Vocalization toward conspecifics in silver foxes (*Vulpes vulpes*) selected for tame or aggressive behavior toward humans

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ABSTRACT

We examined the production of different vocalizations in three strains of silver fox (unselected, aggressive, and tame) attending three kinds of behavior (aggressive, affiliative, and neutral) in response to their same-strain conspecifics. This is a follow-up to previous experiments which demonstrated that in the presence of humans, tame foxes produced *cackles* and *pant*s but never coughed or snorted, whilst aggressive foxes produced *coughs* and *snorts* but never cackled or panted. Thus, *cackle/pant* and *cough/snort* were indicative of the tame and aggressive fox strains respectively toward humans. Wild-type unselected foxes produced *cough* and *snort* toward humans similarly to aggressive foxes. Here, we found that vocal responses to conspecifics were similar in tame, aggressive and unselected fox strains. Both *cackle/pant* and *cough/snort* occurred in foxes of all strains. The difference in the use of *cackle/pant* and *cough/snort* among these strains toward humans and toward conspecifics suggest that silver foxes do not perceive humans as their conspecifics. We speculate that these vocalizations are produced in response to a triggering internal state, affiliative or aggressive, that is suppressed by default in these fox strains toward humans as a result of their strict selection for tame or aggressive behavior, whilst still remaining flexible toward conspecifics.

1. Introduction

The process of historical domestication primarily included the selection of animals demonstrating tolerance toward humans. A long-term experiment on silver foxes *Vulpes vulpes* with strict selection for behavior showed that the goal of a new domesticated canid species with behavior comparable to that of the domestic dog *Canis familiaris* could be achieved in principle (Belyaev, 1979; Hemmer, 1990; Trut, 1999, 2001). In addition to the physical and physiological changes associated with domestication in many unrelated species (Belyaev, 1979; Trut, 1999, 2001), changes in vocal behavior were reported for domestic dogs (Cohen and Fox, 1976; Pongrácz et al., 2005, 2007; Molnár et al., 2006); guinea pigs *Cavia aperea* (Monticelli and Ades, 2001), domestic cats *Felis catus* (Nicastro and Owren, 2003; Nicastro, 2004) and for silver foxes (Gogoleva et al., 2008a, 2008b, 2009).

Gogoleva et al. (2008a, 2008b, 2009) studied silver foxes' vocal responses toward humans at the experimental fur farm of the institute of cytology and genetics RAS, Novosibirsk, Russia, focus-ing on a population of silver foxes strictly selected for tame or aggressive behavior toward humans. According to their non-vocal behavioral responses to human approach, each fox of a tame and aggressive strains received a "behavioral score", ranging between −4 for extreme aggressiveness to +4 for extreme tameness (Belyaev, 1979; Trut, 1980, 1999; Kukekova et al., 2008a,b; Gogoleva et al., 2009). Current generations of tame foxes are friendly towards humans, aggressive foxes attack them, and unselected foxes exhibit the typical faint aggressive-fearful responses found in farmed foxes (Trut, 1999; Kukekova et al., 2008a,b; Trut et al., 2009). Cross-fostering, cross-breeding and embryo transplantation experiments have shown that behavioral differences between tame and aggressive foxes in their attitudes toward humans are genetically determined (Trut, 1980, 2001). As early exposure to humans can effect the further reactions of foxes to people, it is forbidden to pet any particular fox on this farm. Fox pups socialize with conspecifics when they live together with their mothers until weaning and then live together with their littermates up to separation into individual cages at the age of 2 months. After separation, they remain in visual, olfactory and auditory contact with foxes from neighboring and opposing cages. This holding regime has been standardized since 1960 when the selection for behavior began and is uniform for all foxes on the farm, thereby

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excluding the influence of new factors on the behavior of these animals.

Eight call types were exhibited in the presence of humans (Gogoleva et al., 2008a, 2008b, 2009), but tame foxes produced *cackles* and *pants* but never coughed or snorted, whilst aggressive foxes produced *coughs* and *snorts* but never cackled or panted. Thus, these vocalizations were established as indicative of these strains respectively toward humans. As aggressive and tame fox strains were selected without account to vocalization, this conclusion was based on the precise knowledge of their attitudes toward humans.

Crosses between tame and aggressive foxes and back crosses to these strains produced either *cackle/pant* or *cough/snort.* No one single fox (either tame, aggressive or crossbred) produced both *cackle/pant* and *cough/snort* toward people. Thus vocal indicators for tameness and aggressiveness toward people were suggested to be discrete phenotypic traits in the silver fox (Gogoleva et al., 2009). As the genetic mechanisms underlying any kind of behavior are still poorly understood in any species, these findings represent important facts for research focused on genetic basis and inheritance of behavioral traits in aggressive and tame strains of silver foxes and their hybrids (Kukekova et al., 2008a, 2008b).

