BEHAVIOURAL AND PHYSIOLOGICAL DIFFERENCES BETWEEN SILVER FOXES SELECTED AND NOT SELECTED FOR DOMESTIC BEHAVIOUR

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Abstract

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*The degree of domestication of an animal is difficult to estimate because the animal's phenotype depends not only on its genetic make-up but also on its experiences during ontogeny. In addition, comparisons between wild and domestic animals suffer from the lack of a proper reference population. In this study, we compared the offspring of silver foxes (*Vulpes vulpes*) that had been selected specifically for tameness for more than 30 generations (NOVO) with normal Finnish farmed foxes (FIN) and with reciprocal hybrids between these two strains. All animals were housed under standard farm conditions without any extra handling. The NOVO foxes had higher domestication indexes and lower fearfulness scores than the FIN foxes, with their hybrids showing values in between. Almost all NOVO foxes started eating in the presence of a human and took a titbit from him, whereas only a few FIN foxes did so. Open field and urinary cortisol tests failed to discriminate between the genotypes. The NOVO cubs had lower levels of serum cortisol both before and after a stressful situation or ACTH injection and showed lower stress-induced hyperthermia than the FIN cubs, with the hybrids showing results in between. NOVO foxes can be used as a reference when developing and validating behavioural tests for use in the selection of less fearful silver foxes. The observed low fear levels and low stress hormone levels suggest better welfare in the NOVO foxes under standard farm conditions.*

Keywords: *animal welfare, attention-seeking behaviour, behavioural test, silver fox, stress,* Vulpes vulpes

Introduction

Traditional farm animals are believed to have become domesticated over thousands of years, through intentional and unintentional selection by humans for or against certain traits (Hemmer 1990). It is assumed that the traits typically found in domestic animals are genetically fixed during the domestication process, that this process takes place only during an extended period of many generations, and that, once fixed, it is irreversible (Price 1999). The feralisation process is often considered to be the reverse of domestication, requiring

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genetic changes over many generations. However, it has also been suggested that feralisation may be an ontogenic process that happens during an animal's lifetime if it is not socialised to (or is desocialised from) people (Daniels & Bekoff 1989). Kittens that are born and live during their juvenile stage without human proximity, packs of feral dogs, or calves that escape from the farm are all extremely timid and their behaviour resembles that of undomesticated wild animals. Thus, from behaviour alone, one cannot conclude whether and to what extent a particular individual is domesticated in the genetic sense. Comparisons between domestic stock and their wild ancestors provide little help in many species, as the ancestors from which the present farm stock has evolved no longer exist (Dawkins 1980). In order to provide information on the speed and extent of changes in the process of domestication, what is required is a systematic longitudinal study, during which certain traits typical of domestic animals are systematically monitored. Fortunately, such an experiment has been carried out in silver foxes (Trut 1999). About 40 years ago, Professor Dmitri K Belyaev and his team at the Institute of Cytology and Genetics of the Russian Academy of Sciences in Novosibirsk began an experiment in which they selected farmed silver foxes for domestic behaviour. As one of the most common characteristics of domestic animals is lack of fear of humans, Belyaev selected foxes for tameness and subsequently for contact-seeking behaviour. After about 30–35 generations the foxes were not only tame, but also eager to make contact with and to please people, no matter whether the people were familiar to them or not.

For the present experiment we purchased tame Novosibirsk silver foxes (NOVO) for our research station. The foxes gave birth to cubs and these cubs served as a reference with which to compare the normal Finnish (FIN) silver fox cubs. As the behaviour of NOVO foxes had already been assessed using different behavioural tests and their tameness score estimated using a well-validated domestication index (Vasilyeva 1995), they served also as a reference when developing and validating other behavioural tests. Domestication includes not only tameness, but also other traits not directly selected for, such as lower stress levels and certain morphological features (Trut 1999). We compared physiology and behaviour of Finnish farmed silver foxes not intentionally selected for domestic behaviour with those of domestic Novosibirsk foxes. In this study, "domestic foxes" refers to foxes that have lost their fear of humans and that display positive contact-seeking behaviours towards them. To minimise the possible effects of human influence during ontogeny (Pedersen 1992, 1993, 1994; Pedersen & Jeppesen 1990), all cubs were housed using standard farming practice and extra human contact was intentionally avoided. Mixing the NOVO cubs among the FIN cubs eliminated any possible learning of behaviour through imitation of neighbours. In addition, the characteristics of the hybrids between the NOVO and FIN foxes were compared with those of the pure-line animals.

