

Systematics and osteometry of Late Glacial foxes from Belgium

by Mietje GERMONPRE & Mikhail V. SABLIN

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Abstract

Collections of Late Glacial fox remains from the sites of Chaleux, Furfooz and Goyet (Belgium) were studied. The bones were examined, measured and compared with samples of extant and fossil arctic fox (*Alopex lagopus*) and red fox (*Vulpes vulpes*). The Late Glacial red foxes from Belgium are in general larger than recent Belgian red foxes and compare more in size to those of present-day Nordic populations. The change in size in the red fox follows Bergmann's rule and can be correlated with climatic changes during the time period studied. The size of the lower carnassial of arctic fox does not differ significantly among the Late Pleniglacial, Late Glacial and Holocene samples studied. A well-defined progressive trend can, however, be traced in the postcranial size of the arctic foxes. The Pleniglacial foxes are the smallest, ranging well below recent continental foxes in size, whereas Late Glacial arctic foxes are almost comparable in body size with those of recent Siberian populations. The arctic fox appears to be adapting to a very cold climate throughout the Weichselian.

Key-words: red fox, arctic fox, Bergmann's rule, Late Glacial, Belgium

Résumé

Les collections de renards tardiglaciaires de Chaleux, Furfooz et Goyet (Belgique) ont été étudiées. Les ossements ont été examinés, mesurés et comparés avec du matériel moderne et fossile du renard polaire (*Alopex lagopus*) et du renard commun (*Vulpes vulpes*). Les renards communs du Tardiglaciaire en Belgique sont plus grands que les renards actuels belges et sont comparables aux renards modernes boréaux. Le changement de taille chez le renard commun peut être expliqué par la règle de Bergmann et être corrélé avec les changements climatiques pendant la période étudiée. La taille de la carnassière inférieure des renards polaires n'a pas changé pendant le Pléniglaciaire, le Tardiglaciaire et l'Holocène. Les modifications du squelette post-cranien chez les renards polaires suivent une tendance progressive, les renards pléniglaciaires étant plus petits que les renards actuels et les renards tardiglaciaires approchant les dimensions des populations sibériennes récentes. Le renard polaire s'adapte à un climat très froid durant le Weichselien.

Mots-clefs: Renard commun, renard polaire, règle de Bergmann, Tardiglaciaire, Belgique

Introduction

Fossil foxes have been reported in several studies of the Belgian Late Glacial (PATOU-MATHIS, 1994; GAUTIER, 1997; GERMONPRÉ, 1997; CHARLES, 1997, 1998). However, little attention has been paid to the precise identification of the foxes and to their osteometry. In this paper we give a detailed osteometric description of arctic and red fox remains from Late Glacial assemblages stored in the Dupont collection at the Royal Belgian Institute of Natural Sciences. We analysed these remains and compared them with those of fossil foxes from the Late Glacial and Pleniglacial of Russia, and with recent Nordic arctic and red fox populations, living today in ecological and climatological conditions comparable to those prevailing during glacial phases in Belgium. Furthermore, we studied the osteometry of recent Belgian red foxes. These measurements proved useful in distinguishing between the bones of fossil and recent red foxes from sites where recent, intrusive material may have become mixed with the fossil assemblage. For purposes of reference we have included these measurements in this paper, since osteometric data for fossil and recent canids is rarely found in the literature.

The foxes in the Dupont collection are from four cave sites in the Condroz, a region south of the Sambre and Meuse valleys in Belgium (Fig. 1). The landscape comprises steep-sided valleys dissecting high plateaux of relatively constant altitude, locally reaching 350 m (PEETERS *et al.*, 2003). The cave of Trou de Chaleux (50°13'18''N, 4°56'30''E) is situated in a Carboniferous limestone cliff in the valley of the river Lesse, a tributary of the Meuse river, at an altitude of around 115 m and located some 15 m above the river. Several samples from the Late Glacial horizon excavated by DUPONT (1873) yielded an AMS age of c.12,850 y BP (CHARLES, 1998). The caves of Furfooz (Trou des Nutons, Trou du Frontal) are also situated in Carboniferous limestone cliffs on the banks of the Lesse. In Trou du Frontal (50°12'45''N, 4°57'30''E), the studied faunal assemblage was discovered associated with Magdalenian artefacts. An AMS age of 12,800 y BP was obtained from a horse bone from this layer (CHARLES, 1998). The main bone horizon from Trou des Nutons (50°12'45''N,

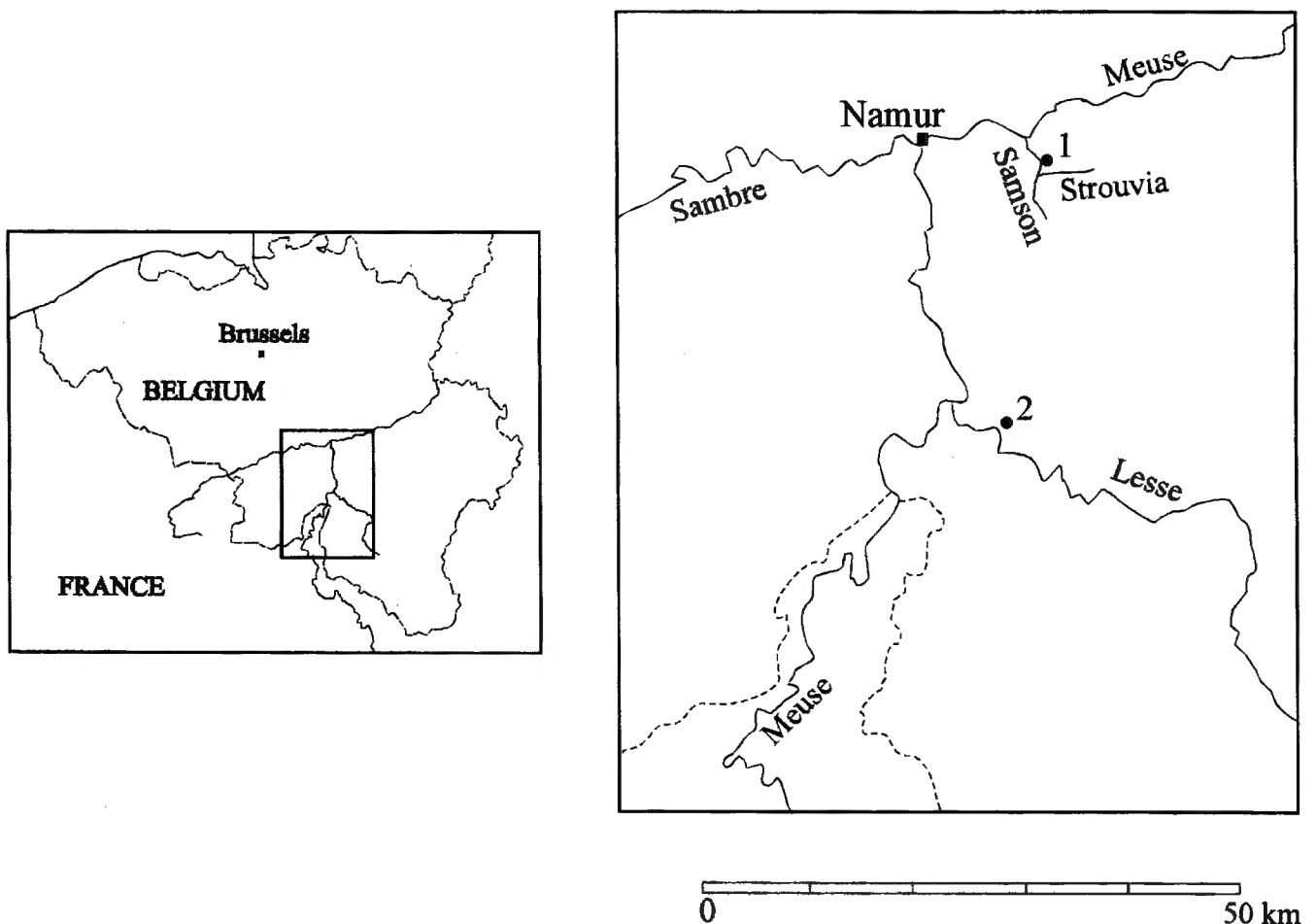


Fig. 1 — Location of the Belgian sites: 1: Goyet, 2: Chaleux and Furfooz (Trou des Nutons, Trou du Frontal).