Wild-type unselected foxes produced *cough* and *snort* toward humans similarly to aggressive foxes (Gogoleva et al., 2008a, 2008b, 2010). This suggests that the directional selection for aggressiveness toward humans did not affect vocalization toward humans in the silver fox, whilst the directional selection for tameness, mimicking the process of historical domestication targeted at the tolerance of animals toward humans (Belyaev, 1979), drastically affected vocalization toward humans in the silver fox. However, it remains unknown whether vocalization toward conspecifics was also affected by this process. Here, we examined vocalization attending aggressive, affiliative and neutral behavior in tame, aggressive and unselected silver foxes toward conspecifics for evidence of variation in call production aligned with previous results toward humans. We specifically examine:

- whether the indicative vocal types of tameness *cackle/pant* disappeared completely from the vocal repertoire of aggressive foxes as a result of directional selection for aggressiveness toward humans;
- whether the indicative vocal types of aggressiveness *cough/snort* disappeared completely from the vocal repertoire of tame foxes as a result of similar selection for tameness.

2. Materials and methods

2.1. Subjects, site and dates of work

Our subjects were 120 adult female silver foxes, aged from 1 to 5 years, kept at the experimental fur farm of the institute of cytology and genetics, Novosibirsk, Russia, as described in Gogoleva et al. (2009). Three study groups included 40 tame (selected for tameness toward humans, 44–48 generations since the start of selection), 40 aggressive (selected for aggressiveness toward humans; 34–38 generations since the start of selection), and 40 unselected for behavior vixens. Tests with exposing same-strain conspecifics on neutral territory were made from July 4 – August 24 2008. Overall, we tested 60 same-strain pairs of vixens, 20 tame, 20 aggressive and 20 unselected. Test pairs of foxes were matched by year of birth and by similarity in their behavior scores toward humans (for tame and aggressive strains).

2.2. Test setup

The experimental setup consisted of two identical wire mesh enclosures of $210 \times 85 \times 90$ cm, on four 65 cm metallic legs; containing three compartments of $70 \times 85 \times 90$ cm abreast; with

entrances 20×20 cm between them, with partitions that were only open during test trials. The short test duration of 15 minutes ensured the safety of the animals, providing enough time for them to make the acquaintance of a conspecific and evaluate its strength and attitude of but not enough time to start a serious conflict. The experimenter was always on hand to interrupt a test trial within a few seconds in case of any serious conflict. The compartments of the test enclosure were similar to home cages of foxes, and all the animals were acclimatized to having other neighboring foxes nearby. Thus, the experimental design reminded them of their holding conditions. The testing area was outside the holding area. We tested two fox pairs per day, one pair per enclosure; one test trial after another, between 08.00 and 09.00 a.m., before feeding. The experimental enclosures were out of direct line of sight of one another and separated by an observation house. Each enclosure was 3 m distant from the observation house and 12 m distant from the other. Thus, the two pairs of foxes tested on the same day were unable to see each other. The order of testing was set randomly among tame, aggressive and unselected foxes. In each test trial, a test pair was made up of new foxes that had not been tested previously. After tests, the experimental enclosures were cleaned.

For individual identification, one fox per test pair was dye-marked with ethyl green (MosFarma, Moscow, Russia) before being placed into the experimental enclosure. Only vixens were used as they are potentially more tolerant to conspecifics than males. Tests were conducted outside breeding or pup rearing seasons, i.e. at a time when the animals were least aggressive to adult conspecifics. No foxes was bitten or otherwise injured during the tests. As these tests were conducted under careful human control, they provided a certain kind of behavior enrichment for the study foxes within the uniform environment of the fur farm. Before and during the tests, water was available *ad libitum*. The animals were fed after testing in their home cages as part of their everyday routine. The research protocols were approved by the Committee of bio-ethics of Lomonosov Moscow State University, protocol # 2008-03.

As the video recording of more than one animal at a time precludes the possibility of specifying callers for all vocalizations (see also audio analysis section), we only tested same-strain pairs of vixens to ensure that all vocalizations within a test were coming from the same strain. For video recording of fox behavior during tests, we placed a Panasonic-NV-GS320 digital camcorder (Panasonic Corporation, Kadoma, Japan) atop a tripod at distance of 3 m in front of the front wall of the experimental enclosure. For audio recording, we used a digital tape recorder Marantz PMD-660 (D&M Professional, Kanagawa, Japan) at a sampling rate of 48 kHz in stereo mode with two microphones: the less-sensitive microphone AKG-C1000S cardioid electret condenser microphone (AKG-Acoustics Gmbh, Vienna, Austria) to record loud calls without distortion and the more sensitive Sennheiser K6 ME64 cardioid electret condenser microphone (Sennheiser electronic, Wedemark, Germany) to record soft calls. The microphones were placed 0.8 m above ground level, atop tripods 0.5 m away from each other, and 0.5 m in front of the front wall of the experimental enclosure.

