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Variation in fur farm and wild populations of the red fox, *Vulpes vulpes* (Carnivora: Canidae). Part II: Craniometry

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Abstract. The skulls of 165 red foxes (75 wild and 90 farm-bred individuals) collected in Poland in the years 2012-2014 were measured, analysed and compared to further investigate the effect of ancestry and selective breeding on craniometrical variation between wild and farm red fox populations. Univariate comparisons of skull measurements (19 cranial traits) as well as 4 craniometric indices revealed significant differences between vast majority of the studied measurements. Principal component analyses and two dimensional plots showed almost complete separation of the two studied populations of the red fox as well as clear separation of sexes between populations and within the farm population. This may suggest that the selective forces (artificial vs. natural selection) acting upon cranial morphology of the red fox vary between wild and farm populations. Furthermore, the second important factor which cannot be ignored when considering morphological differences between wild and farm foxes is the origin of compared populations (the Eurasian wild red fox population vs. the red foxes of North American origin - a founder population of farm foxes). Thus, the ancestry of the farm foxes is discussed as well.

Keywords: Craniometry, Farm red fox, Wild red fox, *Vulpes vulpes*

Introduction

Evolutionary change is a result of selection pressure on heritable characters that are related to fitness (Falconer & Mackay, 1996). Intensive selection pressure can result in rapid morphological changes in wild populations as well as captive ones (e.g. selective breeding of livestock) (Stockwell *et al.*, 2003; Hendry&Kinnison, 1999). Morphological changes may take place when genetic variance underlies the phenotypic variance of evolving characters (Lynch & Walsh, 1998). Artificial selection experiments have confirmed the genetic basis of traits and their rapid evolutionary change under strong selective pressure (Trut, 1999; Trut *et al.*, 2009). Rapid changes in the body structure and proportions are especially seen in domesticated animals or those being domesticated. There are several anatomical features of domestic animals that may be indicative of processes leading to domestication. These include an altered body size compared to wild counterparts, reduced brain size and changes of skull

dimensions (O'Regan & Kitchener, 2005). In homeothermic animals a change in skull size and body mass can occur rather rapidly, as reported for animals introduced into new environments (Yom-Tov *et al.*, 2003).

The red fox (*Vulpes vulpes*) belongs to the order Carnivora. Species belonging to this order are extremely diverse in size, diet, social behaviour, locomotion and activity patterns (Macdonald 1992; Kruuk 2002). This variability is reflected in dimensions and shape of carnivore skulls (Frafjord, 1993; Simonsen *et al.*, 2003; Yom-Tov *et al.*, 2003; Abramov & Puzachenko, 2005; Meiri *et al.*, 2005; Goswami, 2006; Tamlin *et al.*, 2009; Griciuvienė *et al.*, 2013). Wild canids exhibit visible differences in the morphology of both sexes, particularly the skull and dentition (Gittleman & Valkenburgh, 1997; Schutz *et al.*, 2009). Craniometrical variation is not solely due to environmental effects - morphological differences between populations are often proportional to genetic distance (Huson & Page 1979, 1980).

The rate of change in the morphological traits of red foxes resulting from artificial selection carried out on fur farms considerably exceeds the rate of change resulting from natural selection. This is well documented by studies carried out by Onar *et al.*, (2005), Wierzbicki *et al.*, (2000), Wierzbicki & Filistowicz (2001, 2002, 2003). Long-term artificial selection aiming at genetic improvement of traits related to fur quality, animal size and pelt length has led to the increasing differences in terms of the exterior and body dimensions between the farm foxes and their wild ancestors as well as between sexes (Zatoń-Dobrowolska *et al.*, 2012; Lorek *et al.*, 2001). Furthermore, the association between phenotypic changes and delay in the developmental rate as early as during embryonic morphogenesis was noted. Some behavioral and morphological changes (elongation of the lower jaw, elongation of face skull, widened skulls, shortened snouts, floppy ears, curly tails, emotional expression of positive responses to human) appeared together with delayed development of normal traits in domesticated silver fox (Trut *et al.*, 2009). It was also found that farm silver foxes tend to have higher nutrient and energy digestibility, and daily nitrogen balance and retention than their wild counterparts (Gugolek *et al.*, 2014).

Apart from intensive selective breeding carried out on fur farms the second important factor which may be responsible for significant morphological differences between wild and farm foxes is the origin of compared populations (Statham *et al.*, 2011). This may lead to different gene pools and genetic structures of red fox populations inhabiting different regions of the Northern Hemisphere (Mullins *et al.*, 2014; Atterby *et al.*, 2015). Genetic distinctiveness of populations of the same species may produce favourable conditions for

divergence between populations and the evolution of a new species (e.g. *Vulpes fulva*, Statham *et al.*, 2014).

The aim of this paper was to compare the craniometric measurements of wild and farm populations of the red fox to further investigate the effect of ancestry and selective breeding on craniometrical variation between the studied fox populations. A comparative analysis of the morphological traits (9 characters and 2 proportion coefficients) of farm red foxes and their wild counterparts has been reported in the first part of the study (Zatoń-Dobrowolska *et al.* 2016). The origin of both groups of foxes as presumably important, decisive source of phenotypic differences between them will be investigated and discussed in the third, phylogenetic part of this research.

Material and Methods

Skull collection and measurement

The study was carried out in the years 2012 – 2014. Skulls of wild adult red foxes (n=75, 32 females, 38 males, 5 unknown sex), obtained from the Polish hunters, were collected in 21 regions of Poland scattered across the country. The individuals originated from regions where no fox farms or only single ones were located. Thus, it was rather unlikely they were produced as a result of crossbreeding (wild foxes x captive foxes – farm escapees). The animals collected for the study (all of them were red coloured) were evaluated by hunters and experienced fox breeders. Skulls of farm red foxes (n=90, 33 females, 57 males) came from two farms located in the western part of Poland. The foxes were adult (11 months or older) and unrelated. The farm foxes represented 3 colour variants: silver (86 individuals), red (3 individuals) and cross (1 individual).