Materials and methods

The study was approved by the Institutional Animal Care and Use Committee of the University of Kuopio. The stock population of domestic Novosibirsk silver foxes, eight vixens and five males, was purchased in winter 1996. Five of the vixens had been mated in Novosibirsk with different males that were not brought to Finland, and three of the vixens were mated in Finland with the purchased males. Thus, all NOVO foxes used in the present experiments were descendants of these eight vixens and ten males. The purchased foxes were placed in the research station of the University of Kuopio, where five vixens weaned a total of 23 cubs in summer 1996. Three vixens were barren in 1996, but they were used for

breeding in later years. In 1997 and 1998, pure-bred NOVO cubs and hybrids between NOVO and FIN strains were produced. The limited number of NOVO foxes meant that almost all pure NOVO and hybrid cubs were used in the experiments, and the relatedness of cubs within and between the experimental groups could not be fully avoided.

All the cubs used in the present series of experiments were weaned in July and housed thereafter singly in standard wire-mesh fox cages (115 × 105 × 70 cm) in a standard two-row shed. All cubs were fed and cared for according to standard fox-farming practice. Between September and January the cubs were subjected to the tests used in the series of three experiments.

Experiment 1

In 1996, nine NOVO cubs were housed adjacent to one another so that they had only NOVO cubs as their neighbours, while 10 NOVO cubs were distributed throughout the shed so that they had FIN cubs as their neighbours. Nine cubs from the FIN population served as controls. They had only FIN cubs as their neighbours.

The domestication index of the NOVO and FIN foxes was assessed by Dr I Plyusnina, a researcher with much experience of foxes and their testing, on an ordinal scale from –6 to +4. Note that the scale is not exactly the same as that used in Belyaev (1979) or Plyusnina *et al* (1991), but was modified for our purposes. The fear scale ranged from 0 to –6:

0 = Complete absence of fear.
–1 = When a stranger approaches, the fox shows no fear. When he/she opens the cage, the fox avoids him/her.
–2 = When the stranger approaches, the fox keeps still, somewhat huddled up. When he/she opens the cage, the fox huddles up more, and occasionally steps aside.
–3 = The fox huddles up very much when the stranger comes nearer by a few steps. When he/she opens the cage, the fox immediately steps aside.
–4 = When the stranger approaches, the fox runs away. When he/she opens the cage, the fox runs further away.
–5 = The fox runs away immediately upon seeing the stranger, and huddles up in a corner when he/she opens the cage.
–6 = The fox runs away immediately upon seeing the observer, trembles and huddles in a corner, and stands on its front legs raising up its rear end. Urination is often observed.

The plus side of the scale described the contact-seeking behaviour of the foxes:
+1 = The fox does not flee from humans. It accepts some stroking but may occasionally bite the hand.
+2 = The fox lets itself be petted and handled but shows no emotionally friendly response to the stranger.
+3 = The fox is friendly towards the stranger, wagging its tail and whining.
+4 = The fox is eager to establish human contact, whimpering and wagging its tail to attract attention. When the human opens the cage, the fox allows stroking on all parts of its body, greets the hand with sniffing, licking and inhibited bite, turns on its back and actively exposes its belly allowing and requiring stroking, and whimpers all the time with a characteristic vocalisation (not found in normal farmed foxes).

In the feeding test (Rekilä *et al* 1997, 1999), the experimenter placed the usual fresh food by hand onto the roof of the cage (ie in the same place that the foxes' food is normally placed). After food delivery, the experimenter stayed in front of the cage (at a distance of

0.5–0.7 m) without making eye contact with the animal, and recorded whether the fox started eating within 30 s.

In the titbit test, the fox was handed a dog biscuit through the wire mesh by hand. The reaction of the fox was recorded in terms of whether or not it took the titbit within 20 s (Dale & Bakken 1992).

In the pair contest situation (Bakken 1992), a hungry NOVO cub and a hungry, randomly selected FIN cub were placed together in a new standard fox cage. They were given food in one place, and the observer recorded which one of the two foxes defended and monopolised the food. The observer stood in front of the cage (at a distance of 0.7 m) during the test.

In the open field test (Harri *et al* 1995; Rekilä *et al* 1998), a cub was captured from its home cage with neck tongs and carried in an opaque box (55 × 29 × 41 cm) to one end of an open field arena. After a calming-down period of 1 min, a sliding door in the opaque box was opened by remote control, allowing the fox to enter the arena. The open field arena comprised a closed, wire-mesh-floored runway (7.5 × 1.05 m) with opaque walls. The floor of the arena was divided into nine sub-fields of equal size. The number of squares entered and the latency to reach the far end of the arena was monitored during a 5 min test situation.

