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Snowy owl *Nyctea scandiaca* (Aves: Strigiformes) in the Pleistocene of the Ural Mountains with notes on its ecology and distribution in the Northern Palearctic

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A review of the Middle and Late Pleistocene sites containing remains of snowy owl *Nyctea scandiaca* in the Urals, European Russia, Siberia and Europe is given. Analyses of the rodent and bird fauna from the European and Siberian Pleistocene sites allowed to map the southern boundary of the distribution range of snowy owl and to determine the sites that snowy owl visited during seasonal movements to the south. The remains of snowy owl recovered within the rich avifauna in the Ural and Crimean caves are the result of eagle owl hunting activity. It was found that ranges of snowy and eagle owls significantly overlapped in the vast territory of the Middle and Late Pleistocene periglacial steppes. Since the Günz glacial in Europe and Late Würm glacial in Siberia snowy owl had a high predation pressure from the eagle owl. On the Pleistocene-Holocene boundary the ranges of snowy owl and eagle owl separated, following the formation of modern zonal landscapes.

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INTRODUCTION

The presence of snowy owl remains in Pleistocene deposits was considered by earlier researches as an indication of cold climate and was an important element in the reconstruction of paleo-environments (Tugarinov 1937; Voous 1960; Bochenski 1974; Mourer-Chauviré 1975, 1993). Such interpretations can be ascertained only correct whether the species was a year-round residential or seasonal. It is particularly important in cases of recovering bird's remains in the south and west thousands of kilometres off the current breeding range – in the West, Central and south Eastern Europe and south Siberia. Nowadays *Nyctea scandiaca* is an extremely rare victim of *Bubo bubo* (Mikkola 1976) due to their separated ranges. Recovering snowy owl remains in Pleistocene deposits far in the south of its current breeding range reveals the different position and role of snowy owl in ecosystems, its different inter-relations with other nocturnal birds of prey, and particularly, eagle owl. The purpose of the paper is to put together all available data on Pleistocene records of snowy owl, its main predator (eagle owl *Bubo bubo*) and main prey (lemmings) in Palearctic area in general and in Ural mountains in particular. Based on the analyses of collected data, our goal was to reconstruct the breeding range of the Pleistocene snowy owl, the places where species migrated, species ecology, appearance and interrelations with eagle owl.

CHARACTERISTICS OF THE SITES AND CHRONOLOGY

Medvezhya cave

Medvezhya cave (Figs. 2, 3 and 5) is situated 500m from the Pechora River, in the central range of western foothills of the Severnyy Ural at 62°03'N 58°10'E. Its mouth opens 24 m above the ravine bottom and 40 m above the river in the limestone cliff of Iordanskii Ravine coming up to the 55m high terrace. The total length of the cave is about 480 m, making it the longest karst cave in the north Urals (Guslitzer & Kanivets 1965).

The entrance of the cave was excavated between 1960-1962 by Guslitzer & Kanivets (1965) and in 1982-1984 by Guslitzer and Pavlov (Guslitzer *et al.* 1990). The total excavated area was 176 m^2. During excavation of the eastern part of the cave in 1960-1962 the deposits were not screened. Faunal remains were collected by hand sorting (I.E. Kuzmina, pers. comm. 1997). The main postglacial bone-bearing deposits were layers of brown and grey loamy clays, the lower humus horizon in the south-western part and the layer of mixed brown and grey loamy clays in the south sloping part of the excavation area.

During the excavations of 1982-1984 of the western part of the cave (see Fig. 1, Column A) the layer of brown clay (horizon 5) was subdivided into horizons 5A (brown sandy loamy clay) and 5B (brown silty clay). The latter is the oldest deposit of the cave containing faunal remains. All layers were numbered. The greenish-grey sandy, loamy clay (horizon 3) in the western part corresponds to the grey loamy clay layer in the eastern part of the cave. All deposits in the western part of the cave were screened, but in general only mammalian bones were collected. Very few bird bones were added to the existing checklist (Potapova 1990) of the Pleistocene birds from these excavations.