Nineteen measurements were taken on each skull using digital sliding calipers to the nearest 0.1 mm. These were: skull length (SL), maximum zygomatic width (SW), skull height (SH), median palatal length (PL), internal nares length (INL), internal nares width (INW), bone wedge (BW), palate width (PW), nostril length (NL), nostril width (NW), comb height (CH), comb width (CW), least breadth of skull (SS), frontal breadth (SSWP), mastoid height (M), I₃ – C length (SL1), I – C length (SL2), C – P₁ length (SL3), I₃ – P₁ length (SL4). The scheme of cranial measurements used is shown in Figure 1. Because some of skulls provided by hunters and breeders were partly damaged, not all measurements could be taken from all skulls owing to missing or damaged parts. Thus, unequal numbers of measurements for a few skull dimensions were used when calculating their means.

Statistical analyses

The basic descriptive statistics (the arithmetic mean, maximum and minimum, standard deviation – SD, and the coefficient of variation – CV) were used to describe skull measurements. Then, the skull measurements were analysed using the general linear model (GLM) procedure and the following linear model:

$$y_{ijk} = \mu + P_i + S_j + e_{ijk},$$

where:

y_{ijk} – is the studied measurement;

μ – is the overall mean;

P_i – is the i -th population effect;

S_j – is the j -th sex effect;

e_{ijk} – is the random error associated with y_{ijk} -th phenotype, $N(0, \sigma^2)$ was assumed.

The least-squares means (LSM) and their standard errors (SE) were estimated to investigate the simultaneous effect of the population (wild or farm) and sex (male or female) on the studied skull measurements. The statistical significance of differences between population means were verified using the Wilcoxon test for independent samples. The *lsmeans* package in the R program was used for this statistical analysis (Russell, 2016).

Moreover, a comparison was made between four groups of animals: farm females (FF), wild females (WF), farm males (FM) and wild males (WM). The Kruskal-Wallis test, a non-parametric method for comparing two or more independent samples was used in this analysis.

Pearson's correlation coefficients between 19 skull measurements were estimated for each population and their significance was verified. The statistical significance of differences between correlation coefficients in considered groups (wild vs. farm foxes) was verified with the significance test of differences of two correlation coefficients.

Furthermore, four craniometric indices, showing the percentage relationship between different skull dimensions were calculated (Onar, 1999; Onar *et al.*, 2001):

$$\text{Skull Index (SI)} = \frac{\text{Zygomatic width} \times 100}{\text{Skull length}}$$

$$\text{Palatal Index (PI)} = \frac{\text{Greatest breadth of the palate} \times 100}{\text{Palate length}}$$

$$\text{Palato – basal Ratio (BR)} = \frac{\text{Palatal length} \times 100}{\text{Basal length}}$$

$$\text{Length – width Index (WI)} = \frac{\text{Skull length} \times 100}{\text{Maximum zygomatic width}}$$

The principal component analysis (PCA) of investigated measurements and individuals was performed with *ade4* (Dray and Dufour, 2007) and *factoextra* (Kassambara and Mundt, 2016) packages to identify the variables that were most correlated with variation in the skull morphology and to investigate the morphological differences between farm and wild foxes. The principal components with eigenvalues >1.0 were kept in the analysis (Jackson, 1993).

All statistical analyses were performed in the R package (R Core Team, 2016).

Results

Variation between populations

The descriptive statistics of different skull measurements of investigated wild and farm red foxes are presented in Table 1. We observed significant between-populations variation in 14 of the 19 morphological traits considered. Only 5 skull measurements (PL, INL, BW, PW, SSWP) did not differ significantly between the two red fox populations. The reported results show that the skull of farm red foxes was significantly longer (SL) and higher (SH) than the skull of wild foxes (151 mm vs. 147.33 mm, 50.83 mm vs. 50.46 mm, respectively), being at the same time significantly narrower (SW) as compared to the skull of wild foxes (76.49 mm vs. 77.78 mm, respectively). Significant differences were also found between the comb measurements – the skull of farm foxes had wider comb (CW) than the skull of wild ones (26.22 mm vs. 25.01 mm, respectively). Also CH was significantly higher in farm foxes as compared to wild ones (23.39 mm vs. 21.80 mm, respectively). The same tendency was noted for NL and NW, where both measurements were significantly higher in farm foxes as compared to wild counterparts (21.37 mm vs. 20.61 mm, 12.78 mm vs. 12.34 mm, respectively). Furthermore, farm foxes had significantly smaller M than wild foxes (14.58 mm vs. 14.95 mm, respectively).

Dentition analysis revealed significant differences in distance between the studied teeth of farm and wild red foxes (Table 1). SL1, SL2 and SL4 were significantly longer in farm foxes, while SL3 was longer in wild foxes.

When comparing variation of the studied skull measurements (Table 1) it can be noted that vast majority of the measurements taken in wild foxes (13 out of 19) have higher CV than the ones taken in farm foxes. The highest CV was estimated for SL3 (23.73% and 25.20% for farm and wild foxes, respectively), followed by SL1 (16.36% and 13.28% for farm and wild foxes, respectively) and INW (13.96% and 10.83% for farm and wild foxes, respectively).

The lowest CV was estimated for SH (3.19% and 7.21% for farm and wild foxes, respectively) and for SW (3.95% and 5.95% for farm and wild foxes, respectively).

Table 2 shows descriptive statistics of skull indices calculated for farm and wild red fox populations. All indices differed significantly between the studied populations. Two of them (PI and WI) had significantly higher values for farm foxes, while SI and BR had higher values for wild foxes.

Pearson's correlation coefficients between 19 skull and dentition measurements of the studied fox populations are shown in Table 3. The correlation coefficients were estimated within farm and wild red fox populations and their significance was tested. In the farm population 95 correlations were found to be significant, while in the wild populations 80 correlations were significant. A comparison of corresponding correlations between populations revealed that 85 of them differed significantly. In the farm foxes correlation coefficients ranged from very weak (0.01 between CW and SS) to strong (0.83 between PL and SL). Comparable range of values was found for the correlations estimated in the wild foxes (from -0.02 between BW-SH and CH-SS to 0.81 between PL and SL). In both populations most correlation coefficients were low or moderate, ranging from 0.11 to 0.30 (68 and 73 correlations reached this level in farm and wild populations, respectively), while only a few correlations (4 in both populations) were strong, reaching the level of 0.61 - 0.90. Quite often (26 times) the corresponding correlations had opposite signs (+ or -). For example the correlation coefficient between SH and SW reached 0.55 in farm foxes, while in wild ones it was estimated at -0.48.