Adrenal cortex function was measured by means of serum cortisol concentration. The animals were captured using neck tongs. The first blood sample (baseline level) was taken from the left cephalic vein within 2 min after capturing the animal, and the second sample (response to acute stress) was taken from the right cephalic vein 20 min after the open field test. The concentration of serum cortisol (nmol l^{-1}) was analysed using a competitive immunoassay technique (Coat-A-Count Cortisol Assay, Diagnostic Products Corporation, Los Angeles, CA) (cf Rekilä *et al* 1997, 1999).

Experiment 2

In 1997, NOVO vixens were mated with FIN males (NOVO female × FIN male) and *vice versa* (FIN female × NOVO male). The characteristics of their offspring (ie the reciprocal hybrids) were compared with pure-line NOVO and pure-line FIN offspring.

Stress-induced hyperthermia (SIH; Moe & Bakken 1997) was measured during the daytime (0800h–1500h). Cubs belonging to different groups were successively caught in their home cages and their rectal temperature was immediately measured with a digital thermometer (Omron) inserted 5 cm. The first blood sample was taken immediately after temperature measurement. After blood sampling, the fox was released into its home cage, and after 20 min its rectal temperature was measured again and a second blood sample was taken. Immediately after the second blood sampling, the foxes were injected with 0.3 ml synthetic adrenocorticotrophic hormone (ACTH) (Synacthen Depot; cf Rekilä *et al* 1999). A third blood sample was taken and rectal temperature measured 2 h after ACTH administration. The blood samples were analysed for serum cortisol (baseline level; response to handling with rectal temperature measurement and blood sampling procedure; and response to ACTH administration) as in Experiment 1.

For urine collection, a funnel was constructed below the cage and urine collected for 24 h (cf Rekilä *et al* 1999). The concentration of urinary cortisol (nmol l^{-1}) was analysed using the same competitive immunoassay technique as used for blood, and expressed as urinary cortisol:creatinine ratio to correct for the dilution of urine. Creatinine (mmol l^{-1}) was analysed using kinetic Jaffe's reaction.

Experiment 3

In 1998, offspring of pure-line NOVO vixens and pure-line FIN vixens and their reciprocal hybrids were placed in a random order into a shed. A person with no prior experience of foxes was asked to assign scores to the cubs, blindly (ie without knowing their origin), using the minus side of the domestication index used in Experiment 1. This score is thus not identical to the domestication index used in Experiment 1, but describes only the fearfulness of the animals. Foxes that would have received positive scores for their domestication index received a score of zero in this fear index.

Statistical analysis

In Experiment 1, NOVO foxes were treated as two groups, those with NOVO neighbours (domestic group) or those with FIN neighbours (mixed group), while the FIN cubs comprised one group only (FIN). In Experiments 2 and 3, comparisons were carried out between the offspring of pure-line parents (NOVO × NOVO or FIN × FIN) and their reciprocal hybrids (NOVO × FIN or FIN × NOVO). Comparison between groups was carried out using one-way ANOVA (followed by Scheffe's test for *post hoc* comparisons; SPSS 1999) for interval data (Experiments 1 and 2) and using Kruskall-Wallis test (followed by *post hoc* comparison; Siegel & Castellan 1988) for ordinal data (Experiments 1 and 3). Frequencies were compared using Fisher's exact test (Experiment 1). The *P*-values from pairwise group comparisons with Fisher's test were calculated using the Bonferroni correction (ie the *P*-values were multiplied by three).

All experimental groups comprised cubs of both sexes. The cubs used in the present study had reached their final body size at the time at which the experiments were carried out, but were not yet sexually active. It is therefore likely, as supported by earlier studies (Ahola *et al* 2000; Rekilä *et al* 1997, 1999), that there were no sex differences in the parameters measured in this study, and only sex-pooled data are presented.

The number of animals in each behavioural test and physiological measurement in Experiment 1 varies, because some randomly chosen animals were killed before these measurements in order to collect data (not presented here) of their body and organ sizes.

Results

Experiment 1

The domestication index of the NOVO cubs, whether they had NOVO cubs or FIN cubs as their neighbours, was higher than that of FIN cubs (Table 1). In the feeding test and the titbit test, almost all NOVO cubs started eating or took a titbit despite a man standing in front of them, whereas FIN foxes did not. The open field test, whether measured as the number of squares entered or as the latency to reach the far end of the field, did not discriminate between the groups. The NOVO foxes had a lower concentration of serum cortisol before and 20 min after the open field test. Although the NOVO foxes with FIN neighbours showed different values for some behavioural and physiological parameters from the NOVO foxes with NOVO neighbours, the difference was never significant.