Guslitzer & Kanivets (1965: 79) stated that the horizons of grey and brown loamy clay with gravel, containing the most numerous remains of Pleistocene fauna, were accumulated during the period of relatively warm climate in the last (Paudorff, or Karginskii) interstadial of Würm. Guslitzer *et al.* (1990) assigned horizon 5AB to the cold stadial preceding the Bryansk interstadial of Würm, between 32,000 and 29,000 yBP based on lithic artifacts, the morphology of molars of collared lemming *Dicrostonyx guilielmi* Sanford (Kochev 1984, 1993) and faunal composition. Horizon 5B was believed to have been deposited between 37,000 and 33-32,000 yBP, with formation of the cultural layer between 31,000-35,000 yBP. Horizon 3 and 4 were assigned to the Dunaevskii or Bryansk interstadial, dated 24,000-29,000 yBP (Guslitzer *et al.* 1990). Later, Guslitzer & Pavlov (1993: 180) dated the Pleistocene deposits of Medvezhya cave "to the end of the middle and beginning of the Late Valdai (Würm), between 30,000 and 20,000 BP". However, their results (Guslitzer *et al.* 1990; Kochev 1993) contradicted the conclusions made on the basis of analyses of megafauna, avifauna (Kuzmina 1971; Potapova 1990; Smirnov 1996) and radiocarbon dates (i.e. LE-233). The samples of mammal's bones from the horizon 5B were dated by C14 with the results 18,700 ± 180 yBP (GIN-8399), 17,980 ± 200 yBP (LE-2333), 16,130 ± 150 yBP (LE-3060), and the contact of the horizons 5A and 5B: 13,260 ± 230 yBP (T-13476; P. Pavlov, pers. comm. 1996). Horizon 5A yielded 12,230 ± 100 yBP (LE-3059) and 11,840 ± 50 yBP (GIN-8400), and horizon 3 yielded 12,670 ± 90 yBP (GIN-8398) and 13,810 ± 110 yBP (LU-4486) (Sinitsin & Praslov 1997; Vartanian pers. comm. 2000).

There are some discrepancies in 'overlapping' dates received for the horizon 5A and layer 3. However, the radiocarbon dates of the latter seems quite reliable, since the sample of reindeer bones (GIN 8398) comes from the section 13-14 (Potapova, unpublished data), from non-sloped entrance of the