2.3. Test procedure

Twelve hours before the tests, a test pair of vixens were taken from their home cages and isolated in the non-central compartments of the experimental enclosure. So, individuals were given 12 hours to get used to the experimental enclosure before the test. During the test trial, the individuals of a test pair were exposed to each other for 15 minutes. Each test trial began with the removal of the partitions between the compartments of the experimental enclosure separating the animals and ended with their re-installation. During test trials foxes could communicate with each other or remain in their own compartments. All the

trials were conducted by the same experimenter (SG). The experimenter observed the trials through a small window in the wall of the observation house, hidden from the animals.

2.4. Audio analysis

Call recordings (one per test pair) were analyzed with Avisoft SASLab Pro software v. 4.33 (Avisoft Bioacoustics, Berlin, Germany), separately from the video recordings to analyse calls blindly to fox strain and behavior; each recording as a separate file. Calls were downsampled to 22.05 kHz and spectrograms for analysis produced using Hamming window, FFT-length 1024 points, frame 50%, and overlap 87.5%. These settings provided a bandwidth of 56 Hz, frequency resolution of 21 Hz and time resolution of 5.8 ms. We measured the onset and termination of each call in the sound file with the standard marker cursor in the main window of Avisoft. The measurements were exported automatically to Excel (Microsoft Corp., Redmond, WA, USA).

We classified each call visually to one of eight structural types as in Gogoleva et al. (2008a) (Fig. 1). In total, we examined 21,310 calls. For each test pair, we attributed calls to the whole pair, not to individuals. We applied pair based analysis to all tests, because individual based analysis was not possible when the caller was fenced with a conspecific, called in the opposite direction from the camcorder, called turning or moving, or when both test animals called simultaneously. For some call types, *moo*, *growl*, *snort*, and *pant*, callers could not be specified even with good orientation to the camcorder, as foxes produce them softly, with a closed mouth (Gogoleva et al., 2008a), and the accompanying stomach movements are poorly visible. Moreover, a human observer is not able to determine from a video recording from which direction a sound is coming, because video recordings do not provide binaural cues for hearing.

2.5. Video analysis

Videotapes were digitized and analyzed with K-Lite Codec Pack v. 6.4.9.1 (Gabest, Budapest, Hungary), irrespective of fox strain or vocalization, with 1 s precision, each test as a separate file. For each pair, we attributed the behaviors to the whole pair, not to individuals. We considered behavior as neutral when both foxes were not interested in each other; as affiliative when both foxes were friendly toward each other; and as agonistic, when at least one fox behaved aggressively.

The following traits were used to segregate behavior:

Neutral behavior – animals not contacted; stayed in opposite parts of the experimental enclosure; paid no attention to each other, showed their sides or backs, looked in different directions, expressed interest in something else outside; sniffed the fence; groomed themselves; drank water.

Affiliative behavior – moving on half-bent paws; wagging the entire tail (not a part of the tail) quickly from side-to side; mouth ajar; ears pressed to the head or erect: body pressed to the ground but animal moving in a lively manner and turning occasionally onto its side or back, or belly up. Foxes could play, chase each other, mount and jump over each other, but mouths were not opened widely and ears were not tightly pressed to the head; foxes wished to contact, chased and sniffed each other, and wagged their entire tails smoothly.

Agonistic behavior – attack with gaping jaws and ears pressed to the head; one or both forelegs extended; foxes stand on their hind legs and push each other with their forelegs; trying to bite; attacking their opponent through the fence; standing erect on forelegs with head lowered and hind legs spread against the wall (to get as far away from an opponent as possible); body pressed against the ground in immobility, freezing, often with ears tightly pressed

against the head when approached; tail either stationery or wagging furiously, or tail tip twitching (~1/3); an attacked animal turns its side or back to an attacker, lowering its head or crouching on forelegs; keeping its distance from its opponent, a fox shifts from one foreleg to another or scratches furiously at the cage floor with its hind legs, with its head down and ears tightly pressed to its head.

Each video file (one per test pair) was segmented successively according to the number of switches between neutral, affiliative and agonistic behavior displayed by the tested pair. For different pairs, the numbers of the behavior segments varied from 20 to 135 (mean ± SE = 82.5 ± 3.4 segments). For each tested pair, the sums of the segment durations for neutral behavior, affiliative behavior and aggressive behavior were calculated, to achieve the total durations for neutral, affiliative and agonistic behavior respectively.

2.6. Superposed audio and video analyses

For each tested fox pair, the numbers of calls of each of the eight types attending each of the three behaviors were calculated. We superposed the onset and termination of each call of the audio file with corresponding place of the video file of the test. For each tested fox pair, the sums of durations of segments for each behavior were calculated. For each tested fox pair, the sums of numbers of calls of each vocal type during each behavior were calculated. Then for each tested fox pair, the overall calling rate (calls of all types/minute) and the calling rates for each of the eight call types for each behavior was calculated. To calculate calling rates (calls/minute) for each call type during each behavior, we divided the number of calls of the given type by the duration of each behavior within test (in minutes).