The PCA of the data demonstrates five components (PC1,..., PC5) with eigenvalues >1.0, explaining 63.125% of the total variation in the data (Table 4). There is a big drop in eigenvalue between PC1 and PC2, and a smaller drop between PC2 and PC3. On a scree plot PC3 to PC5 appear as scree at the base of the cliff composed of the first two components. Together PC1 and PC2 account for 43.2% of the total variance (34% and 9.2%, respectively). Thus, for further analyses the first two components were retained. All factor loadings for PC1 were negative, while for PC2 eleven loadings were negative and the rest had positive values. Factor loadings for PC1 were rather small and did not exceed 0.4 (absolute value). They ranged from -0.043 for SL3 to -0.344 for SL. The most strongly loaded on PC2 were SS and SL3 (-0.466 and 0.410, respectively). The remaining loadings ranged from -0.024 for SL4 to -0.296 for SL2 (negative values), and from 0.064 for SL to 0.271 for M (positive values).

The PCA suggests almost complete separation of the two studied populations of the red fox. Two dimensional plot of PC1 and PC2 axes in skull and dental measurements (Figure

2) shows sizeable differences between the studied fox populations and correlates with the results presented earlier in Table 1 and Table 2.

Variation within and between sex-population groups

LSM of craniological measurements estimated in four groups on animals (FF, FM, WF, WM) are given in Table 5, while Figure 3 shows largest skulls (illustrative examples) selected from each of the studied groups. A comparison of sexes within populations (FF vs. FM and WF vs. WM) shows evident sexual dimorphism. In the farm population 15 out of 19 measurements studied were significantly larger in males than in females. Only 4 measurements (INW, CH, SS, SL3) showed no differences between sexes. None of the measurements was significantly larger in females than in males. The same situation was noted in the population of wild foxes. Again, 15 measurements were significantly larger in males than in females, while only 4 measurements (INW, CH, SS, SL3) were significantly larger in females. The comparison of sexes within the studied populations revealed that of the total 19 skull measurements, 15 (same in both populations) are subject to sexual dimorphism.

The comparison of sexes between populations (FF vs. WF and FM vs. WM) shows that vast majority of measurements are significantly larger in farm individuals than in wild individuals (Table 5). 10 skull measurements taken from FF (SL, INW, NL, NW, CH, CW, SS, SL1, SL2, SL4) were significantly larger than in WF, 7 measurements did not differ significantly (SH, PL, INL, BW, PW, SSWP, M), while only 2 measurements (SW, SL3) were significantly smaller in FF. The similar results were obtained for males. Significantly larger measurements of FM were noted for 9 (SL, INW, NL, NW, CH, CW, SL1, SL2, SL4) out of 19 measurements studied, 7 measurements (SH, PL, INL, BW, PW, SSWP, M) did not differ significantly between FM and WM, while only 3 measurements (SW, SS, SL3) were significantly smaller in FM than in WM.

Craniometric indices calculated for four groups of foxes (FF, FM, WF, WM) are shown in Table 6. No significant differences were found between all studied groups of foxes as regards PI. Values of SI did not differ significantly between sexes within population (FF vs. FM and WF vs. WM), while significant differences were noted between populations (FM vs. WF and FM vs. WM). A similar situation was found in case of WI. Significant differences were found for indices calculated for sexes between populations (FF vs. WF and FM vs. WM), while no significant differences were noted between sexes within population (FF vs. FM and WF vs. WM). As regards last craniometric index – BR, no significant differences were found between sexes within the wild population (WF vs. WM). Significant differences

were noted for craniometric indices calculated for sexes within the farm population (FF vs. FM) as well as for sexes between populations (FF vs. WF and FM vs. WM).

The PCA shows almost complete separation of sexes between populations (FF vs. WF and FM vs. WM) as well as sexes within the farm population (Figure 4). The separation of sexes in the wild population (WF vs. WM), although visible, is not that indisputable. These findings are generally in agreement with the results presented in Table 5 and Table 6.

Discussion

The family *Canidae* exhibits a wide range of differences in cranial shape and dimensions (Van Valkenburgh & Koepfli, 1993; Wroe & Milne, 2007), but the factors that drive the evolution of differences in shape remain unclear (Slater *et al.*, 2009). Morphological variation is the result of the selection pressure (e.g. competition, available resources, sexual selection, climate, energy waste, etc.) (Gittleman, 1985; Sandell, 1985; Meiri, 2004; Melero *et al.*, 2008) which favours advantageous variants, causing them to become more common in the population. However, this holds true for natural selection, but not necessarily for artificial selection. Selective breeding carried out on farms prefers rather those phenotypes that bring economic profit for breeders (De Vries, 1989; Wierzbicki, 2005; Wierzbicki *et al.*, 2007). In consequence of different natural and artificial selection pressures phenotypic variation in different traits of the same species (e.g. *Vulpes vulpes*, *Neovison vison*) may be induced (Melero *et al.*, 2012; Zatoń-Dobrowolska *et al.*, 2016).

The cranial dimensions and shape in the family *Canidae* have already been studied (Wayne, 1986; Frafjord, 1993; Gittleman & Van Valkenburgh, 1997; Simonsen *et al.*, 2003; Meiri *et al.*, 2005; Goswami, 2006; Yom-Tov *et al.*, 2007; Slater *et al.*, 2009; Hartová-Nentvichová *et al.*, 2010; Viranta & Kauhala, 2011; Griciuvienė *et al.*, 2013) showing that different evolutionary forces may have affected morphology of the skull. However, to our knowledge detailed comparative univariate and multivariate analyses of cranial measurements of wild and farm red foxes have not been reported. This kind of study may give better insight into morphological change brought about by ancient evolutionary paths as well as selective breeding (artificial selection), which according to McDougall *et al.* (2006) is perhaps the most important process of evolutionary change in captive populations.