Table 1 — AMS dates and their calibrations of bones from Trou de Chaleux, Goyet (upper horizon), Furfooz (Trou des Nutons) and Furfooz (Trou du Frontal).

| number | AMS date | 95,4% probability |
|------------------------|------------------|-------------------|
| <i>Chaleux</i> | | |
| OxA-3632 (1) | 12760 +/- 100 BP | 15850 BP 14350 BP |
| OxA-4192 (2) | 12860 +/- 140 BP | 16050 BP 14350 BP |
| OxA-3633 (1) | 12880 +/- 100 BP | 15950 BP 14350 BP |
| <i>Goyet</i> | | |
| UtC-8957 (1) | 12560 +/- 50 BP | 15550 BP 14250 BP |
| GrA-3238 (2) | 12620 +/- 90 BP | 15650 BP 14250 BP |
| GrA-3237 (1) | 12770 +/- 90 BP | 15850 BP 14350 BP |
| <i>Trou des Nutons</i> | | |
| OxA-4195 (1) | 12630 +/- 140 BP | 15750 BP 14150 BP |
| <i>Trou de Frontal</i> | | |
| OxA-4197 (1) | 12800 +/- 130 BP | 15950 BP 14350 BP |

Atmospheric data from Stuiver *et al.* (1998); Oxcal v3.5 Bronk Ramsey

4°57'29''E) produced Magdalenian artefacts and has been dated by AMS to 12,630 y BP (CHARLES, 1998). Goyet cave (50°26'44''N, 5°00'48''E) is located at an altitude of 130 m in a Carboniferous limestone cliff about 15 m above the river Samson, a tributary of the Meuse. The two youngest bone horizons near the cave entrance contained bones associated with Magdalenian artefacts. Three AMS dates from the upper horizon gave a mean of 12,650 y BP (GERMONPRÉ, 1997, 2001). The lower bone horizon has not been dated so far. Table 1 presents all AMS dates and their calibrations from the horizons described above. The material can be assigned to the end of the Oldest Dryas or the very beginning of the Bølling. The onset of the Bølling-Allerød interstadial event is considered to have occurred at ~14,600 cal BP (WEAVER *et al.*, 2003). During the Late Glacial, wooded areas were present in the valley of the Lesse; elsewhere open landscapes dominated (NOIREL-SCHULTZ, 1994). In the Samson valley gallery forests probably bordered the river (DAMBLON, pers. com.).

All of the bone assemblages from these caves include some Holocene intrusive materials (domesticated animals, badgers) (GERMONPRÉ, 2001; GERMONPRÉ & SABLIN, 2002).

Table 2 — Number of identified specimen (NISP) and minimal number of individuals (MNI) of the foxes found in the Belgian Late Glacial assemblages from the Dupont collection in the Royal Belgian Institute of Natural Sciences.

| Species | Trou de Chaleux | | Goyet Horiz. 1 | | Goyet Horiz. 2 | | Trou des Nutons | | Trou du Frontal | |
|-----------------------|-----------------|-----|----------------|-----|----------------|-----|-----------------|-----|-----------------|-----|
| | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI |
| <i>Alopex lagopus</i> | 380 | 16 | 29 | 4 | 42 | 6 | 286 | 52 | 29 | 7 |
| <i>Vulpes vulpes</i> | 63 | 9 | 19 | 2 | 19 | 3 | 118 | 15 | 44 | 5 |

Material and methods

The palaeontological collections of Chaleux, Furfooz (Trou des Nutons, Trou du Frontal) and Goyet have been stored at the Royal Belgian Institute of Natural Sciences since their excavation by Edouard Dupont in the 1860's. The Late Glacial horizons of the cave sites of Trou de Chaleux, Trou des Nutons, Trou du Frontal and Goyet contained numerous remains of arctic and red fox. 1029 specimens from 119 individuals have been studied in detail (Table 2). These bones were examined, measured and compared with those of Pleniglacial foxes from the Kostenki sites (Russian Plain) dating from about 21,000 y BP and Late Glacial foxes from Yudinovo (Russian Plain) aged to about 15,000 y BP, and those of recent foxes from Taimir, Siberia (KUZMINA & SABLIN, 1993; SABLIN, 1994) (Fig. 2). Recent comparative material stored in the Royal Belgian Institute of Natural Sciences, the Zoological Institute of the Russian Academy of

Sciences of Saint Petersburg and the Geological Institute of the Russian Academy of Sciences of Moscow was also utilized for comparative purposes. Additional measurements of recent and fossil specimens were obtained from published sources. The measurements, expressed in mm, were taken following VON DEN DRIESCH (1976). In contrast with the Taimir fox skeletons, all fossil studied bones were isolated finds. Descriptive statistics of the data are given. For each skeletal element one measurement was compared based on t-test (two-tailed) or one-way ANOVA using Graph Pad InStat version 3.00 for Windows 95, GraphPad Software, San Diego California USA, www.graphpad.com.

List of abbreviations:

- B: Belgium,
 Bp: greatest breadth of proximal end,
 Bd: greatest breadth of distal end,

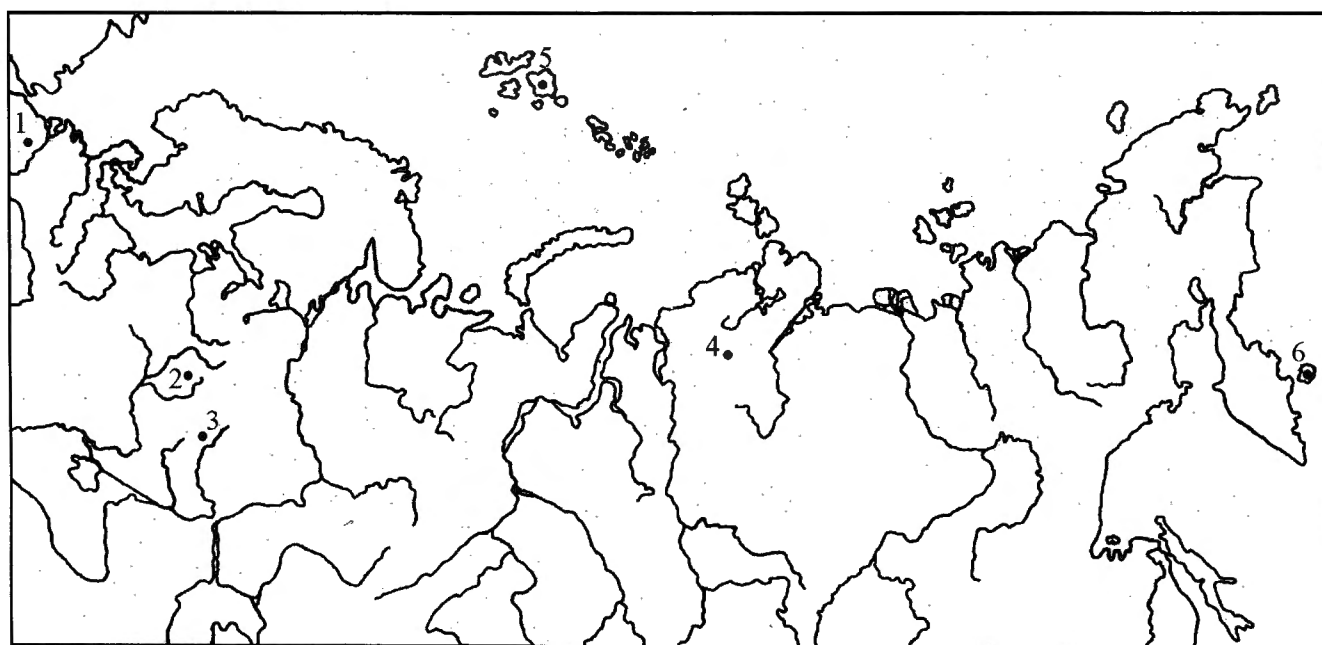


Fig. 2 — Location of the Belgian and Russian sites: 1: Belgium; 2: Yudinovo; 3: Kostenki; 4: Taimir; 5: Franz Josef Land; 6: Komandorski Islands.

| | |
|---------|-----------------------------------|
| cl: | crown length, |
| cw: | crown width, |
| Dc: | greatest depth of caput femoris, |
| Dp: | greatest breadth of proximal end, |
| Dd: | greatest breadth of distal end, |
| F: | female, |
| GL: | greatest length, |
| H: | height, |
| Horiz.: | Horizon, |
| Kost.: | Kostenki, Russia, |
| LG: | Late Glacial, |
| M: | male, |
| m: | mean, |
| MC: | metacarpus, |
| MNI: | minimum number of individuals, |
| MT: | metatarsus, |
| NISP: | number of identified specimens, |
| OR: | observed range, |
| R: | recent, |
| RR: | recent Russia, |
| KD: | smallest breadth of diaphysis, |
| sd: | standard deviation, |
| Yu: | Yudinovo, Russia, |

Results

Vulpes vulpes (Linnaeus, 1758)

The red fox is distributed today throughout Eurasia, North Africa and North America. Red foxes prefer habitats with great diversity, but do not inhabit dense forests (SEIDENSTICHER, 1999). The northern limit of the red fox is determined by resource availability (HERSTEINSSON & MACDONALD, 1992). The geographical distributions of red and arctic foxes are largely separate but overlap in the tundras of North America and Eurasia. In regions where red and arctic foxes are sympatric, red fox dens are found at lower altitudes than arctic fox dens. Red foxes mostly den below the tree line in birch and coniferous forests. Voles are their most important prey in Northern Europe, but hares, birds, eggs and berries are

also included in their diet. Observed differences between the diets of red and arctic foxes – the latter prey mainly on lemmings – is due to their spatial segregation, reflecting prey community composition at different altitudes (ELMHAGEN *et al.* 2002). Voles prefer productive tundra habitats and are generally more abundant at lower altitudes (OKSANEN *et al.*, 1999). Voles and lemmings, the main prey of recent red and arctic foxes, inhabited Belgium during the Late Glacial. The Late Glacial microfaunal assemblage of Chaleux is dominated by voles (*Microtus gregalis*: c. 70%) and lemmings (*Dicrostonyx guilielmi*: c. 25%) suggesting a cold, arid and glacial climate (CORDY, 1994).

