Ann. Zool. Fennici 45: 185–199 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 26 June 2008

Geographic variation of tooth and skull sizes in the arctic fox *Vulpes* (*Alopex*) *lagopus*

Elwira Szuma

Mammal Research Institute Polish Academy of Sciences, ul. gen. Waszkiewicza 1, PL-17-230 Białowieża, Poland (e-mail: eszuma@bison.zbs.bialowieza.pl)

Received 21 June 2007, revised version received 14 Jan. 2008, accepted 26 Sep. 2007

Szuma, E. 2008: Geographic variation of tooth and skull sizes in the arctic fox *Vulpes* (*Alopex*) *lagopus*. — *Ann. Zool. Fennici* 45: 185–199.

The subject of the research was the geographic variation in tooth size and condylobasal skull length (CBL) in arctic fox *Vulpes* (*Alopex*) *lagopus*. The analysis was based on 328 skulls of individuals from 14 different populations. Most of the metric dental characteristics and CBL indicated a significant diversification among the populations. A particularly high inter-population variations was observed in the sizes of C^1, C_1, P^4, and in the CBL. The arctic foxes of Eurasia were larger than the arctic foxes of North America. The largest specimens of the arctic fox were those of Komandorskiye Ostrova, while the smallest ones were on Baffin Land and Greenland. Moderate sizes of dentition and skulls were observed in continental populations (Taymyr, Ust-Yanskiy region, Zaliv Kozhevnikova, Yamal Poluostrov, Yakutskaya oblast'). As regards the variation in the size of the skull and dentition of arctic foxes, a higher variation was noted in arctic foxes from island (St. Lawrence Island, Komandorskiye Ostrova) and "coastal" populations (Yamal Poluostrov, Taymyr), and a lower one in arctic foxes from Asian populations (Zaliv Kozhevnikova, Yakutskaya oblast'). In the Arctic, within the geographical range of the fox, neither the size, nor sexual dimorphism of the metric dental and skull characteristics showed any specific geographic trend. However, the existing hypothesis, (such as Bergmann's rule, or "island syndrome"), do not explain the pattern of size variation in the arctic fox. The arctic fox morphological variation within its range is primarily shaped by climate conditions and food resources, and secondarily by competition within- and between species.

Introduction

On account of its ecological flexibility necessary for its extremely hard life conditions, the arctic fox has always drawn the attention of scientists. At present, the ecology of the species is being particularly investigated (e.g. Prestrud 1991, Hersteinsson & Macdonald 1992, Angerbjörn *et al*. 1999, Anthony *et al*. 2000, Elmhagen *et al*. 2000, Frafjord 2000, Goltsman *et al*. 2005).

Craniometric variation in the arctic fox was a subject of numerous studies (Zalkin 1944, Bisaillon & DeRoth 1980, Frafjord 1993, Prestrud & Nielsen 1995, Zagrebel'nyi & Puzachenko 2006). Ognev (1931) indicated that the arctic fox has low (literally "monolithic") variability within its geographic range. The high mobility and occupation of monotonous tundra-habitat, may explain the observation (Zalkin 1944, Angerbjörn *et al*. 1999). The species includes

This article has been scientifically edited by Philip Starks

eight subspecies in its wide geographic range (Audet *et al*. 2002). Almost entire continental range of the arctic fox is inhabited by one subspecies — *Vulpes* (*Alopex*) *lagopus lagopus*. The other subspecies (*V. l. beringensis*, *V. l. fuliginosus*, *V. l. groenlandicus*, *V. l. hallensis*, *V. l. pribilofensis*, *V. l. spitzbergenensis*, *V. l. ungava*) are mostly isolated, insular populations. In comparison with other, similarly wide-ranging mammals, the arctic fox is characterized by low genetic diversity (Dalén *et al*. 2005).

Despite the morphological and genetic homogeneity, the arctic foxes in the south are larger than those in the north (Bisaillon & DeRoth 1980, Frafjord 1993). Moreover, in comparison with the continental arctic fox, insular populations have visibly larger skulls (Zalkin 1944, Zagrebel'nyi & Puzachenko 2006). Zalkin (1944) found that the arctic fox of Beryngia is characterized by the largest skull sizes. Germonpre and Sablin (2004) obtained similar results by analyzing the lower carnassial in the populations of the arctic fox from Eurasia. They found that the M_1 sizes of the individuals of Komandorskiye Ostrova are relatively larger, while those of Franz Josef Land are relatively smaller in comparison with those of the continental individuals. Geographic variation of the skull size and M_1 in the arctic fox does not confirm the rule of Bergmann (Zalkin 1944, Germonpre & Sablin 2004). McNab (1971) while studying the North-American mammals found, that Bergmann's rule does not apply to the mammals inhabiting areas above 60°N latitude. The arctic fox has exclusively a circumpolar distribution, primarily above 60°N latitude (Wilson & Ruff 1999).

The arctic fox dentition has previously been studied with respect to the historical and geographical variation of M_1 (Germonpre & Sablin 2004), geographic variation of M_1 using the landmark method (Daitch & Guralnick 2007), the ontogenetic and functional aspects of the variation pattern, and the correlation in dentition of the species (Pengilly 1984).

The specific morphometric studies of variation of dentition in the red fox *Vulpes vulpes* indicated that teeth make a sensitive indicator of evolutionary processes occurring in contemporary populations (Szuma 2003, 2007). The analysis of the variation-and-correlation pattern, as well as the geographic variation of the metric and morphotype characteristics in dentition allow one to identify factors determining variation patterns in particular population(s) (Szuma 2003, 2008). In case of the predators the morphometric analysis of the dentition identifies evolution towards adaptation to hypo- or hypercarnivory. The inter-population analysis of the sexual dimorphism in red fox dentition throughout its occurrence showed that the phenomenon is influenced by: the social structure, density of the population or intra- and inter-species competition (Szuma 2008). The geo-climatic or phylogenetic factors are of no less influence on the morphometric variation within the species (Szuma 2007). The specific analysis of the morphometric dental patterns within the populations allows to define both: the past, and the future trends in the evolution of the species (Szuma 2003).

This research showed that changes occurring in both metric and morphotype dental pattern in red foxes result from the high alimentary opportunism (Szuma 2003). The red fox is flexible in its dietary and habitat requirements. Similarly, the arctic fox exhibits distinct, food opportunism as well (Elmhagen *et al*. 2000). The arctic fox is a close relative of the red fox, with which it coexists and competes in the south of its range. During the last century a decrease of the arctic fox range was observed. In the south of its range it yielded to the red fox (Skrobov 1960, Hersteinsson & Macdonald 1992). The phenomenon is explained by climatic warming. The detailed analysis proved that the factors limiting the northern range of fox are: summer temperatures (taken as a habitat productivity index), variables related to winter conditions (Hersteinsson & Macdonald 1992), winter severity (especially mean winter temperature) and seasonality in habitat productivity (Bartoń & Zalewski 2007). Considering this, the question remains why, despite the repeatedly illustrated food opportunism and highly advanced habitat specialization in conditions of interspecies competition, does the arctic fox yields to the red fox? In order to recognize to what extent opportunism of the arctic fox is reflected in its dentition, an attempt was made to examine: (1) the geographic variation of metric characteristics in the arctic fox dentition, (2) the influence of the geo-climatic variables on the pattern of the dentition metric variability, (3) geographic variation in sexual dimorphism of dental metric characteristics, and (4) a comparison of the pattern of geographic variety of the arctic fox dentition with that of the red fox.

Material and methods

The study used 328 skulls of the arctic fox, *Vulpes* (*Alopex*) *lagopus* (Linnaeus, 1758). The material included 14 geographically distant populations that covered almost the entire range of the arctic fox (Fig. 1). The list below includes abbreviations of the populations and in brackets the number of females and males of the arctic fox used in the studies. In some populations the sex of the examined individuals was unknown. The following populations were studied: Ala (Alaska) n = 8 (4, 4); Baf (Baffin Land) n = 22; Ell (Ellesmere Island) n = 4; Gre (Greenland) n = 15 (5, 7); Kom (Komandorskiye Ostrova) n = 58 (18, 26); Koz (Zaliv Kozhevnikova) n = 28 (14, 6); Law (St. Lawrence Island) n = 4 (2, 2); Nov (Novaya Zemlya) n = 2; Sou (Southampton Island) n = 4 (2, 2); Spi (Spitsbergen) n = 1; Tay (Taymyr) n = 58 (25, 24); Ust (Ust-Yanskiy region) n = 44 (21, 23); Yak (Yakutskaya oblast') n = 35 (3, 6); Yam (Yamal Poluostrov) n = 44 (2, 3).