In our study significant craniometric and dental variation has been demonstrated between wild and farm populations of the red fox. The between populations analyses revealed that vast majority of the skull measurements (14 out of 19 studied), corresponding phenotypic correlation coefficients (85 out of all estimated) and 4 calculated cranial indices differed

significantly. The farm fox skulls were generally larger than skulls of the wild foxes. Changed skull dimensions led to significant differences between values of cranial indices, which indicates differences in skull shape of two compared groups of foxes (larger but narrower skull of the farm fox vs. smaller but wider skull of the wild fox). The predominant number of studied cranial features had smaller variation (expressed as CV) in farm foxes than in wild ones, indicating that the captive individuals were more homogeneous group than their wild counterparts.

The between populations differences revealed using univariate comparisons are strongly supported by multiple comparisons. The PCA showed almost complete separation of wild and farm fox populations. Although two principal components (PC1 and PC2) retained in the PCA accounted for less than a half (43.2%) of the total variance in the measurements, the PCA (together with univariate comparisons) seems reliable evidence of morphological distinction between the two compared populations.

The comparison of sexes between populations generally follows the pattern revealed when comparing populations. This means that most of the cranial measurements of farm males were significantly larger than corresponding measurements of wild males, while cranial measurements of farm females were significantly larger than those taken in wild females. This division is also seen when comparing cranial indices computed for sexes from different populations (less pronounced differences are seen when comparing cranial indices calculated for sexes within the population). Also multivariate analyses (the PCA) confirm well seen distinction between sexes (both between and within populations).

It is a common problem in this type of studies to identify and separate factors which are responsible for observed differences. However, it seems that the origin of compared fox populations and selective breeding of farm foxes are two decisive factors that may have caused morphological changes in the skull dimensions.

As regards the origin of the studied fox populations it is believed that most of the breeding stock for the fox farming originated from Eastern Canada, where on Prince Edward Island the first fox farm was established in the 1890s (Balcom, 1916; Westwood, 1989). Strong evidence for this was given by Statham *et al.* (2011) who carried out the phylogenetic study to reveal the origin of the domesticated silver foxes (colour variant of the red fox) in Russia. To assess geographic origin of the studied foxes they used cytochrome *b* and D-loop haplotypes from 5 different regions of the world (Europe, Asia, Alaska and Western Canada, Eastern Canada and the Western Mountains of the USA). The reported results indicated that the Russian domesticated silver fox population was not differentiated from the Eastern

Canada population (extent of genetic differentiation among populations was assessed using pairwise ϕ_{ST}), but was significantly differentiated from all other studied populations. The authors suggest that Eastern Canada is the primary source of ancestry for the farm foxes not only in Russia, but also in other regions of the world. This suggestion seems to be supported by the coat colour (silver) of the studied farm foxes. Because the genes determining silver colour variant are indigenous to North America it can be presumed that the ancestry of the farm foxes was North American (Statham *et al.*, 2011).

The findings reported by Statham *et al.* (2011) are in line with conclusions of Cavallini (1995), who studied variation of the body size in the red fox. The author suggests that morphological variability of the red fox from the different regions of the world rather reflects the phylogenetic distance between populations than differences between colonized habitats.

The commercial success of fur production generated increased interest in fox farming, leading to the establishment of many fur farms in both North America and Europe. The newly established fox farms used imported North American foxes as a breeding stock (Nes *et al.*, 1988). In Poland red fox farming started in 1924 (Piórkowska, 2013). The origin of the Polish breeding stock is not well documented (to our knowledge there is no phylogenetic study reconstructing the evolutionary relationship between Polish red foxes kept on farms and their wild ancestors), but most likely the silver foxes of Canadian descent were imported to the Polish farms as it was in Russia and the Baltic states (Vahrameyev&Belyaev, 1948). This implies that the population of red foxes bred on Polish farms are not of Eurasian origin but rather of East Canadian descent. As a consequence of that, it must be kept in mind that when we compare the wild population of European red foxes with farm red foxes, in fact we compare two genetically distinct populations – the Eurasian red fox population vs. the red foxes of North American origin (a founder population of farm foxes which genetic structure has been changed through selective breeding). Thus, the morphological differences between wild and farm-bred foxes may have been caused, among others, by distinct gene pools of both populations (Zatoń-Dobrowolska *et al.*, 2016).

The second factor which in our opinion affected the skull morphology, leading to significant variation between skulls of wild and farm foxes is selective breeding. According to Lynch&Hayden (1995), who studied genetic influences on cranial form in ranch and feral American mink, if there is a genetic basis to skull variability, there might be variation between captive animals (both between and within a farm), generated through artificial

selection and genetic drift. The authors speculate that skull form and dimensions may have been changed pleiotropically with other traits which have been selected for.

An evidence that the traits associated with captive/domesticated animals were not individually selected for, but they form a group of genetically correlated characters was provided by Dmitry Belyaev (Belyaev, 1979; Trut, 1999). The rigorous selective breeding of the silver fox solely for tameability brought about correlated changes never selected for (so-called correlated response, Falconer&Mackay, 1996). They included, among others, drooping ears, shorter, occasionally upturned tails and shortened snouts.

It can be assumed that the fox breeders do not select for a given skull shape, but for the traits of economic importance (body and pelt size, pelt quality, colour type). Artificial selection for genetic and phenotypic improvement of those traits usually brings satisfactory effects (selected traits have moderate heritabilities, for example h^2 for body size ranges from 0.26 – 0.28, colour type from 0.23 to 0.37, pelt length from 0.20 to 0.22, quality of pelt 0.19, Wierzbicki&Filistowicz, 2002; Wierzbicki&Filistowicz, 2003; Wierzbicki, 2004). Because selected traits are presumably genetically correlated with skull characters the selective breeding promotes also divergence in cranial form and dimensions (for more on the correlated evolution see Goswami, 2006).