Remains of red fox are present in the Late Glacial (Magdalenian) horizons of Trou de Chaleux, Trou des Nutons, Trou de Frontal and Goyet. Fox canines were used as pendants (VAN WETTER, 1920). The scarcity of juvenile remains precludes the use of the cave as a den by foxes. It is likely that the Magdalenian occupants transported the fox carcasses to the cave. Impact notches were observed which had been produced during the extraction of marrow from the fox bones (GERMONPRÉ & SABLIN, *in prep.*).

SZUMA (2000) analysed size variation in the dentition of Polish red foxes and found that the first molars (M^1 and M_1) showed little variability in size. GINGERICH & WINKLER (1979) also noted that carnassial teeth in red foxes show the lowest variability. Thus changes in crown lengths of these teeth can be considered indicative of genuine trends rather than changes in highly variable teeth such as the M_3 . DAVIS (1977) demonstrated a Bergmannian cline in the lower carnassial length of recent red foxes, with populations from colder regions tending to be larger than those from warmer regions. For these reasons the lower carnassial was chosen for further analysis. Measurements of this tooth from Belgian Late Glacial sites, from several European sites dating to the Weichselian, and from recent Belgian, Danish and Finnish foxes are given in Table 3. There is a significant difference

Table 3 — Crown length and crown width of the lower carnassial of *Vulpes vulpes* from the Belgian Late Glacial and (1): DAVID, 1980; KOSINTCEV & BORODIN, 1990; SABLIN (unpubl. data Kostenki sites); (2): KURTÉN, 1965; (3): DEGERBØL, 1933; (4): measured on recent skeletons from Belgium in the Royal Belgian Institute of Natural Sciences.

| <i>Vulpes vulpes</i> M_1 | crown length | | | | crown width | | |
|-------------------------------|--------------|-----------|------|-------|-------------|------|-------|
| | n | OR cl | m cl | sd cl | OR cw | m cw | sd cw |
| fossil | | | | | | | |
| LG Belgium | 27 | 15,5-17,9 | 16,3 | 0,58 | 5,7-6,6 | 6,2 | 0,27 |
| PG East Europe (1) | 5 | 15,3-18,5 | 16,9 | 1,22 | – | – | – |
| Recent | | | | | | | |
| Finland (2) | 32 | 14,4-17,7 | 16,1 | 0,81 | – | – | – |
| Danmark (3) | 52 | 13,6-16,8 | 15,3 | 0,63 | – | – | – |
| Belgium (4) | 65 | 13,4-16,5 | 15,1 | 0,64 | 5,3-6,6 | 5,9 | 0,32 |

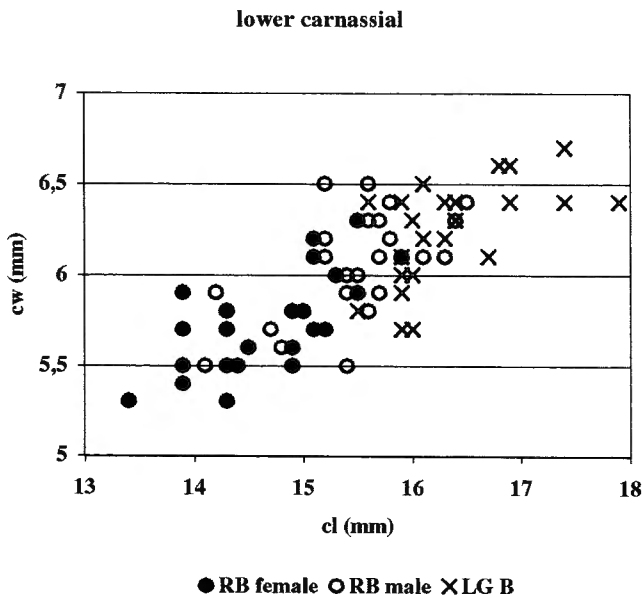


Fig. 3 — Scatter diagram of the lower carnassial (cl, cw) of the fossil and recent *Vulpes vulpes* from Belgium.

between mean carnassial lengths of fossil and recent red foxes (ANOVA; $F_{4,176}=27.191$; $P<0.0001$). Pairwise comparisons (Tukey-Kramer post hoc test for unequal sample size) show that the mean carnassial length of the Belgian Late Glacial foxes is significantly larger than that of both recent Belgian ($P<0.001$) and recent Danish foxes ($P<0.001$). The mean carnassial length of the Belgian fossil foxes is comparable to a recent red fox sample from Finland (KURTEN, 1965) and to a small sample of east European red foxes from Kostenki, Moldavia and the Ural dating to the Weichselian (DAVID, 1980; KOSTINCEV & BORODIN, 1990; SABLIN, unpubl.data Kostenki sites). Figure 3 depicts the relationship of carnassial length to carnassial width for recent female and male foxes and Late Glacial foxes from Belgium.

Measurements of fox limb bones are given in tables 4 and 5, including data from the Belgian cave assemblages and the Russian Pleniglacial Kostenki sites, along with measurements of recent red foxes from Belgium - mainly from south of the Sambre and Meuse axis - and Denmark (DEGERBØL, 1933). Only a few complete bones are present in the Belgian sample. The lengths of a humerus (GL: 120.6 mm), a femur (GL: 121.5 mm) and a tibia (132.2 mm) fall into the observed range for the female subsample of recent Belgian foxes. It is highly likely that these finds are postglacial in age, and they are therefore not included in the tables. A fossil radius and a femur are larger than the mean of the recent Belgian and Danish male foxes and probably date to the Late Glacial.

Since most of the long bones of the Belgian Late Glacial foxes had been broken for marrow extraction, comparative measurements were restricted to the width of the epiphyses. The mean values of distal width of the

humerus (ANOVA: $F_{3,51}=1.349$; $P=0.27$) and proximal width of the femur (ANOVA: $F_{2,56}=1.129$; $P=0.33$) do not differ significantly between the recent and fossil samples. However, significant differences could be observed in the sizes of distal long bones and foot elements in the assemblages studied. A significant variation in the distal width of the radius is shown by ANOVA ($F_{3,36}=11.667$; $P<0.0001$). Tukey-Kramer post hoc test for pairwise comparisons yielded the following P-values: recent Belgian vs. Late Glacial Belgian foxes: $P<0.05$, recent Belgian vs. recent Danish foxes: $P<0.001$, recent Belgian vs. Kostenki foxes: $P<0.001$, recent Danish vs. Kostenki foxes: $P<0.05$. There is also a significant variation between the samples in the mean values of the proximal width of the tibia (ANOVA: $F_{3,49}=4.167$, $P=0.021$). Pairwise comparison (Tukey-Kramer post hoc test) shows that tibia width in Belgian Late Glacial foxes is significantly larger than in recent Belgian foxes ($P<0.05$).

Lengths of the second metacarpal and second metatarsal were also used for comparative purposes (Table 5). There is a significant difference in the mean values for the length of the second metacarpus of fossil and recent Belgian foxes (unpaired- $t=3.552$; $df=31$; $P=0.0012$) and similar results were observed for the second metatarsus of fossil and recent Belgian foxes (unpaired- $t=3.302$; $df=31$; $P=0.0024$).

According to Bergmann's rule, *Vulpes vulpes* inhabiting cooler climates tend to be larger than their congeners inhabiting warmer climates (DAVIS 1977, 1981). DAVIS (1977) calculated regression equations for lower carnassial length of recent foxes to the environmental temperature for the mean temperature of the coldest month ($y=44.19-0.107x$) and the mean maximum temperature of the warmest month ($y=50.13-0.120x$). Regression equations of 27 carnassials of Late Glacial foxes, produced a mean winter temperature of 260.4K ($-12.6^{\circ}\text{C} \pm 5.4$) and a mean maximum summer temperature of 281.7K ($8.7^{\circ}\text{C} \pm 4.8$). These estimates are comparable to average temperatures based on pollen analysis and Coleoptera data for the Netherlands during the pre-Bølling, with about -10°C for the winter month and about 9°C for the summer month. Our mean maximum summer estimation is much lower than the estimated summer temperature of 15°C for the Bølling in the Netherlands (VAN GEEL *et al.*, 1989). According to the regression equations for the Late Glacial foxes, the low summer and winter temperatures could point to an Oldest Dryas age for the assemblages rather than Bølling. SNEYERS & VANDIEPENBECK (1995) give the mean maximum and mean minimum temperature of the region south of the Sambre and Meuse valleys, from 1833 to 1993. The mean maximum and minimum temperatures are $+1^{\circ}\text{C}$ and -4°C for January, and 18°C and 10°C for July. The lengths of the lower carnassials of recent Belgian foxes indicate a mean winter temperature of approximately $-1^{\circ}\text{C} \pm 6.0$ and a mean maximum summer temperature of about $+19^{\circ}\text{C} \pm 5.3$, based on the DAVIS (1977) formula. The mean winter temperature falls in the range

Table 4 — Measurements of long bones of fossil and recent *Vulpes vulpes*, (1): measured on fossil bones from Kostenki in the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, (2): measured on recent skeletons from Belgium in the Royal Belgian Institute of Natural Sciences, (3): DEGERBØL, 1933.