The list of the museums (6 institutions) that made their collections available to the author is given in the Acknowledgements.

The measurements were carried out with the Sylvac digital calliper and were recorded to the nearest 0.01 mm. The upper and lower teeth of the left side were measured (23 measurements were taken on each specimen). Only adult specimens with fully erupted permanent teeth were used. The teeth with worn crowns were not measured. In carnivorous mammals, the size of permanent teeth remains the same during the entire life (with the exception of fractures or wearing), so the arctic fox samples were not divided according to age.

I also used condylobasal skull length (CBL) as a common indicator of body size (e.g. Ralls & Harvey 1985, Meiri *et al*. 2004).

The measurements of the tooth size and CBL were taken as follows:

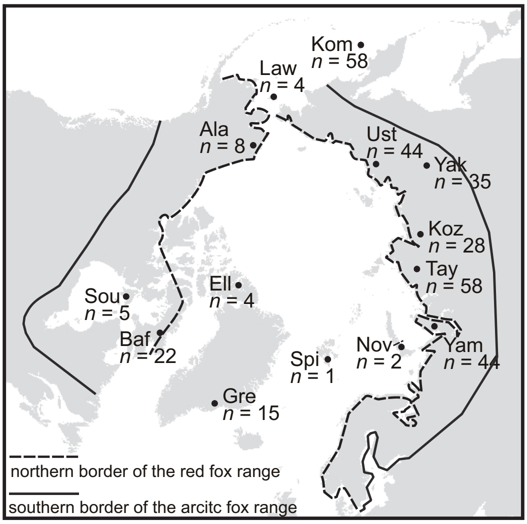

Fig. 1. Distribution of the studied samples of the arctic fox *Vulpes* (*Alopex*) *lagopus*. Abbreviation for particular populations: Ala = Alaska, Baf = Baffin Land, Ell = Ellesmere Island, Law = St. Lawrence Island, Sou = Southampton Island, Gre = Greenland, Spi = Spitsbergen, Nov = Novaya Zemlya, Koz = Zaliv Kozhevnikova, Tay = Taymyr, Ust = Ust-Yanskiy region, Yak = Yakutskaya oblast', Yam = Yamal Poluostrov, Kom = Komandorskiye Ostrova.

LI^3 = length of the crown of upper third incisor (I^3): the greatest mesiodistal distance of the tooth crown;

WI^3 = width of the crown of upper third incisor (I^3): the greatest labiolingual distance of the tooth crown;

LC^1, LC_1 = lengths of the crown of upper and lower canine (C^1, C_1): the greatest mesiodistal distance at the base of the tooth crown;

WC^1, WC_1 = widths of the crown of upper and lower canine (C^1, C_1): the greatest labiolingual distance at the base of the tooth crown;

HC^1, HC_1 = heights of the crown of upper and lower canine (C^1, C_1): the greatest distance between the occlusal tip and the distalmost (i.e., posteriormost) point of the base of the tooth crown;

LP^1, LP_1 = lengths of the crown of first upper and lower premolar (P^1, P_1): the greatest length between the anterior and posterior (mesial and distal) points of the tooth crown;

WP^1, WP_1 = widths of the crown of first upper and lower premolar (P^1, P_1): the greatest width between the lingual and buccal points of the tooth crown;

LP^4b = buccal length of the crown of fourth upper premolar (P^4): the greatest length between the anteriormost point of the anterobuccal lobe of the tooth crown and the distalmost point;

LP^4l = lingual length of the crown of fourth upper premolar (P^4): the greatest length between the anteriormost point of the anterolingual lobe of the tooth crown and the distalmost point;

WP^4 = width of the crown of fourth upper premolar (P^4): the greatest distance between the lingual and buccal points of the tooth crown measured perpendicularly to LP^4b;

LM^1, LM^2, LM_1, LM_3 = lengths of the crown of first upper molar (M^1), second upper molar (M^2), first lower molar (M_1), third lower molar (M_3): the greatest distance between the anterior and posterior (mesial and distal) points of the tooth crown;

WM^1, WM^2, WM_1, WM_3 = widths of the crown of first upper molar (M^1), second upper molar (M^2), first lower molar (M_1), third lower molar (M_3): the greatest distance between the lingual and buccal points of the tooth crown;

CBL = condylobasal length of the skull: the greatest distance between the line connecting the most distal points of the occipital condyles and the line connecting the anteriormost points of the premaxillary bones.

On account of the small number of some samples and numerous specimens of unknown sex, the analysis of geographic variation was accomplished without taking sexes into consideration. Because of the absence of some measurements in some populations, the analysis of agglomeration and of multidimensional scaling (MDS) was carried out on all the characteristics except for the height of the canines and the sizes of I^3.

In the multidimensional analysis the least numerous samples (i.e. Novaya Zemlya, Spitsbergen, and, because of the lack of the data on the upper carnassial — Ust-Yanskiy region) were not included.

In order to estimate to what extent geo-climatic factors determine geographic variation of tooth sizes in the arctic fox, the following independent variables were used: latitude (LAT), longitude (LON), mean annual temperature (MAT), mean amplitude of temperatures between the warmest and coldest months (July and January, respectively) in the year ($AMT_{Jul–Jan}$), and mean annual sum of precipitation (MASP). Each specimen was described by the geographic coordinates with precision to 1°. The climatic data were derived from the WorldClimate database (www.worldclimate.com). For each population the mean longitude and latitude were calculated, and then the nearest meteorological station in the World Climate data base was found. Most meteorological stations provided climatic data allowing calculations of means for several years or several decades. In all the statistical procedures the mean annual temperatures (resolution 0.1 °C) and the mean annual precipitation sums (resloution 0.1 mm) were used.

Sexual dimorphism was calculated as a proportion of the mean measure of certain characters in males and the respective mean in females (M_m/M_f). The index was estimated only in those arctic fox populations in which the number of individuals of each sex exceeded 15. The statistical relevance of sexual dimorphism of dental characteristics was estimated with the *t*-test.

In order to compare the geographic variation of dentition in the arctic fox and its competitor, the red fox *Vulpes vulpes* (Linnaeus 1758), I calculated the coefficient of variation CV (SD × 100/mean) of selected dental and skull characteristics (i.e. LC^1, WP^1, LP^4b, LM^1, WP_1, LM_1 and CBL) for both fox species.

The CV was determined for all arctic fox populations, except the least numerous (Novaya Zemlya, Spitsbergen). I combined the populations of Southampton Island and Baffin Land and, for this analysis, considered them as a single population of northeastern Canada (Can).

I used my own unpublished CVs of dental and skull characteristics for the selected fox populations. In the analysis, I used red fox populations that occurred within the range of the arctic fox [i.e. Alaska, Ala (n = 130); British Columbia, Col (n = 22); Chukchi, Russia, Chu (n = 86); Kenai Peninsula, Ken (n = 13), Kodiak Island, Kod (n = 33), Magadan, Russia, Mag (n = 92); Pechoro-Illycheskiy reserve, Russia, Pec (n = 65); Yakutskaya oblast', Russia, Yak (n = 32); Quebec, Que (n = 20)].

I estimated the relevance of differences between the two fox species with respect to the variation of the selected skull and dentition metric characteristics using the *t*-test. I calculated the mean CV for each of the 9 red fox populations and 10 arctic fox populations using eight metrical characters. I analysed the interpopulation variance using the CV for all the 19 populations

Statistical analyses were carried out using Statistica.PL ver. 6.0.

Results

Statistically significant differences ($p < 0.001$) between the arctic fox populations were found in case of the following dental characteristics: LI^3, LC^1, WC^1, LP^1, WP^1, LP^4b, WP^4, HC_1, WP_1, WM_1, LM_3, WM_3, and CBL. The sizes of the upper molars did not show any significant geographic variations (Table 1).

The means of all the studied dental characteristics of arctic foxes from Eurasia were higher than those of North American arctic foxes. Eurasian arctic foxes were considerably larger ($p < 0.05$) with respect to LI^3, LC^1, LP^1, WP^1, LP^4b, LP^4l, LP_1, WP_1, WM_1, LM_3, WM_3, and CBL (Table 2).