For each tested fox pair, this provided three data sets, for neutral, affiliative and agonistic behaviors respectively. For the total number of 60 tested fox pairs, this provided a total of 180 data sets, each containing calling rates for the eight call types and the overall calling rate. From this analysis, we excluded nine of the 180 data sets, calculated from very short time segments (<0.2 minute). As the calling rate value depended on the time interval during which calls were produced, even few calls, produced within such short time segments could give an unwarrantable high value of the calling rate for the given call type. Two of these nine excluded data sets were from unselected foxes during affiliative behavior, two from unselected foxes during agonistic behavior, three from tame foxes during agonistic behavior and two from aggressive foxes during agonistic behavior.

2.7. Statistical analyses

All statistical analyses were carried out with Statistica, v. 6.0 (StatSoft, Inc., Tulsa, OK, USA). All tests were two-tailed; all means are given as mean ± SE, and differences considered significant where $P < 0.05$. We used one-way ANOVA to compare the durations of neutral, affiliative and agonistic behaviors among unselected, tame and aggressive fox pairs, as the distribution of values for durations of these behaviors did not differ from normality in all the three study groups ($P > 0.05$, Kolmogorov-Smirnov test). We used two-way factorial MANOVA with Neuman-Keuls post-hoc tests to compare calling rates among the three behaviors and among the three fox strains. The values of acoustic variables, not satisfying the criteria of normality, were root square transformed to be introduced to MANOVA. We used Fisher exact test to compare the proportions of foxes producing each call type in the three fox strains.

3. Results

In any study group (tame, aggressive or unselected), the duration of neutral behavior exceeded nearly twice the values for
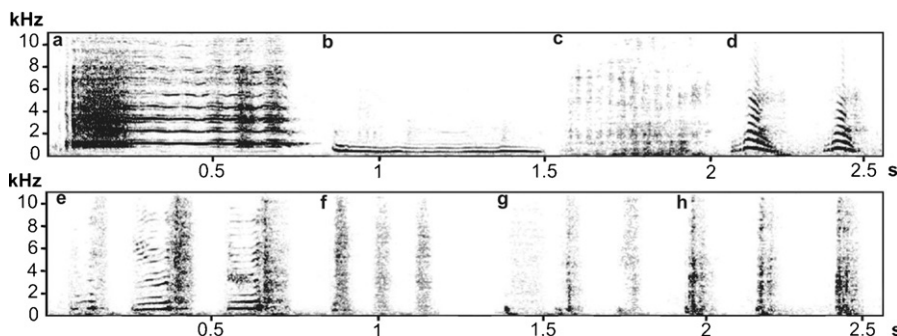
Fig. 1. Spectrogram illustrating call types produced toward conspecifics by silver foxes: a: *whine* of a tame fox; b: *moo* of a tame fox; c: *growl* of a tame fox; d: *bark* of an aggressive fox; e: *cackle* of an aggressive fox; f: *pant* of an aggressive fox; g: *snort* of a tame fox; h: *cough* of a tame fox.

Table 1
Summary durations of segment of neutral, affiliative and aggressive behaviors and one-way ANOVA results for comparison among tame, aggressive and unselected study groups of silver foxes.

Behavior (minute)	Unselected foxes (means ± SE)	Aggressive foxes (means ± SE)	Tame foxes (means ± SE)	ANOVA results
Neutral	8.94 ± 0.49	8.42 ± 0.38	7.65 ± 0.56	$F_{2,57} = 1.81; P = 0.17$
Affiliative	2.77 ± 0.57	3.10 ± 0.38	4.09 ± 0.37	$F_{2,57} = 2.36; P = 0.10$
Agonistic	3.51 ± 0.59	3.50 ± 0.50	2.53 ± 0.50	$F_{2,57} = 1.12; P = 0.33$

affiliative or agonistic behavior (Table 1). A one-way ANOVA, with factor study group, did not reveal significant differences in durations of neutral, affiliative and agonistic behaviors among tame, aggressive and unselected foxes (Table 1).

We estimated the effects of behavior (neutral, affiliative, agonistic) and study group on the calling rate for only six of the eight call types, as *growl* and *bark* occurred rarely and only in a few individuals. A MANOVA revealed the significant effect of behavior on calling rates of all the six call types and on the overall calling rate (Table 2). The MANOVA revealed significant differences between tame, aggressive and unselected study groups only for calling rates of *whines*, *pants*, *snorts* and for the overall calling rate (Table 2). As samples for study group and for behavior were equal, we could compare *F*-ratios from the MANOVA. This comparison indicated that the effect of behavior on the calling rate was stronger than the effect of study group for the overall calling rate and for all call types except *pant*. There were no interaction effects of behavior and study group on the calling rate of any call type (Table 2).