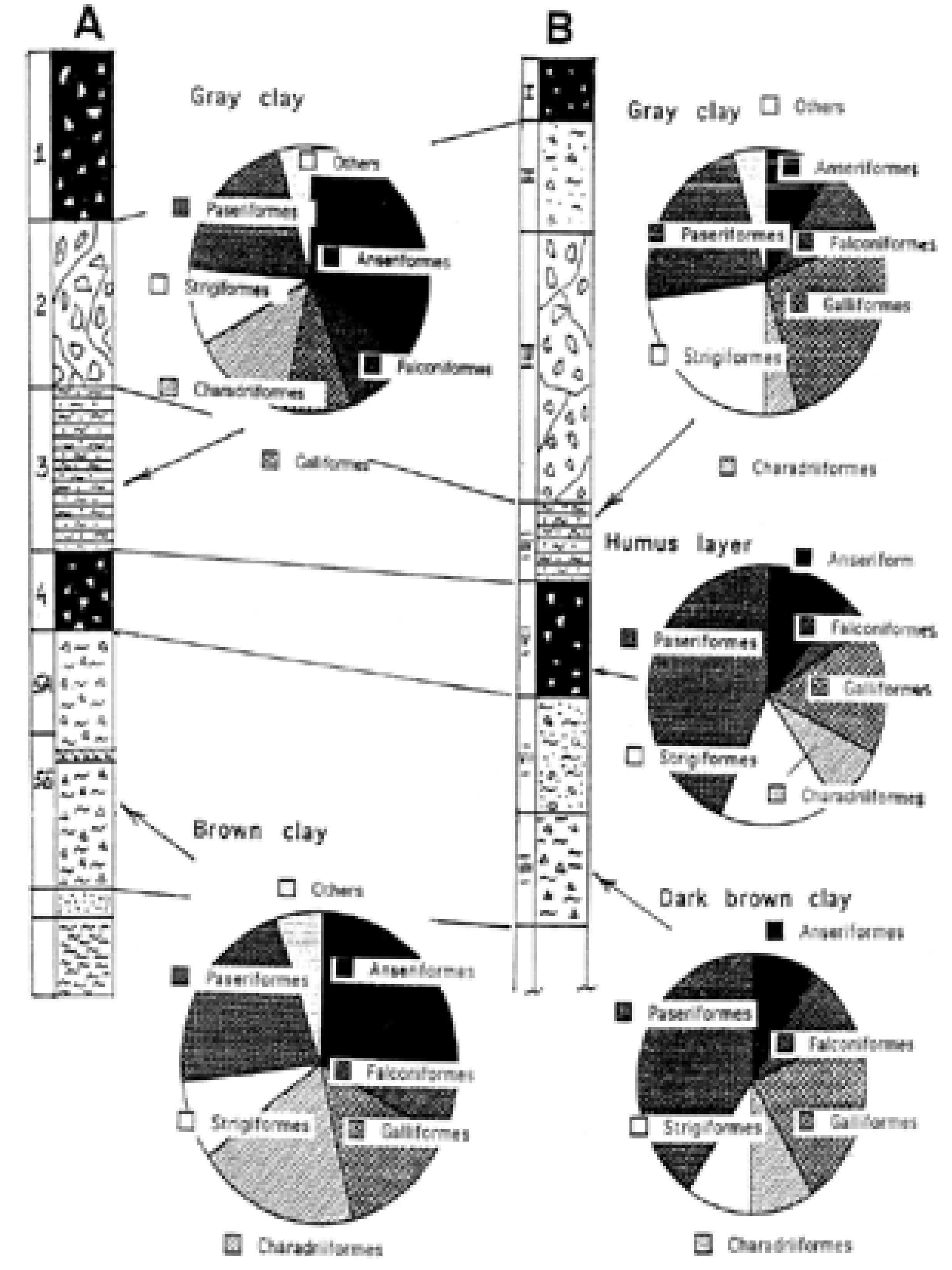

Figure 1 Major taxonomic composition of bird remains (MNI) from the deposits of Medvezhya cave and Grotto Bolshoi Glukhoi. **A** – Medvezhya cave, **B** – Grotto Bolshoi Glukhoi

cave, where the deposits were precisely stratified. Radiocarbon dates for Medvezhya cave received in the 1990's show the lower deposits of the horizon 5 were formed shortly after the maximum cooling of the Valdai glacial (Berezayka and Plyusskij interstadials). The upper part of the horizon 5, layer 4 and 3 were accumulated during the Raunis interstadial, and the terminal cold stadials of the Late Valdai (Lower and Middle Dryas) (Smirnov *et*