The arctic fox population of Komandorskiye Ostrova had the largest dental sizes (Fig. 2 and Appendix). However, M_1 of individuals from Novaya Zemlya was the largest (Fig. 2E, F). The MDS diagram of the dispersion of the arctic fox population, based on Euclidean distances of the dental characteristics, shows that the most remote population is the one from Komandorskiye Ostrova (Fig. 3). Another remote arctic fox population is on St. Lawrence Island. The most similar populations are those of Alaska and Yamal Poluostrov, then of Zaliv Kozhevnikova, Taymyr, Southampton Island, Greenland, Baffin Land, and Yakutskaya oblast'.

The dental metric characteristics indicate a

Table 1. Interpopulation variation (ANOVA) of the arctic fox on the metrical tooth characters and condylobasal skull length (CBL).

	R^2	df	F	p
LI^3	4.172	11	6.81	0.000
WI^3	1.682	11	2.11	0.020
LC^1	6.296	11	3.72	0.000
WC^1	2.118	12	3.49	0.000
HC^1	10.262	6	4.03	0.001
LP^1	3.606	13	2.94	0.000
WP^1	3.090	13	8.11	0.000
LP^4b	13.758	13	3.41	0.000
LP^4l	5.966	12	1.51	0.120
WP^4	7.914	13	3.62	0.000
LM^1	2.175	12	0.96	0.483
WM^1	4.016	12	1.36	0.187
LM^2	2.270	13	1.53	0.106
WM^2	3.489	13	1.03	0.421
LC_1	2.436	12	1.17	0.315
WC_1	0.416	12	0.58	0.853
HC_1	11.866	5	5.74	0.000
LP_1	1.608	13	1.97	0.024
WP_1	2.777	12	9.85	0.000
LM_1	8.491	13	1.90	0.029
WM_1	2.681	13	2.89	0.001
LM_3	4.027	13	4.23	0.000
WM_3	7.441	13	15.40	0.000
CBL	3018.570	13	12.15	0.000

Table 2. Comparison of some metrical dental characters and condylobasal skull length (CBL) of the North American and Eurasian arctic foxes. M_{EU} = mean of the tooth character in Eurasian arctic foxes; M_{NA} = mean of the tooth character in North American arctic foxes.

	M_{EU}	n	M_{NA}	n	df	t	p
LI^3	3.76	227	3.63	29	254	2.60	0.010
WI^3	4.67	241	4.61	36	275	1.33	0.186
LC^1	6.32	207	6.15	36	241	2.38	0.018
WC^1	3.82	211	3.81	42	251	0.14	0.885
HC^1	14.83	79	14.05	3	80	1.87	0.066
LP^1	4.90	239	4.71	48	285	3.66	0.000
WP^1	2.93	246	2.86	54	298	2.59	0.010
LP^4b	12.42	260	12.17	56	314	2.92	0.004
WP^4	6.61	262	6.52	56	316	1.41	0.160
LP^4l	13.97	180	13.79	57	235	2.04	0.042
LM^1	8.39	189	8.39	57	244	0.08	0.938
WM^1	9.81	192	9.75	57	247	0.78	0.436
LM^2	4.68	220	4.62	52	270	1.22	0.223
WM^2	7.16	259	7.11	55	312	0.67	0.505
LC_1	7.21	122	7.16	21	141	0.50	0.619
WC_1	3.93	196	3.91	20	214	0.40	0.692
HC_1	14.14	56	13.90	3	57	0.51	0.609
LP_1	3.81	239	3.72	44	281	2.07	0.039
WP_1	2.70	248	2.63	47	293	2.58	0.010
LM_1	13.71	265	13.65	55	318	0.53	0.596
WM_1	5.13	264	5.03	54	316	2.31	0.021
LM_3	2.84	203	2.65	39	240	3.71	0.000
WM_3	2.49	204	2.32	39	241	3.98	0.000
CBL	120.83	243	118.09	50	291	3.35	0.001

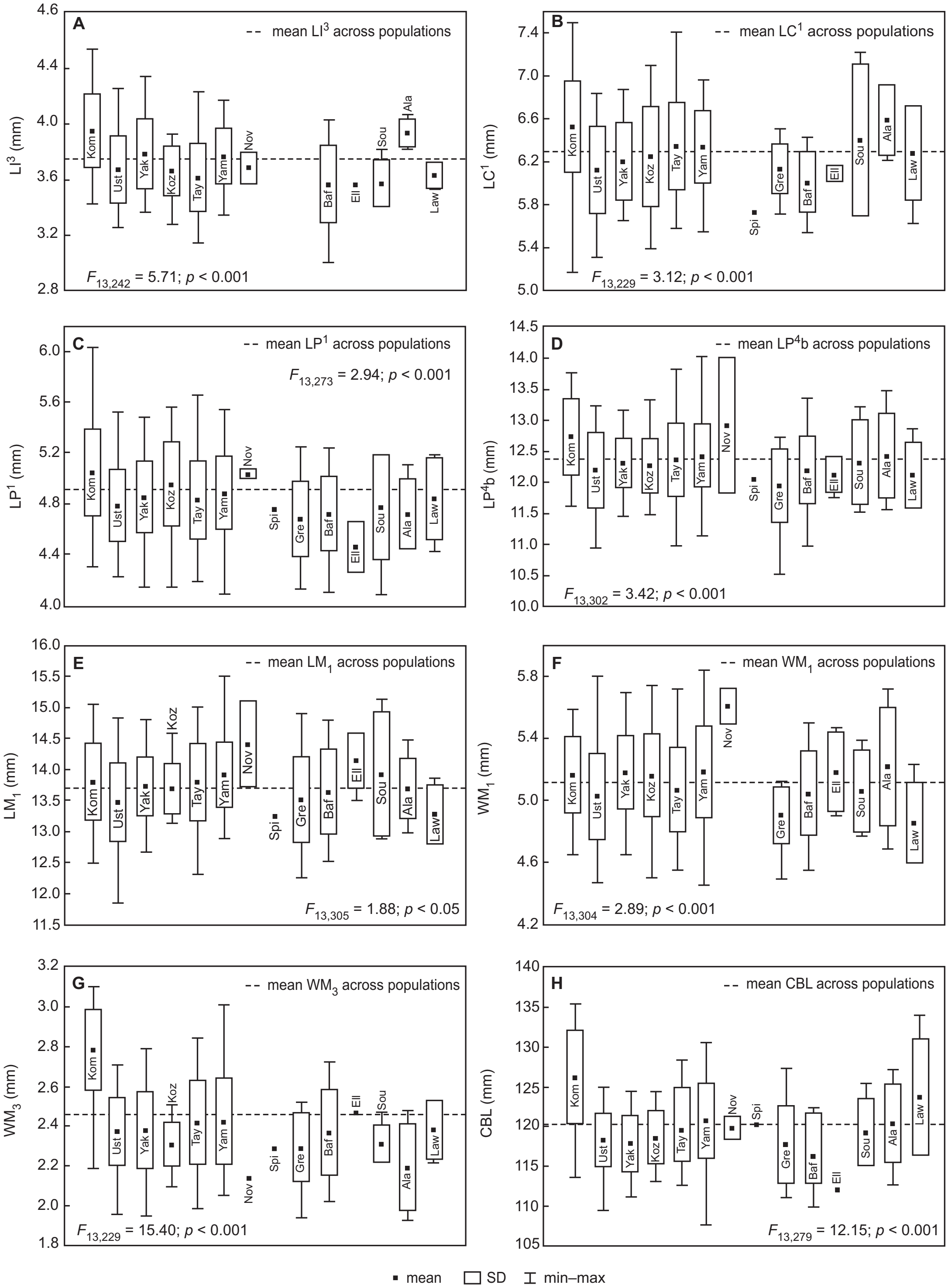

Fig. 2. Variation of (**A**) length of I³–LI³; (**B**) length of C¹–LC¹; (**C**) length of P¹–LP¹; (**D**) buccal length of P⁴–LP⁴b; (**E**) length of M_1–LM_1; (**F**) width of M_1–WM_1; (**G**) width of M_3–WM_3; (**H**) condylobasal skull length (CBL) within geographic range of the arctic fox *Vulpes* (*Alopex*) *lagopus*. Abbreviations as in Fig. 1.

certain gradient related to longitude. The populations of the Far East are characterised by larger dentition sizes. A statistically significant relationship was observed between LM_3 and longitude ($r = 0.74$; $n = 11$; $p = 0.01$).