Distinctive skull morphology of wild and farm foxes may have also been influenced by the limited gene pool of the farm foxes (small founder population), which has further been restricted through family selection (selecting related animals), intensive use for reproduction a very limited number of genetically superior males (or their diluted semen in artificial insemination) and females, which in consequence has led to lowered effective population size.

The results reported in the present paper do not enable to say to which extent distinct origin (evolutionary paths) of wild and farm red foxes is responsible for the observed differences (for the time being we can only speculate). We did not have to our disposal the skull measurements taken from wild North American red foxes to compare them directly with measurements taken from wild and farm red foxes in our study. However, a comparison of two skull measurements (SL and SW) presented in Table 5 with corresponding skull measurements of wild North American red foxes reported by Lariviere&Pasitschniak-Arts (1996) reveals that farm males have larger skulls than their North American counterparts (SL: 154.5 mm vs. 150.2 mm; SW: 77.8 mm vs. 76.7 mm, respectively), while farm females have longer but narrower skulls than wild females from North America (SL: 144.9 mm vs. 142.3 mm; SW: 74.2 mm vs. 75.2 mm, respectively). If we assume as suggested by Statham *et al.*, (2011) that Eastern Canada is the primary source of ancestry for the farm foxes then the

differences in skull dimensions mentioned above (skulls of farm foxes are, on average, larger than those of wild North American foxes) may have been caused by selective breeding and captive rearing environment, while observed differences between wild and farm red foxes reported in our study have rather been caused by ancestry of the studied populations.

In order to find out what is a role of ancestry and selective breeding in observed morphological differences we have additionally undertaken a phylogenetic study. This study is still in progress, but preliminary results (unpublished data) obtained using 24 nuclear markers (canine-derived microsatellites) and Principal Component Analysis indicate complete genetic separation of studied wild and farm red foxes. This supports Statham's suggestions concerning eastern Canadian origin of farm foxes. Furthermore, closer look at genetic structures of both studied fox populations revealed one genetic cluster as the most probable number of genetically distinct populations for wild red foxes (Structure indicated the highest $L(K)$ value as well as lowest standard deviation for $K=1$), while three genetic clusters were indicated as the most probable number for farm red foxes (Delta K presented the highest peak for $K=3$). The preliminary results presented above suggest that ancestry rather than selective breeding is the primary and decisive source of morphological differences between wild and farm red foxes. To have better insight into sources of phenotypic and genetic differences between wild and farm foxes further phylogenetic studies with the use of mtDNA are planned.

In conclusion, despite the fact that different factors drive evolution of skull dimensions and shape, many of which remain unclear, it may be speculated that the origin of foxes as well as selective breeding play a significant role in differentiation of skulls of farm and wild red foxes. Under the strong pressure of artificial selection for economically important traits the farm foxes, having distinctive gene pool as compared to their wild counterparts of Eurasian origin, followed their own microevolutionary pattern of cranial form and dimensions. To attribute the reported morphological changes to the suggested factors (the results presented in this paper are not yet conclusive) the comparative genetic and phylogenetic analyses have been initiated.

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Table 1. Basic descriptive statistics of skull measurements (in millimeters) for wild and farm foxes

	measurement									
	SL	SW	SH	PL	INL	INW	BW	PW	NL	NW
FARM FOXES										
n	90	89	90	90	90	90	90	90	90	90
mean	151.00 _a	76.49 _a	50.83 _a	74.59	9.61	2.61 _a	15.76	18.50	21.37 _a	12.78 _a
minimum	136.40	68.60	46.50	68.10	7.30	1.90	13.00	16.50	18.10	10.90
maximum	165.90	82.80	54.40	80.60	12.40	3.90	18.10	20.40	24.10	15.60
SD	7.75	3.02	1.62	3.10	1.04	0.36	1.08	0.87	1.20	0.86
CV [%]	5.13	3.95	3.19	4.16	10.79	13.96	6.84	4.72	5.63	6.74
WILD FOXES										
n	71	72	73	73	73	73	75	73	72	74
mean	147.33 _b	77.78 _b	50.46 _b	75.18	9.46	2.39 _b	15.79	18.16	20.61 _b	12.34 _b
minimum	133.20	51.70	46.40	67.80	6.90	1.70	12.60	15.00	17.80	10.40
maximum	167.60	85.30	78.60	83.20	12.00	2.90	19.50	20.30	24.00	14.30
SD	6.88	4.63	3.64	3.60	1.13	0.26	1.15	1.20	1.32	0.80
CV [%]	4.67	5.95	7.21	4.79	11.90	10.83	7.26	6.59	6.41	6.46

Note: Different letters in columns indicate significant differences between populations (p-value < 0.05).

Table 1. (continued)

	measurement								
	CH	CW	SS	SSWP	M	SL1	SL2	SL3	SL4
FARM FOXES									
n	90	90	89	89	90	90	90	90	90
mean	23.39 _a	26.22 _a	25.39 _a	37.14	14.58 _a	6.16 _a	15.99 _a	3.62 _a	17.87 _a
minimum	17.50	22.90	21.80	27.20	11.80	3.70	13.80	1.00	15.20
maximum	32.80	31.50	28.70	43.10	16.60	10.20	18.20	6.30	21.70
SD	3.05	1.72	1.48	2.55	1.02	1.01	1.10	0.86	1.30
CV [%]	13.04	6.55	5.82	6.87	7.01	16.36	6.87	23.73	7.26
WILD FOXES									
n	73	73	75	75	73	73	73	73	71
mean	21.80 _b	25.01 _b	23.55 _b	36.83	14.95 _b	5.73 _b	14.93 _b	4.15 _b	16.92 _b
minimum	17.30	21.20	19.20	29.50	12.20	4.20	11.90	1.50	14.50
maximum	27.90	28.60	30.20	42.70	18.00	7.70	17.90	6.70	19.90
SD	2.19	1.51	1.75	2.88	1.21	0.76	1.09	1.05	1.24
CV [%]	10.04	6.04	7.42	7.81	8.12	13.28	7.29	25.20	7.33

Note: Different letters in columns indicate significant differences between populations (p-value < 0.05).