| <i>Vulpes vulpes</i> | | | | | | | | | | | | | | | | | | | | |
|----------------------|----------------------|-----------|------|------|------------------|---------------------|-------------|-------|------|-----------------|-------------|-------|------|-----------------|-------------|-------|------|---------------|-------|-------|
| | Late Glacial Belgium | | | | PG Kost m (1) | R Belgium M & F (2) | | | | R Belgium M (2) | | | | R Belgium F (2) | | | | R Denmark (3) | | |
| | n | OR | m | sd | | n | OR | m | sd | n | OR | m | sd | n | OR | m | sd | M&F m | Mm | Fm |
| <i>humerus</i> | | | | | | | | | | | | | | | | | | | | |
| GL | | | | | | 30 | 113,3-136,4 | 123,1 | 5,99 | 18 | 114,5-136,4 | 125,4 | 6,33 | 12 | 113,3-123,7 | 119,8 | 3,50 | 126,5 | 127,9 | 124,9 |
| Bp | | | | | | 25 | 19,1-23,7 | 20,9 | 1,04 | 14 | 19,1-23,7 | 21,1 | 1,16 | 11 | 19,4-21,6 | 20,7 | 0,88 | 18,2 | | |
| Dp | | | | | | 26 | 24,0-29,4 | 26,1 | 1,15 | 16 | 24,0-29,4 | 26,3 | 1,28 | 10 | 24,4-25,9 | 25,9 | 0,92 | 26,2 | | |
| KD | 11 | 7,2-8,9 | 8,2 | 0,60 | | 26 | 7,7-9,3 | 8,6 | 0,43 | 17 | 7,8-9,3 | 8,6 | 0,42 | 12 | 7,7-9,3 | 8,7 | 0,43 | | | |
| Bd | 8 | 20,0-23,4 | 21,6 | 1,15 | 22,5 | 24 | 20,0-24,8 | 21,3 | 1,08 | 17 | 20,0-24,8 | 21,5 | 1,23 | 10 | 20,2-21,7 | 21,0 | 0,46 | 21,2 | 21,3 | 20,7 |
| Dd | 5 | 15,0-17,5 | 16,2 | 0,60 | | 14 | 14,5-17,9 | 16,0 | 0,98 | 11 | 14,9-17,9 | 16,2 | 0,93 | 5 | 14,5-16,4 | 15,5 | 0,73 | | | |
| <i>radius</i> | | | | | | | | | | | | | | | | | | | | |
| GL | 1 | 127,0 | | | | 25 | 106,3-127,0 | 116,1 | 5,51 | 16 | 112,0-127,0 | 119,0 | 4,37 | 9 | 106,3-118,5 | 111,3 | 3,68 | 118,9 | 121,4 | 115,3 |
| Bp | 6 | 11,5-13,6 | 12,3 | 0,71 | 13,5 | 18 | 11,3-14,9 | 12,2 | 0,90 | 10 | 11,3-14,9 | 12,6 | 1,02 | 8 | 11,3-12,4 | 11,7 | 0,38 | 12,2 | 12,6 | 11,8 |
| Dp | 6 | 7,3-8,4 | 7,8 | 0,52 | | 12 | 7,0-9,1 | 7,8 | 0,75 | 7 | 7,3-9,1 | 8,0 | 0,77 | 5 | 7,0-8,9 | 7,6 | 0,77 | 7,8 | | |
| KD | 11 | 8,3-9,8 | 8,9 | 0,47 | | 21 | 8,1-10,9 | 8,8 | 0,67 | 13 | 8,3-10,9 | 9,0 | 0,72 | 8 | 8,1-8,6 | 8,3 | 0,20 | 8,7 | | |
| Bd | 5 | 15,0-16,6 | 15,8 | 0,71 | 17,5 | 13 | 11,4-15,5 | 14,2 | 1,30 | 9 | 11,5-15,5 | 14,6 | 0,53 | 5 | 11,4-15,2 | 14,1 | 0,89 | 15,8 | 16,3 | 15,1 |
| Dd | 5 | 7,9-9,2 | 8,5 | 0,48 | | | | | | | | | | | | | | | | |
| <i>femur</i> | | | | | | | | | | | | | | | | | | | | |
| GL | 1 | 136,5 | | | | 32 | 120,0-141,8 | 129,6 | 5,90 | 19 | 122,0-141,8 | 131,9 | 5,71 | 13 | 120,0-132,9 | 126,2 | 4,47 | 133,0 | 134,8 | 130,7 |
| Bp | 5 | 25,0-29,0 | 26,5 | 1,85 | | 31 | 24,3-32,4 | 26,7 | 1,62 | 19 | 25,0-32,4 | 27,1 | 1,85 | 12 | 24,3-27,4 | 26,1 | 0,94 | 26,1 | 26,3 | 25,7 |
| DC | 2 | 11,4-12,2 | 11,8 | 0,56 | | 32 | 11,6-14,5 | 12,6 | 0,63 | 20 | 11,6-14,5 | 12,7 | 0,76 | 12 | 12,0-13,0 | 12,4 | 0,32 | | | |
| KD | 3 | 8,5-9,9 | 9,2 | 0,70 | | 31 | 8,4-11,1 | 9,6 | 0,54 | 19 | 8,4-11,1 | 9,6 | 0,62 | 12 | 9,1-10,2 | 9,5 | 0,38 | | | |
| Bd | 1 | 21,0 | | | | 27 | 20,1-25,1 | 22,1 | 1,22 | 17 | 20,1-25,1 | 22,4 | 1,34 | 10 | 20,3-22,2 | 21,4 | 0,61 | 21,5 | 21,9 | 21,0 |
| Dd | | | | | | 19 | 19,5-26,2 | 22,8 | 1,67 | 14 | 20,9-26,2 | 23,3 | 1,55 | 5 | 19,5-22,2 | 21,3 | 1,13 | | | |
| <i>tibia</i> | | | | | | | | | | | | | | | | | | | | |
| GL | | | | | | 29 | 130,0-159,9 | 140,0 | 7,20 | 17 | 131,0-159,9 | 143,8 | 6,80 | 12 | 130,1-143,0 | 135,5 | 4,52 | 144,4 | 145,9 | 141,1 |
| Bp | 7 | 22,4-27,9 | 24,8 | 2,03 | 25,6 | 23 | 21,5-27,0 | 23,0 | 1,16 | 15 | 21,5-27,0 | 23,4 | 1,26 | 8 | 21,6-23,0 | 22,3 | 0,51 | 23,7 | 24,5 | 22,7 |
| Dp | 8 | 24,2-26,8 | 25,6 | 1,00 | | 15 | 23,2-27,8 | 25,3 | 1,24 | 9 | 24,1-27,8 | 25,7 | 1,20 | 6 | 23,2-25,6 | 24,5 | 0,99 | 25,5 | | |
| KD | 20 | 6,6-9,8 | 8,7 | 0,69 | | 13 | 8,3-9,9 | 9,1 | 0,56 | 6 | 8,3-9,9 | 9,4 | 0,59 | 7 | 8,3-9,4 | 8,9 | 0,42 | | | |
| Bd | 20 | 14,8-17,4 | 16,3 | 0,82 | | 15 | 13,4-17,2 | 15,4 | 1,32 | 7 | 14,8-17,2 | 16,1 | 0,81 | 8 | 13,4-16,9 | 14,8 | 1,14 | 16,2 | 16,4 | 15,5 |
| Dd | 20 | 9,9-12,8 | 11,4 | 0,71 | | 20 | 9,2-12,9 | 11,2 | 0,86 | 13 | 9,9-12,9 | 11,5 | 0,84 | 7 | 9,2-11,5 | 10,8 | 0,77 | | | |

Table 5 — Measurements of metapodial bones of fossil and Recent *Vulpes vulpes*.