Most of the dentition characteristics were negatively correlated with latitude. The populations of the highest latitude were characterised by smaller dentition. Significant negative relationships was observed in: WC^1, LP^1, WP^4 (Fig. 4A), LM_3, WM_3 and CBL (Fig. 4B). Only LM^1 was positively correlated with latitude. The most northward populations of the arctic fox had the largest LM^1.

A significant positive relationship existed between MAT and: LI^3 (Fig. 5A), LC^1 (Fig. 5B), LP^1, LP^4b, WP^4, LM^2 (Fig. 5C), and CBL (Fig. 5D).

It has been observed that with the increase of $AMT_{Jul–Jan}$ the size of the dentition and CBL decreases. Although the trends were negative, the relationships, however, were not statistically significant.

With the increase of MASP, the sizes of dentition and CBL grew as well. A significant positive correlation was found between MASP and LI^3, WP^4 (Fig. 6A), WM_3, and CBL (Fig. 6B).

The analysis of the sexual dimorphism of the dental metric characteristics in three populations of the arctic fox, i.e. Taymyr, Komandorskiye Ostrova, and Ust-Yanskiy region, showed, that the highest level of dimorphism occurs in Komandorskiye Ostrova (1.06); intermediate in Taymyr (1.05), and the lowest in Ust-Yanskiy region (1.03). In all the three populations,

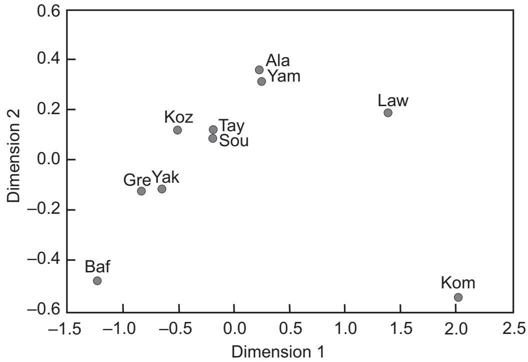

Fig. 3. Dispersion of the arctic fox populations based on the Euclidean distances in respect to the tooth and skull size. Abbreviations as in Fig. 1.

the highest level of dimorphism was found for LI^3, WI^3, LC^1, WC^1, HC^1, LP^1, WP^1 and LC_1. As for the arctic fox populations of Taymyr and Komandorskiye Ostrova the WC_1 and HC_1 exhibited high dimorphism, as well, while in the Komandorskiye Ostrova population the LM^2, WM^2, LM_1, LM_3, WM_3, and CBL showed a higher level of dimorphism (Table 3).

The CV of LC^1, WP^1, LP^4b, WP_1, LM_1 and CBL were slightly different ($p > 0.05$) in red foxes than in arctic foxes (Table 4). In case of LM^1, the CV in both fox species was the same. Despite this, an analysis of variance of the CV in 19 fox populations (9 of the red fox and 10 of the arctic fox) proved the presence of a significant inter-population variation ($F = 1.82$; $p = 0.03$).

The highest CV was found in the arctic fox population of Yakutskaya oblast' (6.9), and the lowest in the Kenai Peninsula (4.3). Considering

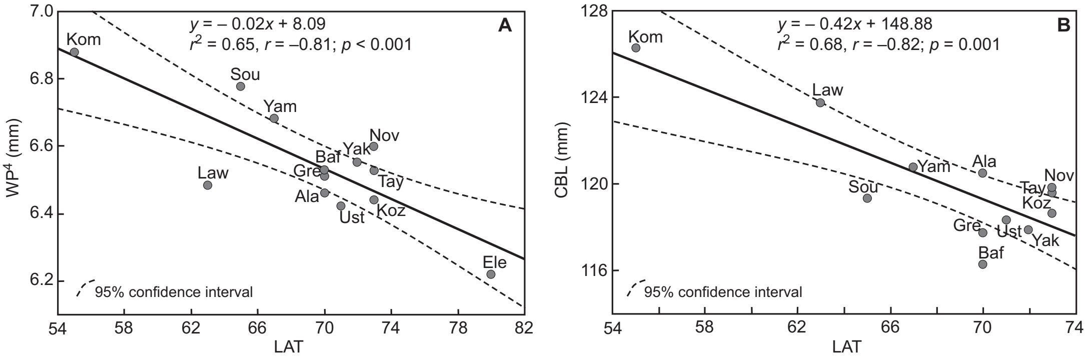

Fig. 4. Relationships between latitude (LAT) and (**A**) width of P^4–WP^4 and (**B**) condylobasal skull length (CBL) in the arctic fox *Vulpes* (*Alopex*) *lagopus.* Abbreviations as in Fig. 1.

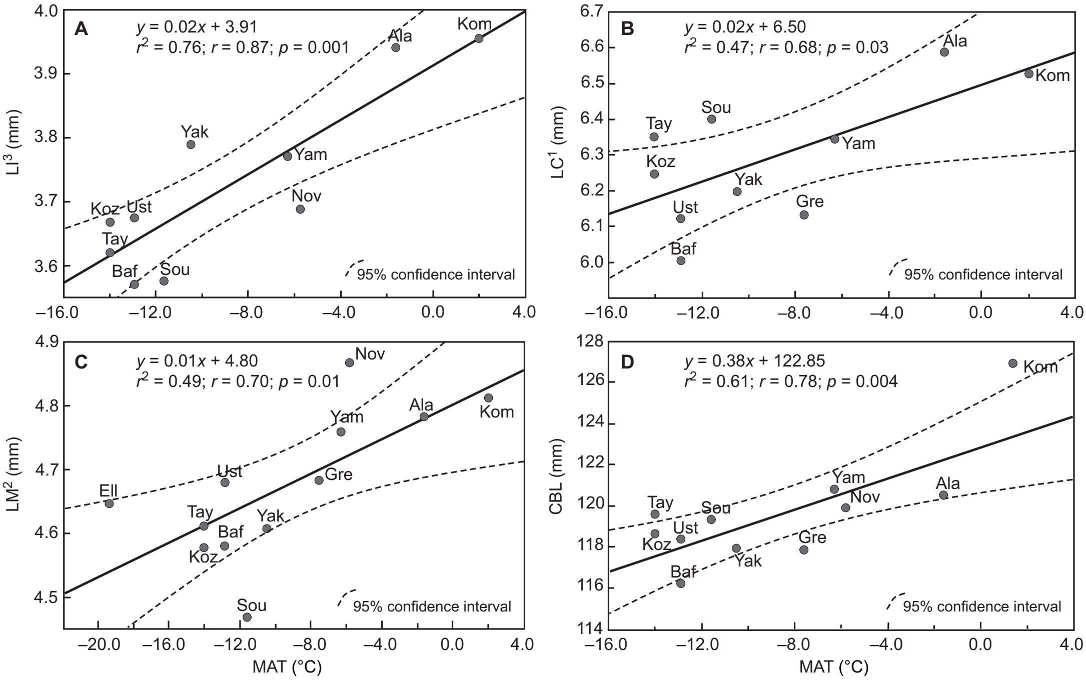

Fig. 5. Relationships between the mean annual temperature, MAT and (**A**) length of I^3–LI^3; (**B**) length of C^1–LC^1; (**C**) length of M^2–LM^2; (**D**) condylobasal skull length (CBL), in the arctic fox *Vulpes* (*Alopex*) *lagopus*. Abbreviations as in Fig. 1.

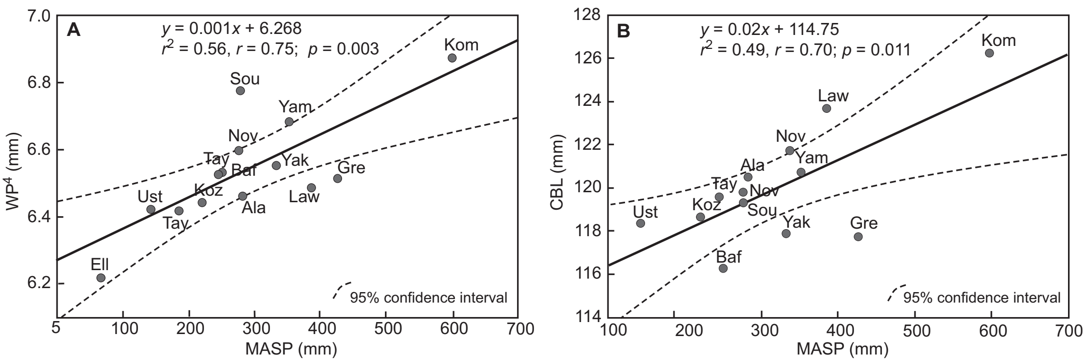

Fig. 6. Relationships between the mean annual precipitation sum (MASP) and (**A**) width of P^4–WP^4 and (**B**) condylobasal skull length (CBL), in the arctic fox *Vulpes* (*Alopex*) *lagopus*. Abbreviations as in Fig. 1.

the dentition metric characteristics in the arctic fox, the most variable were the specimens from Alaska (5.8) and the least variable those from Yakutskaya oblast' (4.0; Table 5).