Table 2. Basic descriptive statistics of skull indices for wild and farm foxes

	index			
	SI	WI	BR	PI
FARM FOXES				
n	89	89	90	90
mean	50.71 _a	1.97 _a	49.44 _a	24.83 _a
minimum	46.05	1.78	46.69	22.42
maximum	56.18	2.17	52.69	27.52
SD	2.01	0.08	1.37	1.22
CV [%]	3.96	3.96	2.78	4.90
WILD FOXES				
n	70	72	73	71
mean	52.87 _b	1.90 _b	51.13 _b	24.19 _b
minimum	35.58	1.74	48.12	20.47
maximum	57.31	2.81	54.25	27.32
SD	2.81	0.13	1.38	1.54
CV [%]	5.31	6.80	2.70	6.36

Note: Different letters in columns indicate significant differences between populations (p-value < 0.05).

Table 3. Pearson's correlation coefficients between skull measurements for wild (lower triangle; 63 individuals) and farm (upper triangle; 88 individuals) foxes

trait	SL	SW	SH	PL	CH	CW	SS	SSWP	INL	INW
SL	1.00	0.63* <i>a</i>	0.54* <i>a</i>	0.83*	0.06	0.42*	-0.09	0.37*	0.40* <i>a</i>	0.20
SW	0.50* <i>b</i>	1.00	0.55* <i>a</i>	0.49*	0.10	0.45* <i>a</i>	0.09 <i>a</i>	0.53* <i>a</i>	0.13	0.20 <i>a</i>
SH	0.23 <i>b</i>	-0.48* <i>b</i>	1.00	0.53* <i>a</i>	0.10	0.34* <i>a</i>	0.08	0.33*	0.07	0.26* <i>a</i>
PL	0.81*	0.39*	0.30* <i>b</i>	1.00	0.13	0.37*	0.04 <i>a</i>	0.40*	0.29* <i>a</i>	0.26*
CH	0.20	0.23	0.10	0.15	1.00	0.43* <i>a</i>	-0.11	0.06 <i>a</i>	-0.16	0.02
CW	0.39*	0.30* <i>b</i>	0.19 <i>b</i>	0.27*	0.29* <i>b</i>	1.00	0.01	0.28*	-0.03 <i>a</i>	0.16 <i>a</i>
SS	0.04	-0.06 <i>b</i>	0.15	0.19 <i>b</i>	-0.02	0.12	1.00	0.44*	-0.03 <i>a</i>	0.22* <i>a</i>
SSWP	0.46*	0.38* <i>b</i>	0.24	0.48*	0.23 <i>b</i>	0.40*	0.54*	1.00	0.03 <i>a</i>	0.03
INL	0.54* <i>b</i>	0.23	0.15	0.60* <i>b</i>	-0.08	0.12 <i>b</i>	0.13 <i>b</i>	0.33* <i>b</i>	1.00	0.16 <i>a</i>
INW	0.09	-0.09 <i>a</i>	0.10 <i>b</i>	0.20	-0.08	-0.28* <i>b</i>	-0.09 <i>b</i>	-0.11	0.35* <i>b</i>	1.00
BW	0.39*	0.37*	-0.02 <i>b</i>	0.41* <i>b</i>	0.12	0.15	0.00	0.31* <i>b</i>	0.30* <i>b</i>	0.19
PW	0.45*	0.45*	0.02 <i>b</i>	0.37*	0.10	0.12	-0.14 <i>b</i>	0.19	0.41* <i>b</i>	0.44* <i>b</i>
M	0.45*	0.08 <i>b</i>	0.27*	0.46*	-0.14 <i>b</i>	0.18	0.31* <i>b</i>	0.44* <i>b</i>	0.36* <i>b</i>	0.14
SL1	0.28* <i>b</i>	-0.02 <i>b</i>	0.17 <i>b</i>	0.32* <i>b</i>	-0.15	0.14	0.11	0.15 <i>b</i>	0.20	0.14
SL2	0.32* <i>b</i>	0.21 <i>b</i>	0.26*	0.40* <i>b</i>	0.14	0.18	0.02	0.26*	0.23	0.04 <i>b</i>
SL3	0.37* <i>b</i>	0.17 <i>b</i>	0.02	0.22 <i>b</i>	0.05 <i>b</i>	0.02 <i>b</i>	0.09 <i>b</i>	0.23	0.25* <i>b</i>	0.05 <i>b</i>
SL4	0.67*	0.17 <i>b</i>	0.30*	0.75* <i>b</i>	0.06	0.28*	0.20 <i>b</i>	0.40*	0.58* <i>b</i>	0.24
NL	0.57* <i>b</i>	0.38*	0.12 <i>b</i>	0.54* <i>b</i>	0.18	0.27*	0.03 <i>b</i>	0.33* <i>b</i>	0.30*	0.26*
NW	0.62* <i>b</i>	0.27* <i>b</i>	0.26* <i>b</i>	0.63* <i>b</i>	-0.08 <i>b</i>	0.20	0.19	0.47* <i>b</i>	0.53* <i>b</i>	0.35*

Note: Coefficients marked with * are statistically significant (p-value < 0.05). Corresponding correlation coefficients with statistically significant differences (p-value < 0.05) are marked with different letters.

Table 3. (continued)

