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Carnivores (Mammalia, Carnivora) of the Urals in the Late Pleistocene and Holocene

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ABSTRACT

Carnivore assemblages from localities of the Late Pleistocene and Holocene of Northern, Middle and Southern Urals were studied. Analysis of species composition of the carnivore fauna was performed for seven chronological periods: MIS 5e, MIS 3, mid-MIS2 (LGT), late MIS 2 (BAIC), early MIS 1 (Preboreal-Boreal), mid-MIS 1 (Atlantic-Subboreal), late MIS 1 (Subatlantic). In the Urals, changes in carnivore fauna were occurring during the Late Pleistocene and Holocene. Faunal composition included the species from European, Siberian and European–Siberian faunal complexes throughout the Late Pleistocene and Holocene, dominated by the species from European–Siberian faunal complexes. The general trend of fauna changes is represented by a decreasing percentage of species from the European faunal complex and an increasing percentage of those from the Siberian faunal complex. Faunal composition has changed due to two main reasons, range shifts and extinction. Sixteen out of 24 species that inhabited the Urals during the Late Pleistocene and Holocene underwent range shifts. The ranges shifted in different directions: reduction, increased and fluctuations. The ranges of several species have not changed. Three species became extinct.

1. Introduction

The Ural region has overlapping ranges of species from the different geographical fauna complexes: European, Siberian, and Euro-Siberian (Kuznetsov, 1950; Kulik, 1980). It is located on the border between Europe and Asia, and crosses tundra, taiga, and steppe natural zones. At present, the Urals is inhabited by 16 species of carnivores belonging to four families (Canidae, Ursidae, Mustelidae, and Felidae) (Marvin, 1969).

The Urals is known for its well-studied Late Pleistocene and Holocene localities, yielding numerous fossil mammal assemblages, including fossil carnivores. The results of these studies have been presented in a considerable number of papers dedicated either to the description of the history of large mammals of selected areas of the Urals (Kuzmina, 1971, 1975; Smirnov et al., 1990; Kosintsev and Bachura, 2005, 2013, 2014; Ulitko, 2006; Bachura and Kosintsev, 2007; Kosintsev, 2007; Kosintsev and Plasteeva, 2009; Danukalova et al., 2011; Ponomarev et al., 2013; Smirnov et al., 2014) or to the description of the fauna of certain localities (Bachura and Strukova, 2002; Bachura and Plasteeva, 2005; Gimranov, 2009; Kosintsev, 1996; Kosintsev and Orlova, 2002; Petrov, Kosintsev, 2005; Kuzmina et al., 1999; Kuz'mina, 2000; Razhev et al., 2005; Strukova et al., 2006; Svendsen et al., 2010; Ulitko et al., 2011; Yakovlev et al., 2006). In these works, carnivores are studied together with other large mammals. Some articles devoted to the history of certain carnivore species of the Urals have been published (Baryshnikov, 2001, 2007; Gasilin and Kosintsev, 2010; Gasilin et al., 2014; Gimranov and Kosintsev, 2015; Kosintsev and Bachura, 2015; Kosintsev and Gasilin, 2011; Kosintsev, Vorob'ev, 2001; Kuzmina, 2002). The purpose of this paper is to reconstruct the history of carnivore fauna of the Urals in the Late Pleistocene and Holocene.

The most ancient carnivore fossils have been found in the Southern Urals. At the site of Baturino, remains of *Ursus* sp. and *Mustela* (small forma) whose size is close to that of *M. erminea* and *M. nivalis*, have been found in the deposits dating to the middle stages of the Early Pleistocene, while the *Mustela* remains (small form) date to the end of the Early Pleistocene (Stefanosvkiy and Borodin, 2002). The Middle Pleistocene deposits of the Ignatievsky cave contain remains of *Canis lupus* and *Canis* sp. (small form), *Vulpes vulpes*, *V. lagopus*, *Ursus savini*, *Martes* sp., *Gulo gulo*, *Mustela erminea*, and *M. nivalis* (Smirnov et al., 1990). The Late Pleistocene deposits yield other Uralian carnivore remains.