Newman-Keuls post-hoc tests for analysis the effects of behavior and study group on calling rates of different call types showed that during agonistic behavior compared to neutral and affiliative, calling rates of *whines* and *coughs* were significantly higher in all study groups, and calling rates of *snort* and *moo* were also significantly higher in unselected foxes (Fig. 2). Among study groups, differences were found in calling rates of *whines* (significantly higher in aggressive compared to unselected foxes during affiliative behavior); of *pants* (significantly higher in tame compared to unselected and aggressive foxes during affiliative behavior);

and of *snorts* (significantly higher in unselected compared to tame foxes during agonistic behavior) (Fig. 2). Six of the eight call types, except the rarely produced *growl* and *bark*, occurred in all the three study groups during all the three behaviors (Fig. 2). In all the three study groups, we found significantly higher overall calling rates during agonistic behavior than during neutral or affiliative behavior (Fig. 3). Among study groups, significant differences were only found in overall calling rates between aggressive and tame foxes during affiliative behavior (Fig. 3).

We examined whether unselected, tame and aggressive foxes differ in the production of different call types, comparing the number of fox pairs of each study group producing each call type with the average value (calculated as the number of fox pairs producing each given call type divided by the number of study groups, i.e. three). Among the study groups, no significant differences was found in numbers of fox pairs producing any of the eight call types higher or lower the average value (Fisher exact test, $P > 0.05$ for all comparisons) (Fig. 4).

We examined whether unselected, tame and aggressive foxes differ in the production of *cackle/pant* and *cough/snort* suggested respectively as indicative of tameness and of aggressiveness toward humans (Gogoleva et al., 2008a, 2009). We did not find significant differences among study groups in proportions of fox pairs producing the indicative call types (Fisher exact test, $P > 0.05$ for all comparisons) (Fig. 5). Forty-four of the 60 (73.3%) tested pairs produced both *cackle/pant* and *cough/snort*. Seven of 60 (11.7%) tested pairs produced *cackle/pant* but no *cough/snort*, eight of 60 (13.3%) tested pairs produced *cough/snort* but no *cackle/pant*,

Table 2
Two-way MANOVA results for separate and interaction effects of factors behavior (neutral, affiliative or agonistic) and fox study group (unselected, aggressive or tame) on calling rates of six call types and on the overall calling rate (of all call types) in silver foxes.

Calling rate (calls/minute)	MANOVA results		
	Study group effect	Behavior effect	Study group & Behavior effect
Whine	$F_{2,162} = 7.73; \textbf{P} < \textbf{0.001}$	$F_{2,162} = 25.81; \textbf{P} < \textbf{0.001}$	$F_{4,162} = 0.44; P = 0.78$
Cackle	$F_{2,162} = 2.08; P = 0.13$	$F_{2,162} = 4.38; \textbf{P} = \textbf{0.014}$	$F_{4,162} = 0.32; P = 0.86$
Pant	$F_{2,162} = 12.12; \textbf{P} < \textbf{0.001}$	$F_{2,162} = 4.58; \textbf{P} = \textbf{0.012}$	$F_{4,162} = 1.87; P = 0.12$
Snort	$F_{2,162} = 3.91; \textbf{P} = \textbf{0.022}$	$F_{2,162} = 13.39; \textbf{P} < \textbf{0.001}$	$F_{4,162} = 0.75; P = 0.56$
Cough	$F_{2,162} = 0.07; P = 0.93$	$F_{2,162} = 23.53; \textbf{P} < \textbf{0.001}$	$F_{4,162} = 0.21; P = 0.93$
Moo	$F_{2,162} = 1.81; P = 0.17$	$F_{2,162} = 10.32; \textbf{P} < \textbf{0.001}$	$F_{4,162} = 0.30; P = 0.88$
All call types	$F_{2,162} = 3.12; \textbf{P} = \textbf{0.047}$	$F_{2,162} = 39.34; \textbf{P} < \textbf{0.001}$	$F_{4,162} = 0.67; P = 0.61$