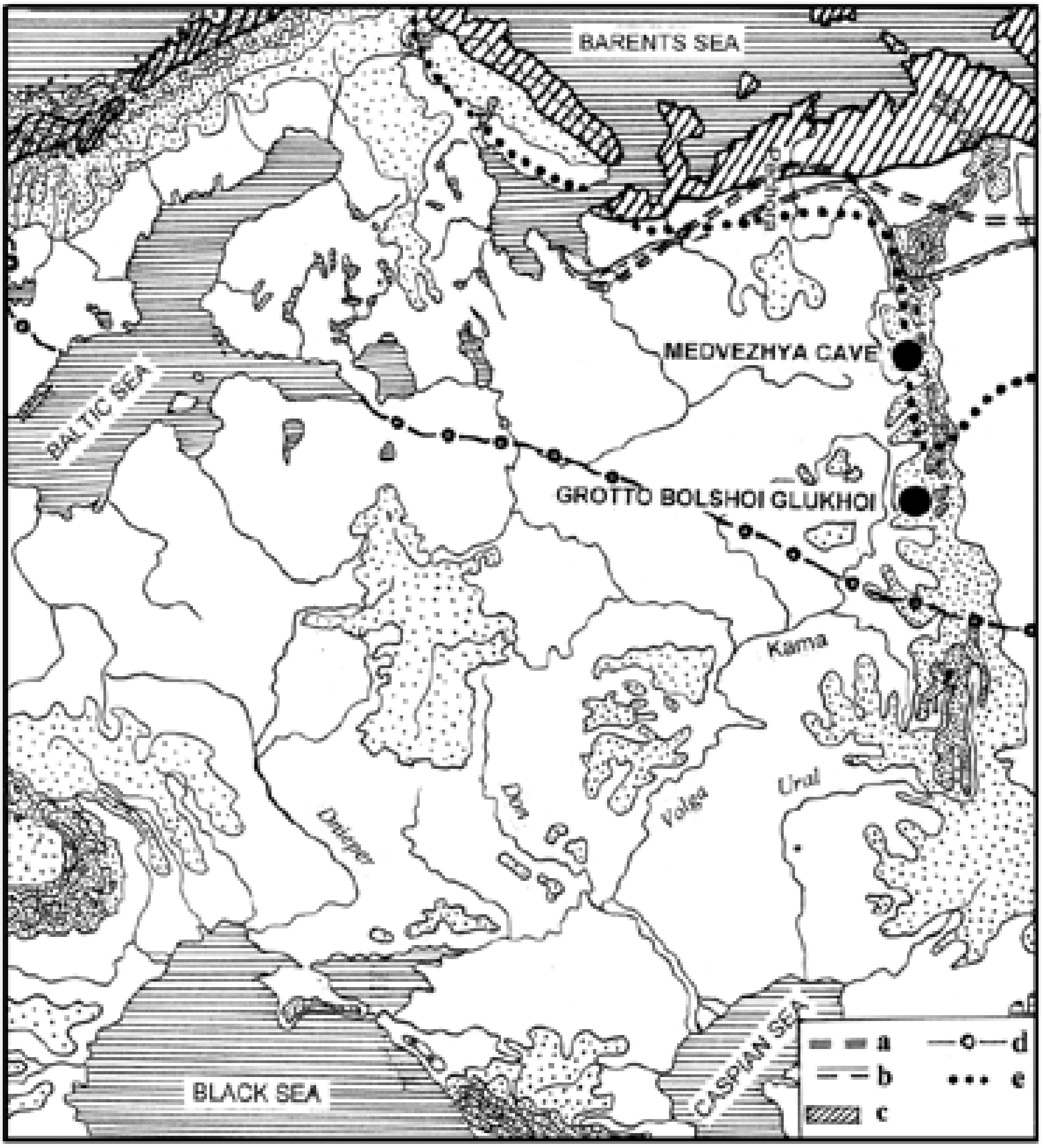

Figure 2 Current ranges of snowy owl *Nyctea scandiaca*, *Lemmus sibiricus* and *Dicrostonyx torquatus* in Europe. **a** – range of Siberian lemming, **b** – range of collared lemming (Markova *et al.*, 1995), **c** – range of snowy owl, **d** – southern boundary of winter occurrences of snowy owl (Snow & Perrins 1998), **e** – southern boundary of permafrost. Dotted areas show uplands and mountains.

Figure 3 Early and Middle Valdai (Würm) sites containing remains of snowy owl *Nyctea scandiaca* (half-shadowed circlets), and lemmings *Dicrostonyx guilielmi* and *Lemmus sibiricus* (asterisks). **1** – Ignatievskaya cave, **2** – grotto Prolom II, **3** – Chokurcha, **4** – Raj cave, **5** - Starun'. **a** – the southern boundary of the range of collared and Siberian lemmings (Markova 1984) in the Russian Plain and Yuzhnyy Ułas, **b** – reconstructed breeding range of snowy owl in the Early and Middle Valdai. Dotted areas shows uplands and mountains.

al. 1999b). Avifauna from horizon 3 characterises the cool and humid climate in the Severnyy Ural (Potapova 1990). New studies of morphological development of upper molars in *Dicrostonyx* species (13 stages) in Ural Mountains, Russian Plain and west Siberia, from the Middle Pleistocene to the recent times, gave a reliable microfaunal chronology of Ural's caves (Smirnov 1999a).