Discussion

The arctic fox has a circumpolar distribution that includes the Arctic and tundra zones of North America and Eurasia, parts of Alpine zones of Fennoscandia, and islands of the Arctic, North Atlantic, and North Pacific Oceans (Audet *et al*. 2002). Despite its wide range, the diversity of arctic fox habitats is minimal in comparison with that of other Canidae species. The above fact reflects a low morphological (Ognev 1931, Zalkin 1944), as well as genetic, diversity of this predator (Dalén *et al*. 2005).

Analysis of the CV of some selected dentition characteristics and of the condylobasal skull length in arctic fox populations from the areas

Table 3. Sexual dimorphism of the metrical tooth and skull characters in three distant populations of the arctic fox. M_f = mean of dental or skull character in female; M_m = mean of dental or skull character in male; M_m/M_f = sexual dimorphism index.

	Komandorskiye ostrova					Taymyr					Ustyanskiy region				
	M_f	n	M_m	n	M_m/M_f	M_f	n	M_m	n	M_m/M_f	M_f	n	M_m	n	M_m/M_f
LI^3	3.83	15	4.05	24	1.06	3.53	19	3.71	18	1.05	3.57	19	3.76	22	1.06
WI^3	4.61	16	4.91	26	1.07	4.48	20	4.77	21	1.06	4.43	20	4.72	23	1.06
LC^1	6.14	15	6.79	23	1.11	6.13	17	6.56	21	1.07	5.94	18	6.32	17	1.06
WC^1	3.81	16	4.04	25	1.06	3.74	18	3.95	21	1.06	3.65	19	3.81	17	1.05
HC^1	15.13	4	15.58	5	1.03	14.48	9	15.05	11	1.04					
LP^1	4.87	16	5.16	24	1.06	4.75	21	5.00	21	1.05	4.71	20	4.87	20	1.03
WP^1	2.99	17	3.19	26	1.07	2.83	21	2.98	22	1.06	2.76	20	2.89	21	1.05
LP^4b	12.31	18	12.98	25	1.05	12.08	25	12.79	23	1.06	11.92	21	12.47	22	1.05
LP^4l	13.72	13	14.3	18	1.04	13.70	23	14.26	20	1.04					
WP^4	6.69	18	7.05	26	1.05	6.47	25	6.69	23	1.03	6.31	21	6.53	23	1.04
LM^1	8.29	13	8.53	18	1.03	8.15	23	8.51	23	1.04					
WM^1	9.6	12	10.11	19	1.05	9.58	24	9.97	23	1.04					
LM^2	4.69	15	5.04	20	1.07	4.62	20	4.66	22	1.01	4.61	19	4.74	22	1.03
WM^2	7.02	18	7.55	25	1.08	7.04	24	7.22	24	1.02	7.1	21	7.22	22	1.02
LC_1	7.00	10	7.36	14	1.05	7.02	9	7.60	6	1.08	6.94	7	7.05	12	1.02
WC_1	3.91	14	4.03	24	1.03	3.77	24	4.08	21	1.08	3.81	15	4.06	17	1.07
HC_1	13.45	2	15.16	8	1.13	13.52	7	14.40	4	1.06					
LP_1	3.88	15	3.94	24	1.02	3.65	23	3.85	24	1.05	3.69	21	3.77	21	1.02
WP_1	2.81	17	2.92	25	1.04	2.57	23	2.71	24	1.06	2.57	20	2.67	23	1.04
LM_1	13.01	18	13.99	25	1.08	13.54	25	14.14	24	1.04	13.33	21	13.62	23	1.02
WM_1	5.03	18	5.26	25	1.04	5.01	25	5.18	24	1.03	4.97	21	5.07	23	1.02
LM_3	2.92	15	3.06	26	1.05	2.82	19	2.79	17	0.99	2.75	18	2.75	16	1.00
WM_3	2.67	15	2.83	26	1.06	2.44	19	2.43	17	1.00	2.37	18	2.38	16	1.01
CBL	122.03	18	130.01	26	1.07	117.76	25	122.70	22	1.04	116.71	21	119.93	22	1.03

Table 4. Comparison of the means of CV (coefficient of variation) in the red fox *Vulpes vulpes* and arctic fox *Alopex* (*Vulpes*) *lagopus* in relation to some metrical dental characters and condylobasal skull length (CBL). M_{VV} = mean of CV for some tooth characters in the red fox; M_{AL} = mean of the CV for some tooth characters in the arctic fox.

	M_{VV}		M_{AL}	df	t	p
LC^1	6.9	>	6.0	17	1.93	0.070
WP^1	6.4	>	5.8	17	1.15	0.268
LP^4b	4.9	>	4.5	17	1.02	0.320
LM^1	4.7	=	4.7	16	–0.06	0.954
WP_1	7.2	>	5.9	17	1.94	0.068
LM_1	4.8	>	4.1	17	1.79	0.091
CBL	4.4	>	3.8	17	0.04	0.134

Table 5. Means of CV (coefficient of variation) in particular populations of the red fox *Vulpes vulpes* and arctic fox *Alopex* (*Vulpes*) *lagopus* calculated on few metrical dental characters and condylobasal skull length (CBL). M_{CV} = mean of CV, SD = standard deviation.

		M_{CV}	n	SD
Vulpes vulpes	Ala	5.0	7	1.1
	Col	5.5	7	1.4
	Ken	4.3	7	0.9
	Kod	5.4	7	1.5
	Mag	5.5	7	0.9
	Pec	5.9	7	1.5
	Que	5.8	7	1.1
	Yak	6.9	7	1.0
Alopex (*Vulpes*) *lagopus*	Ala	5.8	7	2.2
	Can	5.2	7	1.1
	Kom	5.1	7	0.7
	Gre	4.8	7	0.6
	Koz	4.2	7	1.7
	Law	5.3	7	1.3
	Tay	5.2	7	1.3
	Ust	5.1	6	1.3
	Yak	4.0	7	1.0
	Yam	4.9	7	1.2

of their sympatric and sub-arctic range proved that, in almost all of the studied characteristics, the arctic fox is not significantly more variable than the red fox. In arctic fox populations the CV ranges between 4.0 and 5.2, while in red fox in the Arctic CV is from 4.3 to 6.9. The highest CV was observed in arctic foxes from Alaska. It seems that the high value of CV could result from the low sample size (Ala, $n = 8$). The lowest variation was noted in continental arctic foxes from Asia (Yakutskaya oblast', Zaliv Kozhevnikova). Arctic foxes from the insular populations, i.e. from St. Lawrence Island, Komandorskiye Ostrova, Canada (Southampton Island, Baffin Land) were characterised by high variability. The opposite situation occurs in the red fox, in which the population of Yakutskaya oblast' had the highest variability and the least variable were the foxes from the Kenai Peninsula. The variability in size of the arctic fox dentition is most probably shaped by the abundance and diversity of food, as well as the intensity of the competition with the red fox. In more severe continental climate conditions and with permanent pressure of the red fox, the morphological variability of the arctic fox is low. On the contrary, the variability increases on islands, where the food base of arctic foxes is more diverse and the intensity of intra- and interspecific competition decreases.

The characteristic of the coefficient of variation is its strong negative correlation with size. The correlation may artificially inflate the variability, particularly in case of small traits. This is most pronounced when variables whose size differs by more than an order of magnitude are compared or when the index is applied to variables whose size is within an order of magnitude of their measurement error (Polly 1998). On the basis of the sizes of both fox species, and based on an active influence of mathematical factor, a higher variability in the arctic fox then in the red fox should be expected. However, the above-mentioned characteristics of CV does not apply in this case.