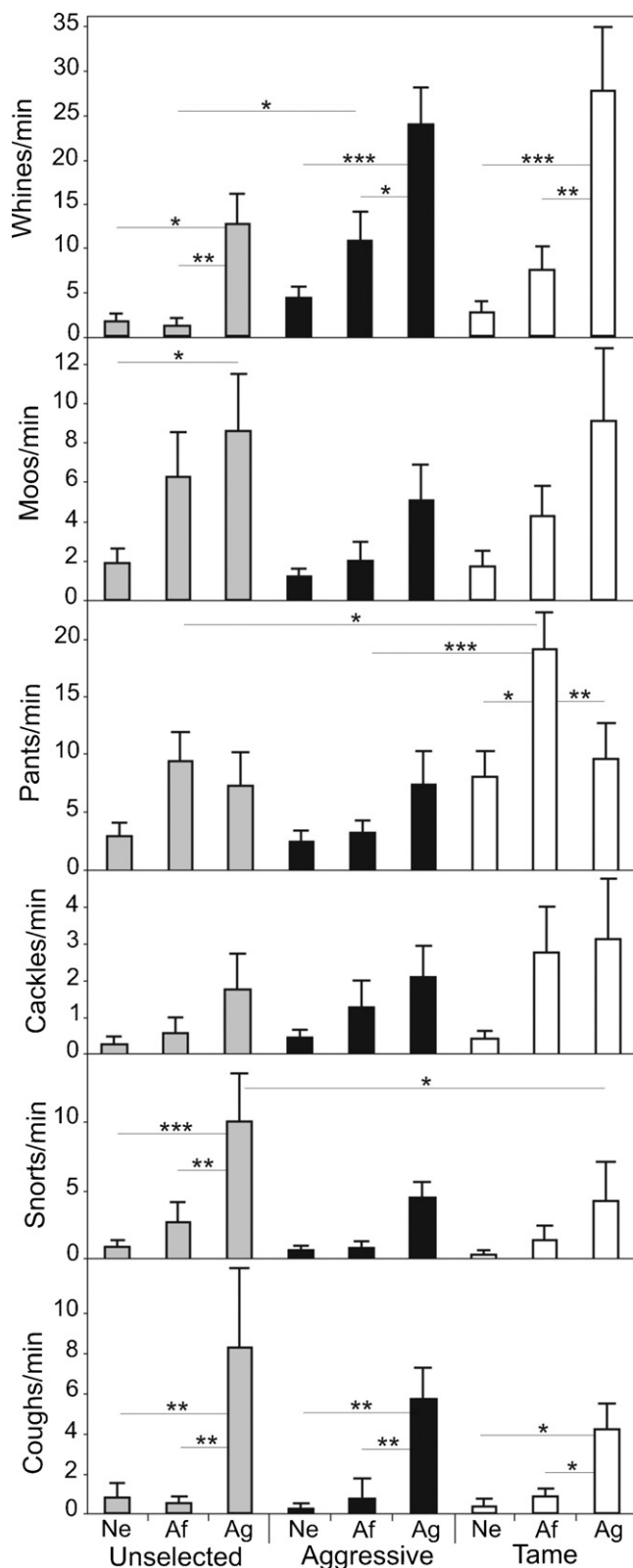Significant *P*-values are shown in bold.

Fig. 2. Mean values (and SE as whiskers) for calling rates of particular call types during neutral (Ne), affiliative (Af) and agonistic (Ag) behaviors in unselected, aggressive and tame study groups, and the differences between the behaviors and groups revealed with MANOVA followed by Newman-Keuls post-hoc tests: *** $P < 0.001$ ** $P < 0.01$; * $P < 0.05$.
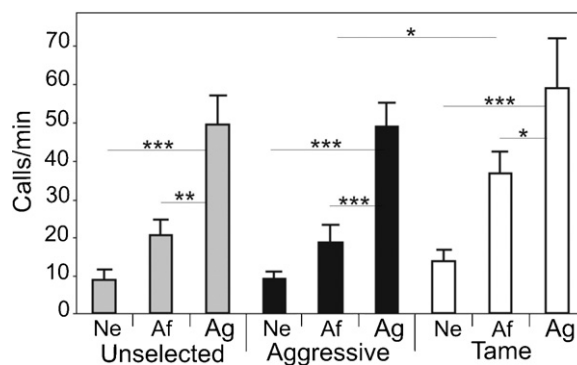

Fig. 3. Mean values (and SE as whiskers) for overall calling rates during neutral (Ne), affiliative (Af) and agonistic (Ag) behaviors in unselected, aggressive and tame study groups, and the differences between the behaviors and groups revealed with MANOVA followed by Newman-Keuls post-hoc tests: *** $P < 0.001$ ** $P < 0.01$; * $P < 0.05$.

and one of 60 (1.7%) tested pairs produced neither indicative call types.

4. Discussion

Toward conspecifics, unselected, aggressive and tame foxes showed much more similarity than differences, both in proportions of neutral, affiliative and agonistic behavior and in vocalizations used during each kind of behavior. This contrasted with the behavioral and vocal responses of these three strains toward people. Although toward people tame foxes display affiliative behavior, aggressive foxes behave aggressively and unselected foxes behave aggressive-fearfully (Trut, 1999; Kukekova et al., 2008a, 2008b; Gogoleva et al., 2009), we found that toward conspecifics all the three strains could display all kinds of behavior. Moreover, unselected, aggressive and tame strains did not differ in preferences in behaving friendly, neutrally or aggressively toward conspecifics.