2. The modern situation: some components of the Urals biota

Four regions are traditionally distinguished within the Urals: the Polar (from 67°30′N to 64°00′N), Northern (from 64°00′N to

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59°15′N), Middle (from 59°15′N to 55°54′N), and Southern Urals (from 55°54′N to 51°00′N) (Urals and Pre-Urals, 1968). Although this division is based on the orography of the Ural Range, each of these regions has its specific natural and climatic features. Here, we consider the Middle and Southern Urals in a broad sense, including the mountains and parts of the Trans-Urals peneplain. We do not have data on the carnivore fauna history in the Polar Urals, so we do not consider this region in this article.

The climate of the Northern, Middle, and Southern Urals is temperate continental. The Urals is disposed across the direction of the prevailing westerly winds, so this western slope is moister than the east slope. The territories of Northern and Middle Urals are located in the taiga where pine and spruce dominate. In the south part of the Middle Urals, there is a large proportion of birch in the composition of vegetation. Almost all the mountainous part of the Southern Ural territory lies in the zone of coniferous small-leaf and coniferous broadleaf forests. Pine, birch, linden, elm and oak (in the south) dominate among vegetation. The southern part of the Southern Urals is located in the steppe zone. In the peneplain of the Middle and Southern Urals, steppe vegetation is present. The mountains of the Northern, Middle and Southern Urals are not high so the altitudinal belt in vegetation is not expressed (Gorchakovskiy, 1975).

Fauna of carnivore of the Urals consist of three main complexes: tundra, forest, and steppe. The carnivores which inhabit the entire territory of Urals are *Canis lupus*, *Vulpes vulpes*, *M. nivalis*, *M. erminea*. A typical tundra species is *Vulpes lagopus* which inhabits the Polar Urals and the extremely northern part of the Northern Urals. The forest complex of carnivores inhabits territory of Northern and Middle Urals as well as mountain-forest zone of Southern Urals. This complex is represented by the taiga (*Ursus arctos*, *Gulo gulo*, *Martes zibellina*, *Martes martes*, *M. putorius*, *M. sibirica*, *Lynx lynx*) and taiga-wetland species (*M. lutreola*, *M. vison*, *Lutra lutra*). The species of forest-steppe species (*Meles leucurus)* inhabits the southern Northern Urals, the Middle, and Southern Urals. Distribution of carnivores of the steppe mammal complex is limited by the southern part of the Middle Urals and Southern Urals (*M. eversmanni*) and the Southern Trans-Urals peneplain area (*V. corsac*) (Urals and Pre-Urals, 1968).

3. Materials and methods

We studied data on carnivore species composition from 287 sites located (Table A.1.) in the Urals between 64° and 51°N (Fig. 1). The carnivore remains have been found in localities of several types, i.e. alluvial, swamp, cave, and archaeological localities.

All faunas have been dated. The MIS 5 faunas have been dated on the basis of the species composition of the associated mammal fauna. All the MIS 3 and MIS 2 faunas have been dated using radiocarbon. The MIS 1 fauna has been dated using radiocarbon and archaeological methods. Radiocarbon dates from the Uralian localities were obtained from the bones of several carnivore species (Table A.2.). We use uncalibrated radiocarbon dates.

All radiocarbon dates with indices GIN, LE, LU, SOAN were obtained by conventional radiocarbon dating, while the dates with other indices by accelerator mass spectrometer (AMS) method. Some localities were radiocarbon-dated by both methods. The comparison of radiocarbon dates obtained by different methods for the cave bear bones indicates that sometimes these methods do not give consistent results (Table A.2.). For example, a conventional radiocarbon date of 26980 BP and some AMS dates, ranging between 37190 BP and 47600 BP, were obtained for the Tayn cave. The bones from the Geologov 3 cave were a source for two conventional radiocarbon dates of 27070 BP and 27580 BP, as well as a single AMS date of 38480 BP. The bones from the Zapovednaya cave gave two conventional dates of 28700 BP and 37250 BP and three infinite AMS dates. The general trend is that the conventional ^{14}C dates (i.e., produced by liquid scintillation counting) yield older ages compared to the AMS ^{14}C values from the same strata. Therefore, we will use AMS dates to determine the dates of species extinction.