The analysis of dental metric characteristics in populations of the arctic fox throughout the circumpolar range indicated significant differences between populations. A considerable inter-population variability was observed in case of the lengths of I^3, C^1, P^1, P^4, M_3, widths of C^1, P^1, P^4, P_1, M_1, M_3, heights of C_1 and of CBL. In the red fox throughout its Holarctic range the dentition metric characteristics show highly significant inter-population variability ($p < 0.001$; E. Szuma unpubl. data). Both in the arctic fox and red fox, the inter-population variation is particularly high in C^1, C_1, P^4 and CBL. These characteristics are of vital adaptation importance, and respond to selective pressure. That was proved by the microevolutionary studies of the dentition (Szuma 2003), and the analysis of the geographic variation of the sexual dimorphism of the metric dental characteristics in red fox (Szuma 2008). Most significant microevolutionary changes in the red fox were observed in the shape of its upper carnassial (Szuma 2003). Whereas the geographic variation of the sexual dimorphism in Nearctic and Palearctic was most pronounced in case of the canines, as well as P^4 and CBL (Szuma 2008).

To date only the geographic variation in skull size of arctic foxes has been pointed out by researchers. Zalkin (1944), Zagrebel'nyi and Puzachenko (2006) found, that the largest CBL sizes are found in the arctic foxes of Bering Island followed by populations from Novaya Zemlya, then continental foxes, and, finally the arctic foxes of Spitsbergen having the smallest skulls (Zalkin 1944). Moreover, Frafjord (1993) found that the arctic fox populations of Greenland, Jan Mayen, and Svalbard are smaller than the Fennoscandian and Siberian foxes. The analysis of the size of M_1 by the landmark method in several populations of arctic fox (Daitch & Guralnick 2007) suggests that foxes from Semidi Island and St. Paul Island have the smallest M_1, and the populations of Bering Island, Nunivak Island, and Siberia — the largest.

The studies on the circumpolar range of the arctic fox showed, that the largest are the foxes of Komandorskiye Ostrova and of Novaya Zemlya. The continental populations of Eurasia (Ust-Yanskiy region, Yakutskaya oblast', Zaliv Kozhevnikova, Taymyr, Yamal Poluostrov) are characterised by moderate dentition characteristics and the skull CBL.

The North American arctic foxes are smaller than the arctic foxes of Eurasia. Considering most of the examined characteristics, the smallest North American arctic foxes inhabit Baffin

Land and Greenland. The Daitch and Guralnick (2007) studied of M_1 indicated that the foxes of Greenland are larger than those of small islands: Semidi Island and St. Paul Island.

With respect to the skull CBL, the arctic fox population of St. Lawrence Island is above-average. Their dentition characteristics, however, place that population among the arctic foxes of mean, or even smaller than mean, sizes.

Daitch and Guralnick (2007) pointed out that the geographic variation of the shape of M_1 in the arctic fox of Holarctic result from stochastic processes. In case of the variability of the dentition sizes and the skull CBL of the arctic fox it is difficult to indicate a definite geographic pattern. The largest dentition and skull sizes were found in the Far East populations — primarily in the populations of Komandorskiye Ostrova. It was indicated by a positive, although statistically insignificant relation between the dentition sizes and the latitude. It was also observed that the mean sizes of the examined dental characteristics of the arctic fox are smaller at higher latitudes. This relationship was rarely statistically significant (WC^1, WP^4, WM_3, CBL).

Based on their analysis of the variability of size and shape of M_1, Daitch and Guralnick (2007) concluded that geographic and climatic variables do not significantly influence arctic fox variation within its natural range. The authors based their statement on the analysis of the geographic variation of the shape and size of an individual tooth.

The results of my research show, that climatic variables in the first place shape the pattern of variation of metric characteristics of the arctic fox dentition. Most of the examined dental characteristics were positively and significantly correlated with the mean annual temperatures (LI^3, LC^1, WP^1, LP^4, WP^4, LM^2, CBL) but negatively with the mean annual amplitude of temperature. Whereas, with an increase of precipitation, the sizes of the dentition and CBL would grow as well. The observations suggest that the growth of the size of dentition in the arctic fox is associated with the warmer and more humid areas within the circumpolar range of the predator.

The warmer and more humid areas of the Arctic are usually the coastal areas and smaller islands. The mildness of the climate in these latitudes guarantees richer food sources for the arctic fox. In the studies on the diet of the species two ecotypes are distinguished: 'lemming foxes' that feed mainly on lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) and 'coastal foxes' that feed mainly on eggs, birds and carrion originating from the sea (Braestrup 1941). The differences between highly fluctuating (lemming) and more stable (coastal) food sources led to different life strategies (Tannerfeldt & Angerbjörn 1998), and different migration patterns (Angerbjörn *et al*. 2004).

It seems that the food reserves affect the geographic pattern of the variability of the size of the dentition and skull in the arctic fox. Zalkin (1944) pointed out, that the food base of the arctic fox in Spitsbergen is extremely poor. It is reflected in skull sizes: CBL is between 113 and 136 mm (Zalkin1944). The largest arctic foxes inhabit Komandorskiye Ostrova, where the food base is very abundant. According to Zalkin (1944) the skull CBL of the arctic fox of Komandorskiye Ostrova is 121–139 mm in males and 116–134 mm in females. My research also indicated that, considering the metric dentition characteristics, the foxes of Komandorskiye Ostrova are the largest and highly variable. Also the morphometric analysis of M_1 with the landmark method (Daitch & Guralnick 2007) suggests that the foxes from Bering Island are among the largest ones as compared with those from the other populations. The food resources of the arctic foxes from Mednyi Island, Bering Island and all islands of Komandorskiye Ostrova are much more stable and abundant than those of the mainland arctic foxes. The food items of island foxes (beached carcasses of marine mammals, seashore animals, eggs and nestlings of colony birds) are motionless, often heavy, and are protected by strong skin or hard shells. This might favour a strong skull and greater body mass in the arctic fox (Goltsman *et al*. 2005). It is also indicated by the statistically significant positive correlation of such characteristics as WP^4, WM_3, and CBL with the mean annual sum of precipitation.

The arctic foxes inhabiting St. Lawrence Island exist in an environment with unusually abundant food. They have access to voles at comparatively high densities nearly every year, as well as to large colonies of cliff-nesting birds and plenty of carrion (Fay & Stephenson 1989). In these conditions, in comparison with the North American arctic foxes, these foxes are characterized by higher productivity and survival rate (Fay & Rausch 1992). That is why this population differs from the other North American arctic foxes also in metric dentition characteristics and in skull CBL. Moreover the arctic fox from St. Lawrence Island are distinguished by the highest level of size variability. The situation on Greenland is quite different. The food basis of arctic foxes there is very unstable, and the lemming population occurring in this limited area is liable to strong fluctuations (Kapel 1999). Less stable and reduced availability of food on Greenland (Kapel 1999) is reflected in smaller dentition sizes and lower size variation in foxes inhabiting the island. Also Daitch and Guralnick (2007), while analyzing the variability of M_1, found that the arctic foxes of Greenland are significantly smaller, and they differ in shape from the foxes of Siberia.

The sexual dimorphism of the skull and dentition in arctic fox varies in particular populations. The highest level of dimorphism occurs in the Komandorskiye Ostrova population. Zagrebel'nyi and Puzachenko (2006) observed that the pattern of sexual dimorphism of skull characteristics in arctic fox is geographically diverse. Similarly, the variation of the dentition size as well as the sexual dimorphism in the metric dentition characteristics, are shaped by complex configuration of the climatic, ecological, and phylogenetic factors. The highest sexual dimorphism of the arctic foxes of Komandorskiye Ostrova may indicate a stronger intra-, and inter-species competition than that in the populations of Taymyr and Ust-Yanskiy region. When food is more abundant and climate conditions more favourable, the arctic foxes may show higher densities. Simultaneously, there may occur a stronger competition with the red fox, which coexists in the area, and probably reaches higher numbers, as well. Between the competing species of the red and arctic fox (despite many similarities), significant differences have been observed as to the patterns of the geographic variation of metric characteristics in dentition. These differences concern the molars. The size of the middle-located molars in the arctic fox does not indicate any significant inter-population variation. Daitch and Guralnick (2007) found that all mainland populations of the arctic fox were similar in the M_1 size. They found solely significant differences in the M_1 size between some island populations. In the red fox, on the contrary — both, M^1 and M_1 show a significant geographic variation with regard to the shape (Szuma 2004, 2007), as well as to the size (E. Szuma unpubl. data).