BW	PW	M	SL1	SL2	SL3	SL4	NL	NW	trait
0.33*	0.50*	0.36*	0.51* <i>a</i>	0.44* <i>a</i>	0.01 <i>a</i>	0.64*	0.71* <i>a</i>	0.40* <i>a</i>	SL
0.47*	0.43*	0.30* <i>a</i>	0.47* <i>a</i>	0.43* <i>a</i>	-0.02 <i>a</i>	0.42* <i>a</i>	0.46*	0.41* <i>a</i>	SW
0.16 <i>a</i>	0.29* <i>a</i>	0.23*	0.30* <i>a</i>	0.26*	0.14	0.33*	0.56* <i>a</i>	0.42* <i>a</i>	SH
0.28* <i>a</i>	0.39*	0.35*	0.53* <i>a</i>	0.54* <i>a</i>	-0.03 <i>a</i>	0.60* <i>a</i>	0.69* <i>a</i>	0.39* <i>a</i>	PL
0.08	0.08	0.14 <i>a</i>	-0.10	0.09	0.20 <i>a</i>	0.06	0.07	0.14 <i>a</i>	CH
0.20	0.26*	0.21*	0.20	0.18	0.16 <i>a</i>	0.21	0.37*	0.24*	CW
-0.07	0.07 <i>a</i>	-0.07 <i>a</i>	0.11	0.03	-0.09 <i>a</i>	0.01 <i>a</i>	-0.14 <i>a</i>	0.11	SS
0.13 <i>a</i>	0.29*	0.13 <i>a</i>	0.35* <i>a</i>	0.32*	0.14	0.31*	0.19 <i>b</i>	0.22* <i>b</i>	SSWP
0.12 <i>a</i>	0.24* <i>a</i>	0.21* <i>a</i>	0.19	0.20	-0.01 <i>a</i>	0.41* <i>a</i>	0.32*	0.15 <i>a</i>	INL
0.15	0.22* <i>a</i>	0.13	0.03	0.23* <i>a</i>	-0.12 <i>a</i>	0.19	0.24*	0.24*	INW
1.00	0.41*	0.28*	0.14 <i>a</i>	0.22*	0.01 <i>a</i>	0.24*	0.16 <i>a</i>	0.24* <i>a</i>	BW
0.52*	1.00	0.19	0.23* <i>a</i>	0.29*	0.20	0.58* <i>a</i>	0.29*	0.29* <i>a</i>	PW
0.20	0.08	1.00	0.19	0.27*	0.00 <i>a</i>	0.23* <i>a</i>	0.30*	0.43*	M
0.00 <i>b</i>	0.00 <i>b</i>	0.25*	1.00	0.55* <i>a</i>	0.00	0.49*	0.41* <i>a</i>	0.31*	SL1
0.17	0.24	0.16	0.03 <i>b</i>	1.00	-0.17	0.56* <i>a</i>	0.44* <i>a</i>	0.33*	SL2
0.20 <i>b</i>	0.12	0.24 <i>b</i>	0.05	-0.09	1.00	0.26* <i>a</i>	-0.10 <i>a</i>	-0.04 <i>a</i>	SL3
0.35*	0.20 <i>b</i>	0.39* <i>b</i>	0.39*	0.22 <i>b</i>	0.42* <i>b</i>	1.00	0.47*	0.32* <i>a</i>	SL4
0.36* <i>b</i>	0.35*	0.22	0.26* <i>b</i>	0.07 <i>b</i>	0.32* <i>b</i>	0.57*	1.00	0.36* <i>a</i>	NL
0.52* <i>b</i>	0.44* <i>b</i>	0.46*	0.24	0.22	0.32* <i>b</i>	0.57* <i>b</i>	0.56* <i>b</i>	1.00	NW

Note: Coefficients marked with * are statistically significant (p-value < 0.05). Corresponding correlation coefficients with statistically significant differences (p-value < 0.05) are marked with different letters.

Table 4. The first 5 principal components which account for more than 63% of total variation from the PCA

Variables	PC1	PC2	PC3	PC4	PC5
SL	-0.344	0.064	-0.019	0.006	-0.213
SW	-0.250	0.264	0.263	0.034	-0.059
SH	-0.286	-0.063	0.185	-0.043	-0.090
PL	-0.309	0.189	-0.039	0.094	-0.186
CH	-0.098	-0.291	0.458	-0.336	-0.038
CW	-0.209	-0.262	0.385	-0.086	-0.108
SS	-0.107	-0.466	-0.035	0.336	0.516
SSWP	-0.227	-0.035	0.288	0.405	0.343
INL	-0.191	0.202	-0.401	0.021	0.111
INW	-0.146	-0.254	-0.366	-0.368	0.235
BW	-0.184	0.235	0.039	-0.336	0.267
PW	-0.233	0.094	-0.073	-0.385	0.207
M	-0.169	0.271	-0.004	0.175	0.174
SL1	-0.208	-0.093	-0.178	0.381	-0.306
SL2	-0.232	-0.296	-0.120	0.007	-0.156
SL3	-0.043	0.410	0.252	0.058	0.239
SL4	-0.301	-0.024	-0.165	0.063	-0.025
NL	-0.289	-0.047	-0.061	-0.077	-0.274
NW	-0.273	-0.032	-0.089	-0.047	0.215
Eigenvalue	6.462	1.746	1.457	1.242	1.084
% of variance	34.015	9.192	7.672	6.538	5.708
Cumulative	34.015	43.207	50.879	57.417	63.125

Note: Bold – absolute value of loadings > 0.3

Table 5. Least squares means (LSM) and their standard errors (SE) of skull measurements for farm females, wild females, farm males and wild males

	measurement									
	SL	SW	SH	PL	INL	INW	BW	PW	NL	NW
FARM FEMALES										
n	33	33	33	33	33	33	33	33	33	33
LSM	144.94 _a	74.17 _a	49.63 _a	72.14 _a	9.17 _a	2.55 _{ac}	15.25 _a	17.88 _a	20.61 _a	12.35 _a
SE	0.84	0.50	0.38	0.41	0.15	0.05	0.15	0.14	0.16	0.11
WILD FEMALES										
n	30	30	31	31	31	31	32	31	31	32
LSM	141.79 _b	75.65 _b	49.35 _a	73.01 _a	9.10 _a	2.33 _b	15.39 _a	17.61 _a	19.88 _b	11.99 _b
SE	0.87	0.51	0.39	0.42	0.15	0.05	0.15	0.14	0.17	0.11
FARM MALES										
n	57	56	57	57	57	57	57	57	57	57
LSM	154.50 _c	77.85 _c	51.53 _b	76.00 _b	9.87 _b	2.65 _a	16.05 _b	18.86 _b	21.82 _c	13.03 _c
SE	0.69	0.41	0.31	0.34	0.12	0.04	0.12	0.11	0.13	0.09
WILD MALES										
n	36	37	37	37	38	38	38	38	36	37
LSM	151.35 _d	79.33 _d	51.25 _b	76.87 _b	9.80 _b	2.43 _{bc}	16.19 _b	18.59 _b	21.09 _a	12.67 _a
SE	0.82	0.48	0.37	0.39	0.15	0.05	0.14	0.13	0.16	0.11

Note: Different letters in columns indicate significant differences between sex-population groups (p-value < 0.05).