In the pair contest situation, when a single portion of food was offered to a NOVO–FIN pair of foxes, the NOVO fox monopolised the food in nine cases out of ten and both ate in one case.

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Experiment 2

Comparison between the pure genotypes and their hybrids reveals that parent genotypes differ from each other for most of the parameters measured and the hybrids typically lie between these extremes (Table 2). This conclusion holds true for blood cortisol and rectal temperature values whether measured at baseline or following response to handling or ACTH injection. The urinary cortisol:creatinine ratio did not discriminate between groups.

Table 1 **Behavioural and physiological characteristics of the Finnish silver foxes (FIN) and the domestic Novosibirsk silver foxes (NOVO) housed after weaning singly with domestic cubs (domestic group) or unselected Finnish cubs (mixed group) as their neighbours. NS, not significant.**

Variable	FIN	NOVO		
		Domestic group	Mixed group	*P*
n	9	9	10	
Domestication index	–1.2 ± 1.6[a]	+3.6 ± 0.5[b]	+3.6 ± 0.5[b]	<0.001[x]
Feeding test: eats/does not eat	1/8[a]	7/2[b]	7/3[b]	<0.001[y]
Titbit test: eats/does not eat	0/9[a]	5/0[b]	7/1[b]	<0.001[y]
n	9	5	9	
Open field (OF) test				
No. squares entered in 5 mins	134 ± 40	133 ± 53	114 ± 96	NS[z]
Latency to get to end of OF (s)	54 ± 71	101 ± 126	40 ± 29	NS[z]
Serum cortisol (nmol l^{-1})				
Baseline level	160 ± 57[a]	36 ± 10[b]	76 ± 72[b]	<0.01[z]
Response to open field	234 ± 78[a]	87 ± 41[b]	139 ± 82[b]	<0.02[z]

[x] Kruskall-Wallis two-way analysis of variance (*post hoc* test; see Siegel & Castellan 1988)
[y] Fisher's exact test (Bonferroni correction for *post hoc* comparisons)
[z] Analysis of variance (Scheffe's test as *post hoc* test)
[a,b] Groups with a common superscript do not differ in the *post hoc* test ($P > 0.06$)

Table 2 **Biological characteristics of offspring of pure Novosibirsk silver foxes (NOVO) and pure unselected Finnish silver foxes (FIN) and their reciprocal hybrids. Parents are denoted as female × male. Acute response = rectal temperature/serum cortisol concentration 20 min after first rectal temperature measurement (ie response to handling); ACTH response = rectal temperature/serum cortisol concentration 2 h after ACTH administration (ie 2 h 20 min after first rectal temperature measurement). NS, not significant.**

	NOVO × NOVO	NOVO × FIN	FIN × NOVO	FIN × FIN	*P**
n	12	13	8	10	
Serum cortisol, nmol l^{-1}					
Baseline	22 ± 9[a]	36 ± 22[ab]	53 ± 35.5[b]	58 ± 28[b]	<0.01
Acute response	74 ± 27[a]	146 ± 46[b]	134 ± 44[b]	183 ± 45[b]	<0.001
ACTH response	329 ± 45[a]	422 ± 79[b]	377 ± 51[ab]	442 ± 127[b]	<0.05
Urine cortisol:creatinine (nmol l^{-1}:mmol l^{-1})	3.5 ± 3.0	5.0 ± 7.8	2.9 ± 0.7	4.2 ± 2.1	NS
Stress-induced hyperthermia (°C)	38.8 ± 0.24[a]	38.9 ± 0.28[ac]	38.9 ± 0.41[a]	39.2 ± 0.26[bc]	<0.05
Baseline	39.0 ± 0.29[a]	39.2 ± 0.31[ab]	39.1 ± 0.38[b]	39.5 ± 0.30[b]	<0.01
Acute response	38.7 ± 0.21[a]	38.8 ± 0.29[a]	38.8 ± 0.36[ab]	39.1 ± 0.40[b]	<0.01
ACTH response					

***** ANOVA followed by Scheffe's test
[a,b,c] Groups with a common superscript do not differ ($P > 0.092$)

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Experiment 3

Fearfulness of the FIN cubs was scored at –1.8 ± 1.2 (n = 12), of the pure NOVO offspring at –0.4 ± 0.5 (n = 12), of NOVO × FIN hybrids at –1.4 ± 1.1 (n = 5), and of FIN × NOVO hybrids at –1.0 ± 1.0 (n = 3). Despite the small sample sizes the genotypes differed significantly from each other along the domestication gradient, with the pure-line foxes further apart and their hybrids in between (Kruskall-Wallis test, $P = 0.011$).