| <i>Vulpes vulpes</i> | | | | | | | | |
|----------------------|----------------------|-----------|------|------|----------------|-----------|------|------|
| | Late Glacial Belgium | | | | Recent Belgium | | | |
| | n | OR | m | sd | n | OR | m | sd |
| <i>MC II</i> | | | | | | | | |
| GL | 5 | 40,4-50,3 | 44,6 | 3,89 | 28 | 35-9-45,1 | 40,0 | 2,42 |
| Bp | 6 | 4,3-4,6 | 4,5 | 0,12 | | | | |
| Dp | 6 | 6,7-7,4 | 7,1 | 0,26 | | | | |
| Bd | 5 | 5,8-6,7 | 6,3 | 0,37 | | | | |
| Dd | 5 | 5,5-6,3 | 5,9 | 0,30 | | | | |
| <i>MC III</i> | | | | | | | | |
| GL | 1 | 50,2 | | | | | | |
| Bp | 1 | 6,5 | | | | | | |
| Dp | 1 | 7,0 | | | | | | |
| Bd | 1 | 6,3 | | | | | | |
| Dd | 1 | 6,1 | | | | | | |
| <i>MC V</i> | | | | | | | | |
| GL | 3 | 40,1-43,7 | 41,9 | 1,80 | | | | |
| Bp | 3 | 7,1-7,7 | 7,4 | 0,31 | | | | |
| Dp | 3 | 6,3-6,8 | 6,5 | 0,25 | | | | |
| Bd | 4 | 6,7-7,4 | 7,1 | 0,29 | | | | |
| Dd | 3 | 5,1-6,2 | 5,7 | 0,57 | | | | |
| <i>MT II</i> | | | | | | | | |
| GL | 3 | 61,0-64,7 | 63,0 | 1,86 | 30 | 52,0-64,1 | 57,2 | 2,97 |
| Bp | 5 | 3,9-4,2 | 4,1 | 0,13 | | | | |
| Dp | 4 | 10,0-10,5 | 10,3 | 0,24 | | | | |
| Bd | 3 | 6,5-7,3 | 6,8 | 0,44 | | | | |
| Dd | 1 | 6,5-6,6 | 6,6 | 0,07 | | | | |
| <i>MT III</i> | | | | | | | | |
| GL | 2 | 66,0-68,4 | 67,2 | 1,70 | | | | |
| Bp | 6 | 5,8-6,8 | 6,2 | 0,37 | | | | |
| Dp | 7 | 9,6-11,4 | 10,3 | 0,59 | | | | |
| Bd | 2 | 6,3-6,3 | 6,3 | | | | | |
| Dd | 2 | 6,2-6,2 | 6,2 | | | | | |
| <i>MT IV</i> | | | | | | | | |
| GL | 2 | 60,8-64,1 | 62,5 | 2,33 | | | | |
| Bp | 2 | 4,3-4,7 | 4,5 | 0,28 | | | | |
| Dp | 2 | 8,5-8,6 | 8,6 | 0,07 | | | | |
| Bd | 2 | 5,5-5,8 | 5,7 | 0,21 | | | | |
| Dd | 2 | 5,8-6,1 | 6,0 | 0,21 | | | | |
| <i>MT V</i> | | | | | | | | |
| GL | 4 | 57,8-63,4 | 61,7 | 2,62 | | | | |
| Bp | 5 | 4,2-5,4 | 4,9 | 0,50 | | | | |
| Dp | 5 | 7,3-8,7 | 8,0 | 0,60 | | | | |
| Bd | 4 | 5,2-7,0 | 6,2 | 0,80 | | | | |
| Dd | 4 | 506-6,5 | 6,0 | 0,40 | | | | |

given by SNEYERS & VANDIEPENBEECK (1995), the mean maximum summer temperature is comparable to the recent mean maximum temperature of July in south Belgium.

Alopex lagopus (Linnaeus, 1758)

The arctic fox is an inhabitant of tundra and tundra-forest regions and is distributed today throughout continental Eurasia, North America and the northern ocean islands, primarily above 60°N latitude. The ears, muzzle and limbs are reduced in size to prevent heat loss and its luxurious fur provides an enormous amount of insulation, even the foot pads are covered with fur (PRESTRUD, 1991; PULLIANEN, 1993; ANDERSON, 1999). But despite these differences, arctic and red foxes are very similar in morphology, ecology and behaviour (FRAFJORD, 2003). The southern distribution limit of the arctic fox is determined by interspecific competition with the red fox (HERSTEINSSON & MACDONALD, 1992). Arctic and red foxes are sympatric in a narrow overlap zone in the low Arctic, but are spatially segregated. In Fennoscandia arctic foxes are found on the mountain tundra possibly because of increased competition with red foxes at lower altitudes (ELMHAGEN *et al.*, 2002). Arctic foxes may be killed or chased by red foxes. Arctic fox breeding is restricted to less productive high altitude areas above the tree line. They avoid breeding in the vicinity of red foxes, otherwise their young can be at a high risk of mortality (TANNERFELDT, 2002). Red foxes can also dominate limited food supplies (FRAFJORD *et al.*, 1989). Arctic foxes in inland habitats use lemmings as their primary prey, but they also feed upon voles, birds, berries and carcasses of reindeer. The differences between red and arctic fox diets are better explained by altitudinal segregation than by differences between their fundamental food niches. Lemmings are more common in unproductive tundra habitats and at relative high altitudes (ELMHAGEN *et al.*, 2002).

Arctic fox remains from Trou de Chaleux, Trou des Nutons, Trou du Frontal and Goyet are undoubtedly glacial in age. Impact notches and cut marks on several bones show that arctic fox carcasses were skinned, butchered and used as a source of marrow by the Magdalenian people (GERMONPRÉ & SABLIN, *in prep.*). Since recent arctic foxes den above the tree line and avoid river valleys with birch and coniferous forest (LANDA *et al.*, 1998), it is likely that prehistoric people trapped arctic foxes on the treeless plateaux.

Measurements of the lower carnassials of Late Glacial foxes from Belgium were compared with those of recent continental foxes (*Alopex lagopus lagopus*) from Taimir, Siberia, and Late Pleistocene arctic foxes (*Alopex lagopus rossicus*) from the Upper Palaeolithic sites of Avdevo, Kostenki, Sungir and Yudinovo (central Russian Plain) (KUZMINA & SABLIN, 1993; SABLIN, 1994) (Table 6). There are no significant differences in the mean crown lengths of the lower carnassial from the Late Pleniglacial, Late Glacial and Holocene samples (ANOVA; $F_{5,237} = 1.837$; $P = 0.11$). Table 6 also includes

Table 6 — Measurements of the lower carnassial of fossil and recent *Alopex lagopus*: (1) Geological Institute, Russian Academy of Sciences, Moscow, (2) SABLIN, 1994, (3) measured on recent skeletons from Taimir, Russia, in the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, (4) measured on recent skeletons from Komandorskiye Islands, Russia, in the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, (5) measured on recent skeletons from Franz Josef Land, Russia, in the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg.

| <i>Alopex lagopus</i> M ₁ | age | crown length | | | crown width | | | |
|--|--------------|--------------|-----------|------|-------------|---------|------|-------|
| | | n | OR cl | m cl | sd cl | OR cw | m cw | sd cw |
| fossil | | | | | | | | |
| Late Glacial Belgium | c. 12,700 BP | 82 | 12,7-15,4 | 14,3 | 0,59 | 4,7-5,8 | 5,4 | 0,23 |
| <i>Alopex lagopus rossicus</i> | | | | | | | | |
| Sungir, Russian Plain (1) | c. 21,000 BP | 20 | 13,2-15,6 | 14,3 | 0,72 | 4,8-5,7 | 5,4 | 0,34 |
| Avdeevo, Russian Plain (1) | c. 21,000 BP | 34 | 13,0-15,5 | 14,2 | 0,75 | 4,6-5,9 | 5,4 | 0,37 |
| Kostenki, Russian Plain (2) | c. 21,000 BP | 47 | 12,2-15,5 | 14,1 | 0,66 | 4,5-6,0 | 5,3 | 0,42 |
| Yudinovo (2) | c. 15,000 BP | 31 | 12,7-15,5 | 14,5 | 0,61 | 4,5-5,6 | 5,2 | 0,25 |
| recent | | | | | | | | |
| <i>Alopex lagopus lagopus</i> (3) | | 29 | 12,9-15,1 | 14,2 | 0,60 | 4,8-5,9 | 5,4 | 0,33 |
| <i>Alopex lagopus beringensis</i> (4) | | 25 | 13,8-15,2 | 14,6 | 0,35 | 5,2-5,7 | 5,5 | 0,20 |
| <i>Alopex lagopus spitzbergenensis</i> (5) | | 11 | 12,6-14,4 | 13,7 | 0,63 | 4,4-5,0 | 4,8 | 0,17 |

measurements of carnassials of recent island forms from the Komandorskiye Islands (*A. l. beringensis*) and from Franz Josef Land (*A.l. spitzbergenensis*), which are slightly larger and smaller respectively than carnassials of continental arctic foxes.

Comparative measurements of postcranial bones of arctic foxes from the Belgian Late Glacial, from the Pleniglacial Kostenki sites, from Yudinovo, and from recent arctic foxes from Taimir (KUZMINA & SABLIN, 1993; SABLIN, 1994) are given in tables 7 and 8. Significant differences between the length of the humerus of the fossil and recent arctic foxes were confirmed by ANOVA ($F_{3,54} = 6.978$; $P = 0.0005$). Pairwise comparisons (Tukey-Kramer post hoc test for unequal sample size) show that humerus length in the recent foxes is significantly greater than that of the Kostenki ($P < 0.001$) and Yudinovo ($P < 0.05$) foxes. A scatter diagram plotting greatest length and distal width of the humerus of fossil and recent foxes is shown in figure 4. Significant differences were observed in the greatest length of the radius (ANOVA; $F_{3,66} = 4.267$; $P = 0.0082$). Tukey Kramer's post hoc test for pairwise comparison yielded following P-values for the radius: Kostenki vs. recent foxes ($P < 0.05$) and Kostenki vs. Belgian Late Glacial foxes ($P < 0.05$). The mean values for the greatest length of the femur of the Kostenki, Yudinovo and recent arctic fox samples do not show significant differences (ANOVA, $F_{2,43} = 2.172$, $P = 0.13$). Complete femurs were not preserved in the assemblages of Late Glacial arctic foxes from Belgium. Also the mean values for the greatest length of the tibia do not differ notably (ANOVA, $F_{3,51} = 2.068$, $P = 0.12$).