The available data allowed us to perform the analysis of the species composition of the carnivore fauna for seven chronological periods: MIS 5e, MIS 3, mid-MIS 2 (LGT), late MIS2 (BAIC), early MIS 1 (Preboreal-Boreal, Early Holocene), mid-MIS 1 (Atlantic-Subboreal, Middle Holocene), late MIS 1 (Subatlantic, Late Holocene). Data for the other periods are not sufficient.

In the Late Interglacial (MIS 5e, Eemian, Mikulino, Streletsk, Kazantsevo), the climate was warmer than now, and forest vegetation was more widespread (Mangerud, 1989; Grichuk, 2002; Kühl, Litt, 2003). The mega-interstadial of the Last Glaciation (MIS 3, Middle Weichselian, Bryansk Interstadial, Karginsk Interstadial) with an age of 60–24 ka BP is characterized by relatively warm climate but also by the occurrence of a large number of climatic fluctuations which differ in intensity (Zagwijn, 1974; Vanderberge, 2002; Rasmussen et al., 2006; Svensson et al., 2008; Velichko and Faustova, 2009). As for the end of the Late Pleistocene (MIS 2, Late Weichselian, Late Valdai, Sartan), we have studied two periods that occurred after the Last Glacial Maximum (LGM), i.e. Deglaciation or Late Glacial Transition (LGT; 17–12.4 ka BP) and the Bølling – Allerød interstadial warming divided by short and weak pronounced Older Dryas Stadial (BAIC; Late Weichselian, Late Valdai, Late Sartan; 12.4–10.3 ka BP) (Markova et al., 2008; Faustova, 1994). At the onset of the Holocene, the climate became warmer (Svensson et al., 2008) and the forests spread rapidly (Chotinsky and Klimanov, 2002). The chronology of the localities examined in the paper covers the entire the Late Pleistocene and Holocene, from MIS 5e to late MIS 1. The boundaries of the chronological periods are given as radiocarbon years.

The faunas of separate localities within one area (Northern, Middle and Southern Urals) have been chronologically classified into several groups (Table A.1.). The Southern Urals includes two large geomorphologic units: the mountain region and the Transuralian peneplain. Within the territory of the Southern Urals, all the Late Pleistocene localities are situated in mountains region. Therefore, we consider them as one geographical group. The Holocene localities are situated in both regions. Thus, the localities of each Holocene period form two geographical groups, namely the “mountain” and the “peneplain” groups.

The analysis of the Late Pleistocene and Holocene and modern ranges of each species allowed us to assign all the carnivore species to one of three faunal complexes, European, Siberian, or European–Siberian complex. The ranges of many species cover the territory of both Europe and Asia. The European faunal complex is represented by the species whose range lies mostly in Europe, and its eastern margin in Asia is restricted to the Yenisei River. The Siberian faunal complex contains the species whose range lies mostly in Asia and its western margin in Europe is restricted to the Volga basin. The European–Siberian faunal complex includes the species with their ranges represented mostly in both Europe and Asia. It is difficult to assign the Asiatic black bear (*Ursus tibethanus*) and dhole (*Cuon alpinus*) to a particular faunal complex. At present, their ranges lie entirely in Asia, though their Pleistocene ranges were different. During the Saalian glaciation the Asiatic black bear's range covered central (Musil, 2005–2006; Nagel, Rabeder, 2000) and southern Europe and extended into the Iberian Peninsula (Torres, 1988; Crégut-Bonnoure, 1997). This range apparently remained unchanged until the end of the Eem interglacial and was drastically reduced at the onset of the Weichselian Stage. The dhole's range covered southern and central Europe in the Late Pleistocene (Sommer and Benecke, 2005). The dhole persisted in