Consistently, there were no differences between unselected, aggressive and tame strains in proportions of fox pairs producing any call type. Also, there were no differences between fox strains in proportions of fox pairs producing the indicative call types of tameness *cackle/pant* and of aggressiveness *cough/snort*. Earlier, we showed (Gogoleva et al., 2008a, 2009) that toward people, the unselected and aggressive foxes never *cackled* or *panted*, whilst the tame foxes never *coughed* or *snorted*. Thus, the indicative vocal types of tameness *cackle/pant*, lacking in aggressive foxes toward people, nevertheless remained intact in this strain toward conspecifics, in spite of the directional selection for aggressiveness toward people. Similarly, the *cough/snort* remained intact in tame foxes toward conspecifics but disappeared toward people as a result of directional selection for tameness. These findings suggest that the production of vocal types, established as indicative of tameness and aggressiveness toward humans, depends on whether a fox perceives a human or conspecific positively or negatively. That is, it seems that the production of the indicative call types is secondary to the inherited tendency of the foxes to respond tamely or aggressively to human approach. These findings are consistent with the evidence from neuro-ethological experiments with a small nonhuman primate squirrel monkey *Saimiri sciureus*. In this model species for studying neural control of vocalization in mammals, most call types were shown to be secondary to the emotional states experienced by an animal (e.g. Jürgens and Ploog, 1970; Jürgens, 1976, 2009), and brain representation was not uniform for call types, correlating respectively to positive and negative emotional states (Jürgens, 1982; Dujardin and Jürgens, 2006).

The difference in use of *cackle/pant* and *cough/snort* vocalizations between strains toward humans and toward conspecifics
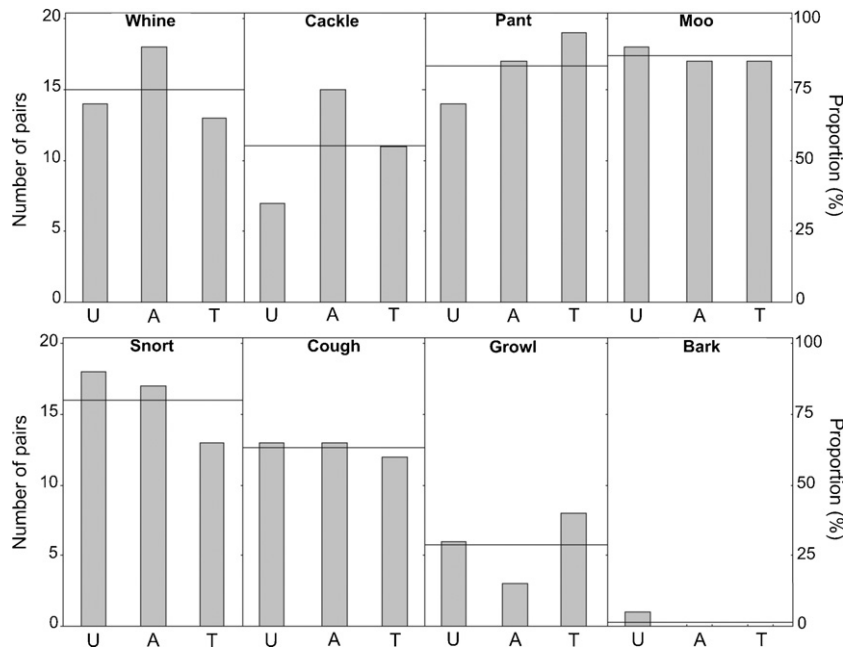
Fig. 4. Numbers and proportions of tested fox pairs that produced particular call types in each study group: U: unselected; A: aggressive; T: tame. Horizontal lines show mean values for numbers of tested fox pairs producing the given call type, the results of all comparisons between the observed and mean values with Fisher exact test are non significant.

suggests that silver foxes of either strain do not perceive humans as their conspecifics. Domesticated tame foxes probably produced greater affiliative vocalization in the presence of humans because domestication has made it more likely that the internal state associated with affiliative vocalizations is induced by the presence of humans. Aggressive foxes on the other hand, exhibited an increased predilection for a negative internal state in the presence of humans and consequently produced more aggressive vocalizations. Thus, our data are consistent with the suggestions of Lord et al. (2009) that the *bark* has increased in the domestic dog not because it was selected for, but because domestication has increased the number of situations in which the internal state associated with the bark is produced. Nevertheless, compared to the domestic dog, in which *bark* is the most widespread vocalization toward people and conspecifics (Yin, 2002; Yin and McCowan, 2004), foxes of any strain very rarely produced *bark* and *growl* toward humans (Gogoleva et al., 2008a, 2008b, 2009) and toward conspecifics (this study). We can suggest therefore that the vocal responses of different canids, even if triggered by apparently similar internal states and produced in apparently similar contexts, may nevertheless be species-specific. Domestic dogs and domesticated silver foxes differ strongly in their preferential vocal responses both toward humans and toward conspecifics, although definitive *bark* vocalization is presented in the vocal repertoire of silver foxes (Gogoleva et al., 2008a).