Since length among the various metapodial bones is probably highly correlative, and similar results would be expected for each element, we decided to limit further

analysis to the third metacarpus and third metatarsus (Table 8). Significant differences were noted in the greatest length of the metacarpus in the samples studied (ANOVA, $F_{3,79} = 4.029$, $P = 0.0101$); third metacarpals from Kostenki ($P < 0.05$) and from Yudinovo ($P < 0.05$) are notably shorter than those of the modern foxes

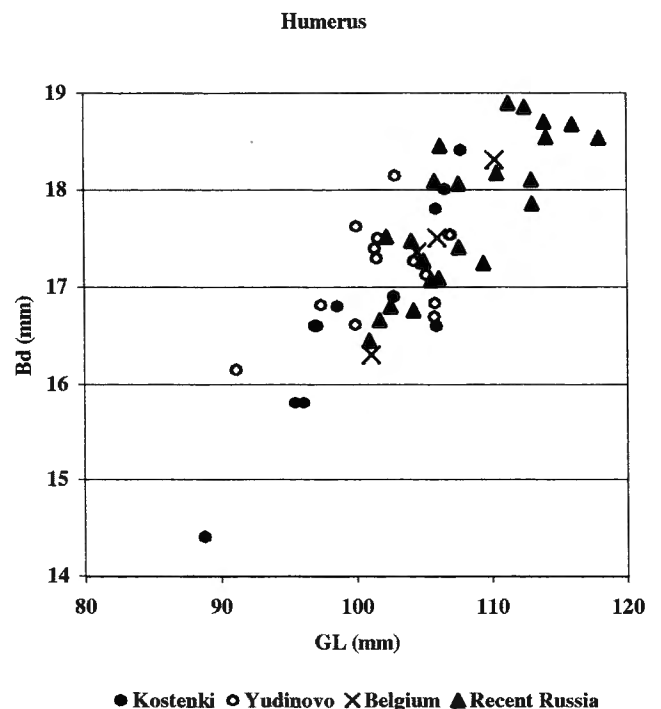


Fig. 4 — Scatter diagram of the humerus (GL, Bd) of *Alopex lagopus*.

Table 7 — Measurements of long bones of fossil and recent *Alopex lagopus*, (1): SABLIN, 1994, (2): KUZMINA & SABLIN, 1993.

| <i>Alopex lagopus</i> | | | | | | | |
|-----------------------|----|----------------------|-------|------|-------------|--------------|------------|
| | n | Late Glacial Belgium | | | PG | LG | R |
| | | OR | m | sd | Kost. m (1) | Yu. m (1, 2) | R m (1, 2) |
| <i>humerus</i> | | | | | | | |
| GL | 4 | 101,3-110,3 | 105,5 | 3,74 | 100,4 | 102,8 | 108,4 |
| Bp | 18 | 14,6-16,8 | 15,5 | 0,75 | | | |
| Dp | 19 | 20,9-24,8 | 22,6 | 1,07 | | | |
| KD | 47 | 5,9-7,3 | 6,6 | 0,33 | | | |
| Bd | 43 | 15,8-18,9 | 17,6 | 0,81 | 17,1 | 17,3 | 17,7 |
| Dd | 34 | 11,6-14,6 | 13,4 | 0,65 | | | |
| <i>radius</i> | | | | | | | |
| GL | 6 | 94,5-109,5 | 101,9 | 5,42 | 95,7 | 98,8 | 99,9 |
| Bp | 27 | 9,3-11,4 | 10,5 | 0,60 | 9,9 | 10,3 | 10,3 |
| Dp | 29 | 5,7-7,2 | 6,4 | 0,37 | | | |
| KD | 56 | 5,8-8,3 | 7,0 | 0,53 | | | |
| Bd | 22 | 12,2-14,4 | 13,5 | 0,60 | 13,0 | 13,4 | 13,5 |
| Dd | 21 | 6,4-8,3 | 7,2 | 0,48 | | | |
| <i>femur</i> | | | | | | | |
| GL | | | | | 105,5 | 107,1 | 109,4 |
| Bp | 11 | 23,1-25,7 | 24,3 | 0,85 | | | |
| DC | 11 | 10,1-11,9 | 11,1 | 0,45 | | | |
| KD | 10 | 7,3-8,1 | 7,7 | 0,23 | | | |
| Bd | 9 | 17,4-18,8 | 18,1 | 0,53 | 17,6 | 17,9 | 18,4 |
| Dd | 9 | 14,1-20,6 | 18,3 | 2,96 | | | |
| <i>tibia</i> | | | | | | | |
| GL | 5 | 117,0-124,7 | 120,7 | 3,56 | 119,1 | 119,1 | 123,4 |
| Bp | 6 | 17,9-20,3 | 19,6 | 0,95 | 19,4 | 19,9 | 20,2 |
| Dp | 7 | 19,1-23,5 | 21,2 | 1,35 | 21,0 | 21,3 | 21,2 |
| KD | 48 | 6,3-8,2 | 7,2 | 0,39 | | | |
| Bd | 48 | 12,2-14,8 | 13,4 | 0,63 | 13,1 | 13,2 | 13,8 |
| Dd | 43 | 8,1-10,1 | 9,0 | 0,55 | 8,8 | 8,8 | 9,4 |

(Tukey-Kramer post hoc test). The length of the third metatarsal also varied significantly between the assemblages examined (ANOVA, $F_{3,83} = 6.680$, $P = 0.0004$). Pairwise comparisons (Tukey-Kramer post hoc test) indicate that the third metatarsus of recent continental arctic foxes are longer than those of Kostenki ($P < 0.01$), from Yudinovo ($P < 0.01$) and from the Belgian Late Glacial sites ($P < 0.05$).

Altogether the total length of the fore leg (GL humerus + GL radius + GL metacarpus III) increased by 14 mm from the Pleniglacial foxes to the recent ones (Fig. 5a). These three elements differ significantly in size in the assemblages studied. Although a similar increase (11 mm) was observed in the total length of the hind leg (GL femur + GL tibia + GL metatarsus III) (Fig. 5b), only the length of the metatarsus differed significantly in length in the samples studied.

Table 8 — Measurements of metacarpal and metatarsal bones of fossil and recent *Alopex lagopus*, (1): SABLIN, 1994.

| <i>Alopex lagopus</i> | | | | | | | |
|-----------------------|----|----------------------|------|------|-------------|-----------|---------|
| | n | Late Glacial Belgium | | | PG | LG | R |
| | | OR | m | sd | Kost. m (1) | Yu. m (1) | R m (1) |
| <i>MC II</i> | | | | | | | |
| GL | 11 | 33,6-40,2 | 36,2 | 1,84 | 35,6 | 36,4 | 37,7 |
| Bp | 12 | 3,8-4,1 | 3,9 | 0,10 | | 3,8 | 4,0 |
| Dp | 12 | 5,5-6,4 | 5,9 | 0,27 | | 5,6 | 5,9 |
| Bd | 11 | 5,4-5,8 | 5,6 | 0,17 | | | |
| Dd | 10 | 4,8-5,6 | 5,1 | 0,23 | | | |
| <i>MC III</i> | | | | | | | |
| GL | 11 | 37,3-45,6 | 42,1 | 2,53 | 41,0 | 41,2 | 42,9 |
| Bp | 12 | 4,2-5,2 | 4,8 | 0,31 | | 4,7 | 4,7 |
| Dp | 12 | 5,1-6,4 | 5,9 | 0,39 | | 5,8 | 5,9 |
| Bd | 15 | 5,0-5,8 | 5,4 | 0,25 | | | |
| Dd | 15 | 4,9-6,0 | 5,4 | 0,31 | | | |
| <i>MC IV</i> | | | | | | | |
| GL | 6 | 38,8-42,0 | 40,3 | 1,16 | 39,8 | 40,1 | 41,8 |
| Bp | 7 | 4,2-4,6 | 4,4 | 0,12 | | 4,3 | 4,7 |
| Dp | 6 | 5,4-5,9 | 5,6 | 0,17 | | 5,8 | 5,8 |
| Bd | 7 | 4,8-5,3 | 5,1 | 0,17 | | | |
| Dd | 8 | 4,9-5,2 | 5,0 | 0,10 | | | |
| <i>MC V</i> | | | | | | | |
| GL | 10 | 32,2-36,6 | 34,4 | 1,42 | 33,6 | 33,3 | 35,6 |
| Bp | 10 | 5,6-6,9 | 6,3 | 0,33 | | 6,2 | 6,4 |
| Dp | 10 | 5,3-5,8 | 5,5 | 0,16 | | 5,4 | 5,6 |
| Bd | 11 | 5,3-6,4 | 5,8 | 0,32 | | | |
| Dd | 10 | 4,7-5,5 | 5,0 | 0,22 | | | |
| <i>MT II</i> | | | | | | | |
| GL | 6 | 44,2-48,9 | 46,4 | 2,18 | 46,0 | 47,0 | 48,7 |
| Bp | 6 | 3,1-3,5 | 3,3 | 0,15 | | 3,2 | 3,4 |
| Dp | 6 | 7,3-8,2 | 7,9 | 0,34 | | 7,9 | 8,1 |
| Bd | 7 | 5,1-5,6 | 5,4 | 0,21 | | | |
| Dd | 6 | 4,6-5,3 | 5,0 | 0,26 | | | |
| <i>MT III</i> | | | | | | | |
| GL | 12 | 46,1-53,3 | 50,7 | 2,18 | 50,9 | 50,7 | 53,6 |
| Bp | 16 | 4,3-5,1 | 4,7 | 0,21 | | 4,8 | 4,9 |
| Dp | 10 | 7,8-8,9 | 8,2 | 0,42 | | 8,3 | 8,4 |
| Bd | 13 | 4,9-5,5 | 5,2 | 0,20 | | | |
| Dd | 12 | 5,1-5,7 | 5,4 | 0,19 | | | |
| <i>MT IV</i> | | | | | | | |
| GL | 5 | 49,0-54,6 | 51,7 | 2,03 | 51,9 | 53,3 | 54,8 |
| Bp | 6 | 3,2-4,0 | 3,5 | 0,29 | | 3,7 | 3,6 |
| Dp | 6 | 7,1-7,6 | 7,4 | 0,19 | | 7,7 | 7,8 |
| Bd | 6 | 4,6-5,3 | 5,1 | 0,25 | | | |
| Dd | 6 | 5,1-5,7 | 5,4 | 0,20 | | | |
| <i>MT V</i> | | | | | | | |
| GL | 7 | 46,8-54,7 | 49,4 | 2,92 | 47,7 | 48,5 | 49,9 |
| Bp | 10 | 4,0-4,3 | 4,1 | 0,12 | | 4,3 | 4,4 |
| Dp | 9 | 6,3-7,6 | 6,8 | 0,42 | | 6,7 | 7,0 |
| Bd | 12 | 5,0-5,8 | 5,4 | 0,22 | | | |
| Dd | 12 | 4,8-5,6 | 5,1 | 0,26 | | | |