Also the chronological analyses of the sizes of M_1 in the red fox and arctic fox, carried out by Germonpre and Sablin (2004) revealed that these two closely related foxes have two different patterns of the evolutionary changes. From Late Glacial to Holocene, a decrease of M_1 in the red fox was observed, while in the arctic fox, the mean crown sizes of M_1 from Late Pleniglacial, Late Glacial to Holocene, did not changed significantly. The permanence of the sizes of M_1 from Pleistocene to Holocene, indicates low rate of the arctic fox evolution. The red fox, on the contrary, is liable to fast evolutionary changes. In changing environment and climate, and the simultaneous strong inter-species competition in the areas of sympatric occurrence of both fox species, it is the red fox that predominates, because of its better evolutional flexibility.

Acknowledgements

I really appreciate Dr. Matthew W. Hayward for correction of English grammar and style in the manuscript. For the access to specimens in collections and their courteous assistance, I thank G. F. Baryshnikov (Zoological Institute, Russian Academy of Sciences, St. Petersburg), D. V. Ivanoff (National Museum of Natural History, and Zoological Museum, University of Taras Schevchenko, Kiev), P. Jenkins, S. Churchfield, P. D. Polly (Natural History Museum, London), A. G. Rol (Zoological Museum of Amsterdam), O. L. Rossolimo, V. V. Rozhnov (Zoological Museum of the Moscow University), and E. Zholnerovskaya (Siberian Zoological Museum of the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk).

References

Angerbjörn, A., Hersteinsson, P. & Tannerfeldt, M. 2004: Consequences of resource predictability in the arctic fox — two life history strategies. — In: Macdonald, D. W. & Sillero-Zubiri, C. (eds.), *The biology and conservation of wild canids*: 163–172. Oxford University Press.

Angerbjörn, A., Tannerfeldt, M. & Erlinge, S. 1999: Predator–prey relationships: arctic foxes and lemmings. — *Journal of Animal Ecology* 68: 34–49.

Anthony, R. M., Barten, N. L. & Seiser, P. E. 2000: Foods of artcic foxes (*Alopex lagopus*) during winter and spring in western Alaska. — *Journal of Mammalogy* 81: 820–828.

Audet, A. M., Brian Robbins, C. & Larivière, S. 2002: *Alopex lagopus*. — *Mammalian Species* 713: 1–10.

Bartoń, K. A. & Zalewski, A. 2007: Winter severity limits red fox populations in Eurasia. — *Global Ecology and Biogeography* 16: 281–289.

Bisaillon, A. & DeRoth, L. 1980: Cranial measurements in the arctic fox (*Alopex lagopus*). — *Revue Canadienne de Biologie* 39: 81–84.

Braestrup, F. W. 1941. A study on the arctic fox in Greenland. — *Meddelelser om Grønland* 13: 1–101.

Daitch, D. J. & Guralnick, R. P. 2007: Geographic variation in tooth morphology of the arctic fox, *Vulpes* (*Alopex*) *lagopus*. — *Journal of Mammalogy* 88: 384–393.

Dalén, L., Fuglei, E., Hersteinsson, P., Kapel, Ch. M. O., Roth, J. D., Samelius, G., Tannerfeldt, M. & Angerbjörn, A. 2005: Population history and genetic structure of a circumpolar species: the arctic fox. — *Biological Journal of the Linnean Society* 84: 79–89.

Elmhagen, B., Tannerfeldt, M., Verrucci, P. & Angerbjörn, A. 2000: The arctic fox (*Alopex lagopus*): an opportunistic specialist. — *Journal of Zoology, London* 251: 139–149.

Fay, F. H. & Rausch, R. L. 1992: Dynamics of the arctic fox population on St. Lawrence Island, Bering Sea. — *Arctic* 45: 393–397.

Fay, F. H. & Stephenson, R. O. 1989: Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. — *Canadian Journal of Zoology* 67: 1986–1994.

Frafjord, K. 1993: Circumpolar size variation in the skull of the arctic fox *Alopex lagopus*. — *Polar Biology* 13: 235–238.

Frafjord, K. 2000: Do arctic and red foxes compete for food? — *Zeitschrift für Säugetierkunde* 65: 350–359.

Germonpre, M. & Sablin, M. V. 2004: Systematics and osteometry of Late Glacial foxes from Belgium. — *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 74: 175–188.

Goltsman, M., Kruchenkova, E. P., Sergeev, S., Volodin, I. & Macdonald, D. W. 2005: "Island syndrome" in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island. — *Journal of Zoology, London* 267: 405–418.

Hersteinsson, P. & Macdonald, D. W. 1992: Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. — *Oikos* 64: 505–515.

Kapel, Ch. M. O. 1999: Diet of arctic foxes (*Alopex lagopus*) in Greenland. — *Arctic* 52: 289–293.

McNab, B. K. 1971: On the ecological significance of Bergmann's rule. — *Ecology* 52: 845–854.

Meiri, S., Dayan, T. & Simberloff, D. 2004: Body size of insular carnivores: little support for the island rule. — *The American Naturalist* 163: 469–479.

Ognev, S. I. [Огнев, С. И.] 1931: [*Mammals of eastern Europe and northern Asia, vol. 2. Carnivores*]. — Gosizdat, Moskva, Leningrad, Russian Federation. [In Russian].

Pengilly, D. 1984: Developmental versus functional explanations for patterns of variability and correlation in the dentitions of foxes. — *Journal of Mammalogy* 65: 34–43.

Polly, P. D. 1998: Variability in mammalian dentitions: size-related bias in the coefficient of variation. — *Biological Journal of the Linnean Society* 64: 83–89.

Prestrud, P. 1991: Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. — *Arctic* 44: 132–138.

Prestrud, P. & Nielsen, K. 1995: Growth, size, and sexual dimorphism in Arctic foxes. — *Journal of Mammalogy* 76: 522–530.

Ralls, K. & Harvey, P. H. 1985: Geographic variation in size and sexual dimorphism of North American weasels. — *Biological Journal of the Linnean Society* 25: 119–167.

Skrobov, V. D. 1960: On interrelations of the polar fox and fox in the tundra of the Nenets National Region. — *Zoologicheskiy Zhurnal* 39: 469–471. [In Russian with English summary]

Statistica.PL 1997: *STATISTICA PL dla Windows*. — StatSoft Polska Sp. z o.o.

Szuma, E. 2003: Microevolutionary trends in the dentition of the Red fox (*Vulpes vulpes*). — *Journal of Zoological Systematics and Evolutionary Research* 41: 47–56.

Szuma, E. 2007: Geography of dental polymorphism in red fox *Vulpes vulpes* and its evolutionary implications. — *Biological Journal of the Linnean Society* 90: 61–84.

Szuma, E. 2008: Geography of sexual dimorphism in the tooth size of the red fox *Vulpes vulpes*. — *Journal of Zoological Systematics and Evolutionary Research* 46: 73–81.

Tannerfeldt, M. & Angerbjörn, A. 1998: Fluctuating resources and the evolution of litter size in the arctic fox. — *Oikos* 83: 545–559.

Wilson, D. E. & Ruff, S. 1999: *Smithsonian book of North American mammals*. — Smithsonian Institution Press, Washington.

Zagrebel'nyi, S. V. & Puzachenko, A. Yu. 2006: Variability of skulls in the polar fox subspecies: *Alopex lagopus beringensis, A. l. semenovi, A. l. lagopus* (Carnivora, Canidae). — *Zoologicheskiy Zhurnal* 85: 1007–1023. [In Russian with English summary].

Zalkin, V. I. 1944: Geographical variability in the skull structure of the Russian polar fox. — *Zoologicheskiy Zhurnal* 23: 156–169. [In Russian with English summary].

Appendix. Descriptive statistic for metrical dental characters and condylobasal skull length (CBL) in 14 populations of the arctic fox *Vulpes* (*Alopex*) *lagopus*. Abbreviation for particular populations: Ala = Alaska, Baf = Baffin Land, Ell = Ellesmere Island, Gre = Greenland, Kom = Komandorskiye Ostrova, Koz = Zaliv Kozhevnikova, Law = St. Lawrence Island, Nov = Novaya Zemlya, Sou = Southampton Island, Spi = Spitsbergen, Tay = Taymyr, Ust = Ust-Yanskiy region, Yak = Yakutskaya oblast', Yam = Yamal Poluostrov.