Table 5. continued.

	measurement								
	CH	CW	SS	SSWP	M	SL1	SL2	SL3	SL4
FARM FEMALES									
n	33	33	32	32	33	33	33	33	33
LSM	23.08 _{ac}	25.44 _a	25.57 _a	36.17 _{ac}	14.23 _a	5.81 _a	15.38 _a	3.68 _{ac}	17.15 _a
SE	0.39	0.22	0.23	0.38	0.16	0.13	0.15	0.14	0.17
WILD FEMALES									
n	31	31	32	32	31	31	31	31	30
LSM	21.25 _b	24.31 _b	23.65 _b	35.83 _a	14.64 _{ac}	5.47 _b	14.41 _b	4.19 _b	16.30 _b
SE	0.39	0.23	0.23	0.38	0.16	0.13	0.15	0.14	0.18
FARM MALES									
n	57	57	57	57	57	57	57	57	57
LSM	23.56 _a	26.67 _c	25.29 _a	37.68 _b	14.78 _{bc}	6.36 _c	16.34 _c	3.58 _a	18.29 _c
SE	0.32	0.18	0.19	0.31	0.13	0.11	0.12	0.12	0.14
WILD MALES									
n	37	37	38	38	37	37	37	37	36
LSM	21.73 _{bc}	25.54 _a	23.37 _b	37.34 _{bc}	15.18 _b	6.02 _a	15.37 _a	4.08 _{bc}	17.45 _a
SE	0.37	0.22	0.22	0.36	0.16	0.12	0.14	0.14	0.17

Note: Different letters in columns indicate significant differences between sex-population groups (p-value < 0.05).

Table 6. Basic descriptive statistics of skull indices for farm females, wild females, farm males and wild males

	Index			
	SI	WI	BR	PI
FARM FEMALES				
n	33	33	33	33
mean	51.53a	1.94a	50.09a	25.03
minimum	47.77	1.83	48.28	22.42
maximum	54.58	2.09	52.69	27.48
SD	1.75	0.07	1.12	1.26
CV [%]	3.40	3.43	2.24	5.04
WILD FEMALES				
n	29	29	30	30
mean	53.14b	1.88b	51.14b	23.99
minimum	48.21	1.74	48.98	20.49
maximum	57.31	2.07	53.78	27.32
SD	1.86	0.07	1.30	1.66
CV [%]	3.50	3.55	2.55	6.92
FARM MALES				
n	56	56	57	57
mean	50.23a	1.99a	49.06c	24.71
minimum	46.05	1.78	46.69	22.70
maximum	56.18	2.17	52.31	27.52
SD	2.01	0.08	1.37	1.19
CV [%]	4.00	3.95	2.80	4.81
WILD MALES				
n	36	36	36	37
mean	52.74b	1.91b	51.24b	24.40
minimum	35.58	1.75	48.12	20.47
maximum	57.02	2.81	54.25	26.88
SD	3.46	0.17	1.45	1.50
CV [%]	6.57	8.81	2.83	6.14

Note: Different letters in columns indicate significant differences (p-value < 0.05).

Figure 1. Skull measurements: **A. Dorsal view:** 1 - Skull length (SL); 2 - Maximum zygomatic width (SW); 3 - Frontal breadth (SSWP); 4 - Least breadth of skull (SS); 5 - Nostril width (NW); 6 - Nostril length (NL). **B. Ventral view:** 7 - Comb width (CW); 8 - Comb height (CH); 9 - Median palatal length (PL); 10 - Bone wedge (BW); 11 - Palatal width (PW); 12 - Internal nares width (INW); 13 - Internal nares length (INL). **C. Left-lateral view:** 14 - Skull height (SH); 15 - Mastoid height (M); 16 - I3 - C length (SL1); 17 - I-C length (SL2); 18 - C-P1 length (SL3); 19 - I3 - P1 length (SL4).

Figure 2. Principal component analysis (PCA) of 19 skull dimensions measured from wild and farm foxes. Axes represent loadings onto components 1 and 2.

Figure 3. Illustrative examples of studied skulls (left-lateral, dorsal and ventral views): a. farm male; b. farm female; c. wild male; d. wild female.

Figure 4. Principal component analysis (PCA) of 19 skull dimensions measured from 4 sex-population groups: farm males, farm females, wild males, wild females. Axes represent loadings onto components 1 and 2.

Figure 1. Skull measurements: A. Dorsal view: 1 - Skull length (SL); 2 - Maximum zygomatic width (SW); 3 - Frontal breadth (SSWP); 4 - Least breadth of skull (SS); 5 - Nostril width (NW); 6 - Nostril length (NL). B. Ventral view: 7 - Comb width (CW); 8 - Comb height (CH); 9 - Median palatal length (PL); 10 - Bone wedge (BW); 11 - Palatal width (PW); 12 - Internal nares width (INW); 13 - Internal nares length (INL). C. Left-lateral view: 14 - Skull height (SH); 15 - Mastoid height (M); 16 - I3 - C length (SL1); 17 - I-C length (SL2); 18 - C-P1 length (SL3); 19 - I3 - P1 length (SL4).

162x150mm (96 x 96 DPI)

Figure 2. Principal component analysis (PCA) of 19 skull dimensions measured from wild and farm foxes. Axes represent loadings onto components 1 and 2.

154x93mm (96 x 96 DPI)

Figure 3. Illustrative examples of studied skulls (left-lateral, dorsal and ventral views): a. farm male; b. farm female; c. wild male; d. wild female.

102x207mm (96 x 96 DPI)

Figure 4. Principal component analysis (PCA) of 19 skull dimensions measured from 4 sex-population groups: farm males, farm females, wild males, wild females. Axes represent loadings onto components 1 and 2.

154x93mm (96 x 96 DPI)