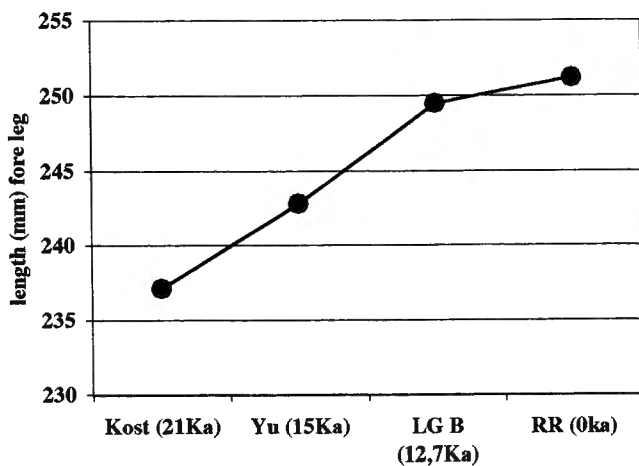


Fig. 5a — *Alopex lagopus*: length of the fore leg (GL humerus + GL radius + GL metacarpus III) from the Pleniglacial over the Late Glacial until recent times.

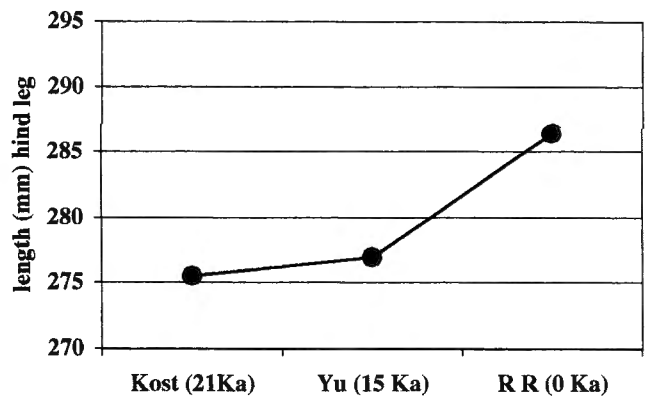


Fig. 5b — *Alopex lagopus*: length of the hind leg (GL femur + GL tibia + GL metatarsus III) from the Pleniglacial over the Late Glacial until recent times.

In the Pleniglacial and Late Glacial arctic fox, *Alopex lagopus rossicus*, from Kostenki and Yudinovo the proximal part of the fore leg is shorter than in recent *Alopex lagopus lagopus* from Taimir, but does not differ in size from the Late Glacial Belgian foxes. The middle part of the fore leg is shorter in Pleniglacial Kostenki foxes than in the Late Glacial Belgian and recent Siberian foxes. The fore foot of *A. l. rossicus* from Kostenki and Yudinovo is shorter than the one of the recent foxes. The lengths of the long bones of the hind leg are comparable in both the fossil and recent arctic foxes. The hind foot of all the fossil foxes is, however, smaller in size when compared with the hind foot of the recent Taimir foxes.

Our results show that the length of the lower carnassial of the fox does not appear to change significantly from the Pleniglacial through to the present-day. However, as

body size increases, the M_1 becomes relatively smaller. This is shown graphically in figure 6 where the carnassial/humerus index is given for the four assemblages. This index was calculated as the ratio of carnassial mean length to the humerus mean length ($(clM_1/GLhumerus) * 100$). The index declines from 14.14 in the foxes from Kostenki to 13.10 in recent arctic foxes.

Discussion

Vulpes vulpes

BERGMANN (1847) observed that latitude and body size are inversely correlated within species or groups of closely related species of warm-blooded vertebrates. Larger bodies have a relatively smaller surface area and can better maintain body heat in a cold environment (DAVIS, 1981). 65% of mammalian species follow Bergmann's rule, including the red and arctic fox (MEIRI & DAYAN, 2003). The red fox exhibits a temperature- and latitude-correlated size gradient in the Palaearctic region (DAYAN *et al.* 1989, DAVIS, 1977, 1989, KURTÉN, 1965). FRAJFORD & STEVY (1998) found that in Norway, foxes increase in size from southern to central Norway, but are smallest in the north. They attribute the small size of the northern foxes to a cooler climate, a longer winter and a reduced food supply, while in southern and central Norway the size of the red fox follows Bergmann's rule.

Foxes from the Belgian Late Glacial sites have large carnassials and robust bones, which point to large body size. Their carnassials are significantly larger than those of recent Belgian foxes and compare in size to those of Finnish red foxes, and fossil foxes from eastern Europe and Russia (Table 9). Temperature may play a role in selection in red fox morphology, as was demonstrated by KURTÉN (1965) and DAVIS (1977, 1981). The foxes in our samples from colder periods (Pleniglacial and Late Gla-

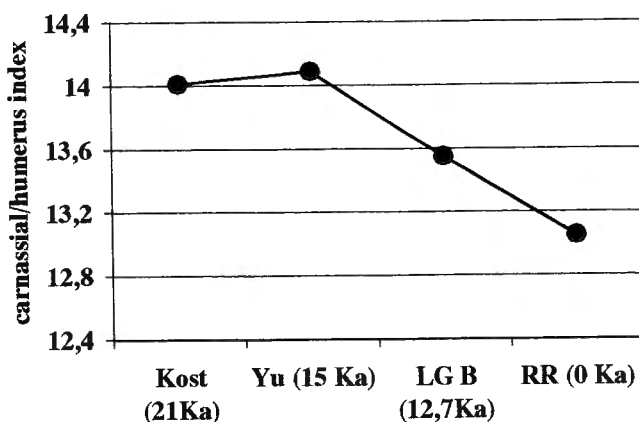


Fig. 6 — *Alopex lagopus*: carnassial/humerus index: $(clM_1/GLhumerus) * 100$ from the Pleniglacial over the Late Glacial until recent times.

cial) or from colder regions (Finland) are larger than their congeners from warmer periods/regions (recent Belgian). The mean winter temperature during the Belgian Late Glacial, based on the length of the lower carnassial was probably around -12°C , close to the critical lower temperature for the Alaskan red fox noted at -13°C (PRESTRUD, 1991). The maximum summer temperature is estimated at around 9°C . These low winter and summer temperatures indicate that the Belgian Late Glacial assemblages should be placed in the Oldest Dryas rather than the Bølling.

Unfortunately, only two complete long bones (a radius and a femur) were preserved in the Late Glacial assemblages in the Dupont collection. Widths of proximal long bones (humerus, femur) do not differ in the samples of fossil and recent red foxes studied (Table 9). However, widths of distal long bones (radius, tibia) in the Late Glacial Belgian sample are significantly larger than those of recent Belgian foxes, falling into the size-ranges of recent Danish and fossil Russian foxes. Second metacarpals and second metatarsals from the Belgian Late Glacial sample are significantly longer than these elements in the recent sample from Belgium (Table 9). MURRAY & LARIVIÈRE (2002) tested geographical differences among populations of recent American red foxes. In particular they found that the foot area in these foxes increased with latitude and was correlated with mean annual snowfall. Size differences in the foot elements of fossil and recent foxes in the samples from Belgium could indicate heavier annual snow falls and colder temperatures during the Belgian Late Glacial than recorded today. This is also shown by the winter and summer temperature of the Late Glacial deduced from the length of the lower carnassial. The large size of the fossil Belgian red foxes could indicate a Bergmannian response to the cold climatic conditions of the Late Glacial. However, according to BENES (1975) Weichselian red foxes from Central Europe are metrically closer to the recent north European subspecies *Vulpes vulpes vulpes* (Linnaeus, 1758) rather than the smaller recent western and central European subspecies *Vulpes vulpes crucigera* (Bechstein, 1789). He assumed that the large glacial foxes retreated at the close of the Weichselian to northern Europe and were replaced by *Vulpes vulpes crucigera*, migrating from southern Europe. HEPTNER *et al.* (1974) and WANDELER & LÜPS (1993), on the other hand, consider that *crucigera* should be a synonym for *vulpes*. More osteometric data, especially measurements of complete bones, and mitochondrial DNA-analyses of the fossil material could help to solve this dilemma.