Discussion

There is no doubt that the foxes of the domestic strain and of the normal Finnish strain used in the present study differed in their behaviour. The difference in foxes' behaviour toward humans was so remarkable that even those with no prior experience of foxes could recognise it. This was demonstrated in Experiment 3, where a person with no experience of foxes and no prior information on their history ranked the FIN foxes as the most fearful, the NOVO foxes as the least fearful, and their reciprocal hybrids in between. The results also show that low fear of humans is highly heritable. Domestication in the sense of genetic tameness through selection can be an astonishingly rapid process if the trait can be reliably measured and if it is strongly selected for, as the history of domestic silver foxes demonstrates (Trut 1999).

In the present study, fearlessness was not determined by intentional or unintentional handling by people, or by learning from neighbouring individuals. This is an important notion because handling by humans, especially at a young age, also leads to tame animals (Pedersen 1992, 1993, 1994; Pedersen & Jeppesen 1990). On the other hand, Vasilyeva (1995) showed that foxes with a higher domestication level respond more easily to handling than do "less domesticated" foxes.

Domestic foxes started eating without fear of humans and they readily accepted a titbit handed to them by a strange person. This demonstrates that the feeding test and the titbit test measure fear of humans, as already demonstrated by Rekilä *et al* (1997, 1999) for silver foxes and blue foxes (*Alopex lagopus*) and by Lankin (1997) and Boissou and Lankin (1998) for other farm animals. However, the discriminative power of these tests in detecting small-scale differences in the degree of fear is limited, because the tests classify animals into only two categories (Rekilä *et al* 1999). In contrast with the domestication test, however, the feeding test and the titbit test can be rapidly carried out, their performance requires no special skill, they are very objective in that the result is clear, and as a result they can be applied to a practical farm situation.

The open field test was devised to measure emotionality (or fear) in rats (Hall 1941), and has been widely used ever since. However, its usefulness for other animals has not yet been properly validated (Harri *et al* 1995; Rekilä *et al* 1996, 1998). In the present study, the open field test failed to discriminate between foxes with different domestication scores. The small group size may partially explain this failure, since Vasilyeva (1995) detected a significant (~20%) difference in the number of squares entered and over 100% difference in the latency to begin moving between two groups of 182 foxes that scored +1.29 and +0.63 on the domestication index. In the present study, the percentage difference between domestic and unselected foxes in number of squares entered was 17% at its highest, although the difference in the domestication index between the groups was very clear. Thus, in accordance with our earlier studies, the discriminative power of the open field test in foxes is poor (Harri *et al* 1995; Rekilä *et al* 1996, 1998).

The NOVO foxes were less fearful in the pair contest situation, which might indicate that they do not fear conspecifics either. However, as the human observer was very near to the test cage, this finding may simply prove that the NOVO foxes were less fearful towards the man than were the FIN foxes in the pair contest situation.

The tame behaviour of domesticated silver foxes is associated with remarkable changes in the function of the hypothalamic–pituitary–adrenal axis (eg Oskina 1996). The present study confirmed these findings. Low fear of humans (measured using the feeding test and the titbit test) is associated with a low level of stress hormones in serum and low reactivity to a stressful situation in normal Finnish farm foxes also (Rekilä *et al* 1997, 1999). It is obvious that the welfare of the domesticated foxes is improved compared to the normal Finnish foxes, and selection for less fearful foxes should be a major breeding goal on commercial farms. Early handling of fox cubs also reduces their later fear of humans without a significant change in cortisol secretion in the urine (Pedersen 1994). It is not known whether it is the lower degree of fear reduction or the different mechanism underlying its development that explains the unchanged urinary cortisol level following early handling of cubs.

The only possible negative characteristic of domestic foxes is their strong requirement for attention from humans. One could speculate that regular human contact is essential to them. Because daily petting of a large number of animals is not possible, the foxes might suffer from frustration resulting from a lack of regular petting.

Animal welfare implications

Silver foxes selected for domestic behaviour can be used as a reference when developing and comparing different behavioural tests. The comparison carried out in this study shows that the feeding test and the titbit test can be used to measure foxes' fear of humans. These tests are practical and are easy to carry out under farm conditions. Low fear of humans is a highly heritable trait that can easily be measured and selected for. Low levels of fear are coupled with low levels of stress hormones in the blood and with less intense stress reactions and, as a result, with better welfare. Thus, selection for an absence of fear towards humans can be recommended as a method to improve the welfare of farmed silver foxes.

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