Toward conspecifics, unselected, aggressive and tame foxes showed much higher calling rates during agonistic behavior compared to affiliative or neutral. This again can be attributed to internal states as higher call rates are indicative of higher arousal (review in Gould, 1983). In particular, the calling rate of fox pups is the critical feature for mother responding (Tembrock, 1958). In unselected foxes, calling rates of *coughs* and *whines* and the overall calling rate increased with increase of arousal in response to a human moving toward a fox during human approach (Gogoleva et al., 2010). In free-living baboons *Papio hamadrayas*, the calling rate of *grunts* was significantly higher in high-arousal conditions compared to low-arousal conditions, in connection with a group

moving and the approach of an adult female to a mother with an infant (Rendall, 2003). In domestic pigs, higher calling rates have been observed in hungry animals compared to feed animals (Weary and Frazer, 1995). Also, an increased rate of alarm calls was reported in ground-dwelling rodents under increasing threat during a predator approach (Blumstein and Armitage, 1997; Warkentin et al., 2001) and the increased rates of *barks* were found in domestic dogs mobbing a stranger than in the same dogs left tethered or soliciting for a toy (Pongrácz et al., 2005). In the current study, the increased overall calling rates during agonistic behavior were due to an increase in the calling rates of *whines* and *coughs* as well as *snorts* and *moos*, but not *cackles* and *pants*. Moreover, *pant* was a single vocalization which Tame foxes produced at higher levels during affiliative behavior compared to agonistic
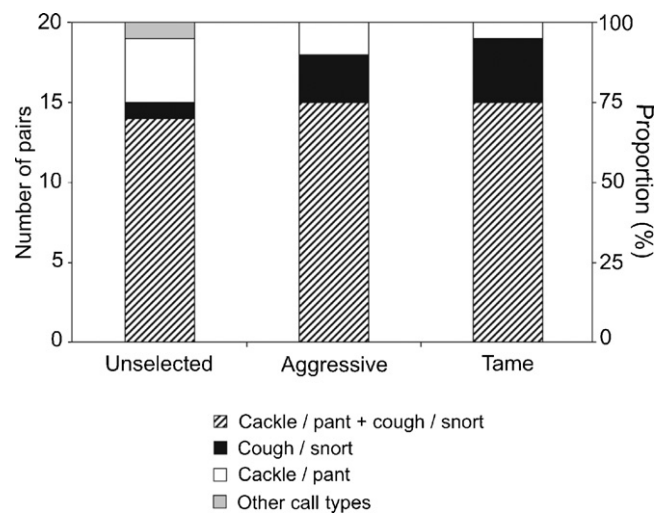

Fig. 5. Numbers and proportions of unselected, aggressive and tame fox pairs that produced along to other call types both *cough/snort* and *cackle/pant*, only *cough/snort*, only *cackle/pant*, or neither *cackle/pant* nor *cough/snort*.

or neutral behavior. This suggests the weaker relation of *cackle* and *pant* to aggressive behavior compared to other call types, not only toward humans (Gogoleva et al., 2008a, 2009), but also toward conspecifics.

However, if we discount the differences between the three fox strains, the vocal responses of silver foxes were very similar toward people and toward conspecifics. All eight vocalizations found toward conspecifics were previously recorded toward humans (Gogoleva et al., 2008a, 2008b). Similar to their use toward people, *growl* and *bark* were rarely produced toward conspecifics by silver foxes of any strain (Gogoleva et al., 2008a, 2008b, 2009). In conformity with current data, in other canids *whine*-like sounds are found in a wide range of contexts (review in Gogoleva et al., 2008a), from greeting conspecifics (Cohen and Fox, 1976) to extreme anxiety (Darden and Dabelsteen, 2006). *Cough* is produced in a short series in the context of warning pups or other conspecifics and in agonistic contexts (Tembrock, 1976; Newton-Fisher et al., 1993; Darden and Dabelsteen, 2006), and *snorts* are met in connection with disturbance (Tembrock, 1976). *Cackle* occurs in non-agonistic interactions between adults and pups or between pups (Darden and Dabelsteen, 2006) or during friendly contacts between family group members (Ovsjanikov et al., 1988). Cohen and Fox (1976) have noticed that, in red foxes and domestic dogs, *pant* occurs during greeting and invitation to play, however, Tembrock (1976) related this vocalization to disturbance.

Current data showed that toward conspecifics, *cackle/pant* and *cough/snort* occurred in any strain at any behavior. In part, it could result from our test design considering behavior of a test pair as agonistic when at least one partner behaved aggressively. Probably, during agonistic behavior, some foxes behaved aggressively producing *cough/snort* whereas their partners behaved submissively producing *cackle/pant*. Nevertheless, we found that *cough/snort* also attended affiliative behavior, when both were friendly. We conclude therefore, that among conspecifics, *cough* and *snort* were not restricted to an aggressive context but probably also attended playful behavior. To confirm that *cackle/pant* in agonistic contexts arises from submissive foxes and that *cough/snort* in affiliative contexts attends play, individual-based analysis is necessary, rather than the analysis based upon the level of interacting fox pairs we have employed. However, this would be technically difficult, as the vocalizations of interacting conspecifics will inevitably overlap.

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