		Ala	Baf	Ell	Gre	Kom	Koz	Law	Nov	Sou	Spi	Tay	Ust	Yak	Yam
LI^3	*M*	3.94	3.57	3.57		3.95	3.67	3.63	3.69	3.58	3.57	3.62	3.67	3.79	3.77
	n	4	17	1		52	23	3	2	4	18	37	41	33	39
	SD	0.10	0.28			0.26	0.18	0.09	0.11	0.17		0.24	0.24	0.25	0.20
WI^3	*M*	4.74	4.56	4.81		4.79	4.69	4.61	4.78	4.55	4.58	4.63	4.58	4.63	4.67
	n	6	20	2		56	26	4	2	4	22	41	43	34	39
	SD	0.30	0.32	0.11		0.25	0.30	0.20	0.03	0.36		0.28	0.29	0.23	0.23
LC^1	*M*	6.59	6.01		6.13	6.53	6.25	6.28		6.40	6.01	6.35	6.12	6.20	6.34
	n	3	15		10	50	19	4		3	15	43	35	26	34
	SD	0.33	0.28		0.23	0.42	0.47	0.44		0.71		0.40	0.41	0.36	0.34
WC^1	*M*	3.96	3.73		3.82	3.93	3.78	3.85	3.70	3.93	3.72	3.84	3.73	3.64	3.86
	n	5	16		13	52	20	4	2	3	16	44	36	24	33
	SD	0.26	0.22		0.22	0.24	0.23	0.29	0.04	0.21		0.23	0.19	0.19	0.24
HC^1	*M*				13.82	15.35	14.58	14.16				14.67		14.17	14.95
	n				1	14	9	2				23		7	26
	SD					0.81	0.60	1.00				0.57		0.57	0.65
LP^1	*M*	4.72	4.72	4.46	4.68	5.05	4.96	4.84	5.04	4.77	4.69	4.83	4.79	4.85	4.89
	n	5	17	2	14	53	23	4	2	5	19	48	40	34	39
	SD	0.28	0.29	0.20	0.30	0.34	0.33	0.32	0.04	0.41		0.31	0.28	0.28	0.29
WP^1	*M*	2.94	2.90	2.87	2.78	3.12	2.88	2.78	3.04	2.86	2.89	2.89	2.83	2.88	2.91
	n	8	20	2	14	56	23	4	2	5	22	50	41	34	40
	SD	0.26	0.15	0.20	0.14	0.18	0.16	0.13	0.10	0.21		0.20	0.16	0.12	0.17
LP^{4}b	*M*	12.43	12.20	12.13	11.95	12.74	12.28	12.12	12.93	12.32	12.19	12.37	12.20	12.32	12.43
	n	8	21	4	13	57	28	4	2	5	25	56	43	34	40
	SD	0.68	0.54	0.29	0.59	0.61	0.44	0.53	1.10	0.68		0.59	0.61	0.40	0.50
WP^4	*M*	6.46	6.53	6.22	6.51	6.87	6.44	6.49	6.60	6.78	6.51	6.53	6.43	6.55	6.69
	n	8	22	2	15	58	28	4	2	4	24	56	44	34	40
	SD	0.55	0.38	0.21	0.45	0.34	0.35	0.19	0.62	0.32		0.47	0.38	0.43	0.45
LP^{4}l	*M*	14.11	13.82	13.95	13.57	14.12	13.74	13.61	14.23	13.81	13.84	13.93		13.88	14.04
	n	8	22	4	13	43	24	4	2	5	26	51		22	38
	SD	0.77	0.54	0.22	0.64	0.63	0.37	0.38	0.88	1.02		0.55		0.49	0.58
LM^1	*M*	8.50	8.49	8.30	8.26	8.48	8.25	8.24	8.64	8.40	8.46	8.33		8.41	8.45
	n	8	22	4	13	44	25	4	2	5	26	55		23	40
	SD	0.43	0.41	0.18	0.44	0.44	0.29	0.37	0.66	0.50		0.53		0.39	0.39
WM^1	*M*	10.02	9.77	10.00	9.54	9.92	9.61	9.45	10.02	9.82	9.81	9.75		9.85	9.84
	n	8	22	4	13	44	25	4	2	5	26	56		24	41
	SD	0.68	0.56	0.35	0.54	0.55	0.43	0.83	1.02	0.54		0.49		0.30	0.44
LM^2	*M*	4.78	4.58	4.65	4.68	4.81	4.58	4.53	4.87	4.47	4.59	4.61	4.68	4.61	4.76
	n	6	20	4	12	47	25	4	2	5	26	50	41	29	26
	SD	0.55	0.39	0.43	0.28	0.39	0.39	0.04	0.04	0.46		0.30	0.27	0.30	0.31
WM^2	*M*	7.25	7.07	7.38	7.05	7.28	6.97	7.04	7.56	7.18	7.12	7.07	7.16	7.17	7.23
	n	6	22	4	13	57	27	4	2	5	26	56	43	35	39
	SD	0.90	0.49	0.24	0.37	0.55	0.66	0.12	0.28	0.57		0.45	0.42	0.46	0.56
LC$_1$	*M*	7.73	7.07		7.16	7.22	7.36	7.50	7.28	6.89	7.07	7.23	7.01	7.11	7.36
	n	1	9		7	33	15	2	2	1	9	19	19	19	15
	SD		0.44		0.36	0.44	0.33	0.13	0.59			0.42	0.42	0.47	0.35
WC$_1$	*M*	4.18	3.88		3.93	3.97	3.87	3.92	4.09	3.72	3.88	3.91	3.94	3.88	3.92
	n	1	8		7	50	21	2	2	1	8	48	32	15	28
	SD		0.36		0.16	0.20	0.24	0.14	0.28			0.29	0.24	0.21	0.23
HC$_1$	*M*				13.90	14.78	13.77					13.80		13.36	14.32
	n				3	14	10					14		4	14
	SD				0.43	0.77	0.53					0.69		0.66	0.54

continued

Appendix. Continued.

		Ala	Baf	Ell	Gre	Kom	Koz	Law	Nov	Sou	Spi	Tay	Ust	Yak	Yam
LP_1	*M*	3.74	3.76	3.65	3.65	3.91	3.84	3.68	3.99	3.83	3.74	3.75	3.73	3.86	3.80
	n	5	16	3	11	50	18	4	2	4	19	54	42	34	39
	SD	0.10	0.21	0.09	0.24	0.20	0.26	0.25	0.20	0.19		0.26	0.25	0.25	0.33
WP_1	*M*	2.62	2.66	2.78	2.58	2.88	2.65	2.55	2.83	2.62	2.67	2.62	2.63	2.68	2.67
	n	7	17	3	11	55	19	4	2	5	20	55	43	34	40
	SD	0.23	0.18	0.09	0.14	0.13	0.10	0.18	0.13	0.11		0.16	0.15	0.10	0.20
LM_1	*M*	13.70	13.64	14.14	13.52	13.63	13.69	13.28	14.41	13.93	13.72	13.80	13.48	13.74	13.92
	n	8	21	4	12	56	28	4	2	5	25	58	44	35	42
	SD	0.48	0.68	0.45	0.69	1.41	0.41	0.48	0.69	1.00		0.62	0.63	0.47	0.52
WM_1	*M*	5.22	5.05	5.19	4.91	5.17	5.16	4.86	5.61	5.06	5.07	5.07	5.03	5.18	5.19
	n	8	21	4	11	56	27	4	2	5	25	58	44	35	42
	SD	0.38	0.27	0.26	0.18	0.24	0.27	0.26	0.11	0.26		0.27	0.28	0.24	0.30
LM_3	*M*	2.58	2.67	2.92	2.66	3.03	2.68	2.68	2.65	2.66	2.68	2.79	2.75	2.78	2.80
	n	7	12	1	10	52	17	3	1	5	13	42	34	23	34
	SD	0.32	0.29		0.23	0.24	0.26	0.16		0.14		0.31	0.26	0.32	0.26
WM_3	*M*	2.20	2.37	2.47	2.29	2.78	2.31	2.38	2.14	2.31	2.38	2.42	2.37	2.38	2.42
	n	6	13	1	10	52	17	3	1	5	14	42	34	23	35
	SD	0.21	0.22		0.16	0.20	0.11	0.15		0.09		0.21	0.17	0.19	0.22
CBL	*M*	120.51	116.27	112.20	117.75	126.26	118.64	123.75	119.88	119.36	116.08	119.59	118.36	117.87	120.78
	n	7	21	1	11	58	26	4	2	5	22	55	43	27	32
	SD	4.89	3.32		4.88	5.87	3.33	7.32	1.39	4.17		3.87	3.32	3.50	4.64