Alopex lagopus

FRAFJORD (1993) found significant differences in skull size in recent arctic foxes, with Fennoscandian and Siberian arctic foxes being larger than those from higher latitudes. He proposed two possible explanations for these size differences. He correlates the reduction in skull size with energetic constraints on body size due to lower primary productivity; and he explains the size decrease in

Table 9 — Comparisons of the measurements of skeletal elements from *Vulpes vulpes* from Kostenki, the Belgian Late Glacial, recent Danish and recent Finnish red foxes with the mean values of recent Belgian foxes; statistical difference: (ns): not significant, (*): significant, (**): very significant, (***): extremely significant, (?): not enough data.

| <i>Vulpes vulpes</i> Recent Belgium | PG Kostenki c. 21 Ka | LG Belgium c. 12,7 Ka | Recent Denmark 0 Ka | Recent Finland 0 Ka |
|---|----------------------------|-----------------------------|---------------------------|---------------------------|
| M/I cl | *** | *** | *** | *** |
| Humerus Bd | ns | ns | ns | ? |
| Radius Bd | *** | * | *** | ? |
| MC II GL | ? | *** | ? | ? |
| Femur Bp | ns | ns | ns | ? |
| Tibia Bp | ? | * | ns | ? |
| MT II GL | ? | ** | ? | ? |

higher latitudes as an adaptation to reduced competition with red foxes. We only compared the fossil arctic foxes with recent ones from the Siberian mainland. According to our results it appears that from the Pleniglacial onwards there is an increase in body size in the continental arctic fox as well in the foxes of the Russian Plain and Belgium. However, this size increase is not equal for all skeletal elements (Table 10). Some elements remain stable in size (lower carnassial, femur, tibia) compared to the recent Taimir foxes. One element (metatarsus III) differs significantly between all fossil and recent foxes. In the Pleniglacial foxes from Kostenki (c. 21 Ka), two long bones (humerus and radius) and the foot bones from the fore leg and the bones from the hind foot are shorter than these bones from the recent Taimir foxes. In the Yudinovo foxes (c. 15 Ka), the proximal long bone of the fore leg, as well as the fore and hind foot bones are notably shorter than those of Taimir. Furthermore, the radius of the Kostenki foxes is significantly shorter than the radius of the Belgian arctic foxes. From the Pleniglacial (Kostenki) through the Late Glacial (Yudinovo, Belgium) to the present-day, the fore leg in particular is increasing in length (Fig. 5a) and to a lesser extent the hind leg (Fig. 5b). A mitochondrial DNA analysis of the arctic foxes from Belgium, Yudinovo and Taimir is currently being performed to check the phylogenetic differentiation between these fossil and recent populations (DALEN *et al.*, *in prep.*).

According to LEHMANN (1954) the arctic fox increased in size during the Late Pleistocene. This author considered that the size increase was an adaptation to lower temperatures and a tundra habitat. BENES (1975) found that the lower teeth of arctic foxes from the Early Weichselian are smaller than those of Pleniglacial and recent arctic foxes. Body size gradually increased during the Weichselian up to the Holocene. He explained the progressive increase of the skeletal elements of the arctic foxes according to Bergmann's rule and believed this

Table 10 — Comparisons of the measurements of skeletal elements of *Alopex lagopus* from Kostenki, Yudinovo and the Belgian Late Glacial with mean values from the recent Russian continental foxes; statistical difference: (ns): not significant, (*): significant, (**): very significant, (***): extremely significant, (?): not enough data.

| <i>Alopex lagopus</i> Recent Russia | PG Kostenki c. 21 Ka | LG Yudinovo c. 15 Ka | LG Belgium c. 12,7 Ka |
|---|----------------------------|----------------------------|-----------------------------|
| M/1 cl | ns | ns | ns |
| Humerus GL | *** | * | ns |
| Radius GL | * | ns | ns |
| MC III GL | * | * | ns |
| Femur GL | ns | ns | ? |
| Tibia GL | ns | ns | ns |
| MT III GL | ** | ** | * |

animal adapted to an extremely cold climate during or after the Pleniglacial. SABLIN (1994) also noted that the body size of the continental arctic fox in the Russian Plain increased during the time interval from 21,000 BP to 10,000 BP.

The size increase observed in the arctic foxes from the beginning of the Last Glacial until the present-day could be related to several factors such as environmental conditions (temperature, snow depth, length of snow cover, etc.), prey availability/choice and interference competition with sympatric red foxes. From our data it is clear that the legs and especially the foot bones were still increasing in size even as late as the Late Glacial (Yudinovo: fore and hind foot, Belgium: hind foot) (Table 10). MURRAY & LARIVIÈRE (2002) found that snow might have contributed to selection for foot size in recent arctic fox. The size increase of the foot bones of the arctic foxes in our samples may indicate an augmentation of the foot surface area pointing to a decreasing foot-load and possible adaptation to a long or deep snow cover. This adaptive morphological change in the arctic fox continued into the Late Glacial. It seems that prior to the Pleniglacial, arctic foxes were less specialized to a very cold climate. Although this process was almost completed during the Late Glacial in Belgium, the hind foot is still smaller than the hind foot of recent Taimir foxes. Following Bergmann's rule, it can be postulated that arctic foxes adapted more and more to an extreme cold climate with heavy snowfall during the Pleniglacial and even the Late Glacial.

HARRIS & STEUDEL (1997) remarked that the evolution of the carnivore hind-limb length is most affected by prey-capture behaviour. In arctic foxes stalking with pouncing or chasing predominates. A possible relationship between canid front-leg length and prey-capture behaviour has not been examined. The length of the lower carnassial remains stable in our sample and the first lower

molar becomes relatively smaller from the Pleniglacial onwards (Fig. 6). A change in diet, related to prey availability or prey-capture behaviour, could be a complementary explanation for the morphological disparity observed in our samples. Isotopic biogeochemistry of fossil bone collagen could provide information about the palaeodiet of the fossil arctic foxes. Stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of the Late Glacial fox bones from Belgium are currently being undertaken (STEVENS & GERMONPRÉ, *in prep.*).

Furthermore, it cannot be excluded that interference competition could have influenced the body size of the animals concerned. FRAFIJORD *et al.* (1989) observed that the outcome of a contest between arctic and red fox depends on the size, sex and age of the individuals involved. Increased competition might select for larger and more competitive arctic foxes (FRAFIJORD, 1993). The Belgian Late Glacial arctic foxes had to cope with sympatric red foxes. In Yudinovo, where red foxes are lacking, the arctic foxes are small. However, the arctic foxes from Kostenki are even smaller and here red foxes were present. The largest foxes in our sample are from Taimir, where a 70% overlap in the spatial distribution of recent red and arctic foxes exists (SABLIN, unpub. data). Yet, the largest Russian arctic foxes are found on the Komandorskiye islands, where red foxes are absent (HEPTNER *et al.*, 1974).

In our opinion, the size increase of the arctic fox has been an ongoing process since the beginning of the Weichselian. Some body parts (front leg, hind foot) were influenced more than others. We agree with LEHMANN (1954), BENES (1975) and SABLIN (1994) that this increase is probably a specialization of the arctic fox to truly cold conditions with heavy snowfall and an adaptation to a tundra habitat. This specialization could furthermore have been influenced by the presence of red fox and changes in the prey availability and prey capture behaviour. To test this explanation more analyses of size trends in sympatric fossil and recent red and arctic foxes are necessary.

Conclusion

Two species of foxes were present during the Late Glacial in Belgium: the red fox (*Vulpes vulpes*) and the arctic fox (*Alopex lagopus*). They were found in several Magdalenian cave sites situated in river valleys of the Condroz. The remains of these animals were studied osteometrically in order to compare the skeletal elements of the Late Glacial foxes from Belgium with fossil foxes from Russia and recent foxes from Belgium, Denmark, Finland, and Russia. Size fluctuations noted in the arctic fox and the red fox are not parallel. Late Glacial red foxes are larger than recent ones and the reverse is true for the arctic foxes. The size change in the red fox can be explained by Bergmann's rule, correlated with climatic changes during the time period studied, with the Weichselian foxes being larger than recent ones from the same latitude. Based on the size of the lower carnassials of the Belgian fossil foxes a mean

winter temperature of -12.6°C and a mean maximum summer temperature of 8.7°C was calculated. These low temperatures assign the Belgian Magdalenian assemblages rather to the Oldest Dryas than to the Bølling. The size change in the arctic foxes follows an opposite trend with the Pleniglacial Russian foxes being distinctly smaller than recent continental foxes and the Late Glacial Belgian foxes approaching the body proportions of the latter. Throughout the Weichselian the arctic fox is adapting to a very cold climate, and reaches its modern continental size only at the end of, or after the Ice Age.

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Mietje GERMONPRÉ
 Department of Palaeontology
 Royal Belgian Institute of Natural Sciences
 Vautierstreet 29
 1000 Brussels
 Belgium
 mietje.germonpre@naturalsciences.be

Mikhail V. SABLIN
 Zoological Institute RAS
 Universitetskaya nab. 1
 199034 Saint Petersburg
 Russia
 msablin@yandex.ru

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