Deposits of layers 5 and 3 yielded a rich large mammal fauna of Late Pleistocene 'mammoth assemblage' with high predominance of Pleistocene hair *Lepus tanaiticus*, arctic fox *Alopex lagopus* , reindeer *Rangifer tarandus* and cave bear *Spelaearctos spelaeus* (Kuzmina 1971). Among micromammal remains the most numerous were Pleistocene collared lemmings *Dicrostonyx gulielmi*, narrow-skulled vole *Microtus gregalus*, steppe pika *Ochotona pusilla* , and Siberian lemming *Lemmus sibiricus* (Sukhov 1976; Guslitzer *et al.* 1990). Among birds the grouse (genus *Lagopus*) was predominant in all horizons of the cave (Guslitzer & Kanivets 1965; Potapova 1986, 1990). The most numerous remains of birds come from the mixed 5A and 5B sub-horizons.

Grotto Bolshoi Glukhoi

Grotto Bolshoi Glukhoi (Figs. 2, 3 and 5) is situated in the western foothills of the Sredniy Ural at 57°30'N; 57°E, about 400 km south of Medvezhya Cave. The grotto opens in a karst wall at several hundreds meters from the Chusovaya River, the left tributary of Kama River, 32 m above the water surface. Guslitzer & Pavlov (1987) excavated 40 m^2 in 1985 and 1986.

The horizons (Fig. 1 column B) of grey-brown (VI) and brown (VII) loamy clay deposits of the grotto have not been radiocarbon dated (Guslitzer & Pavlov 1987). The

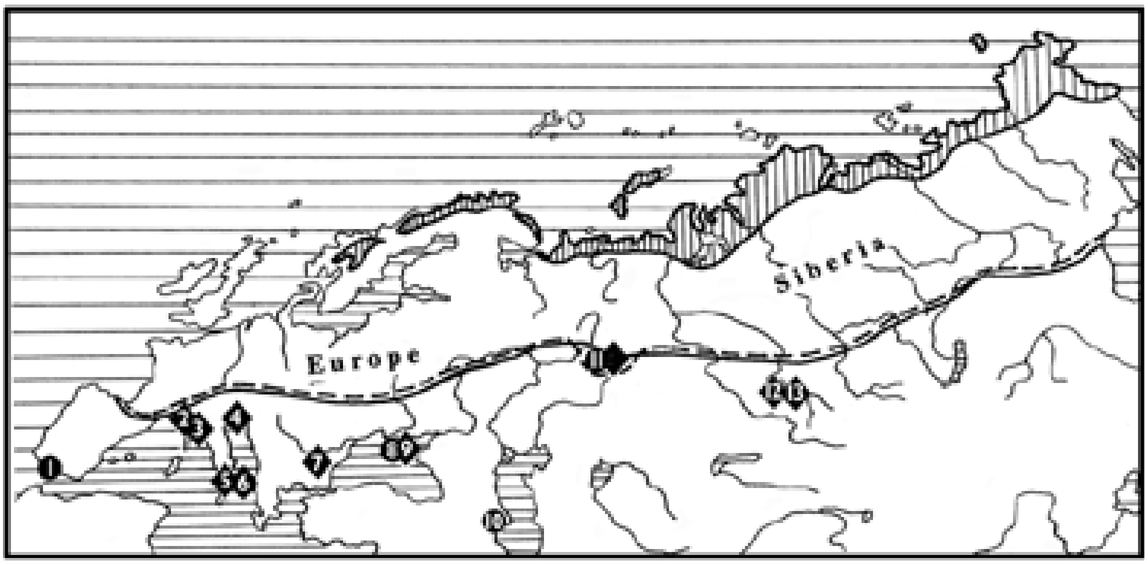

Figure 4 Locations of the most southern sites with remains of snowy owl, modern range of *Nyctea scandiaca* (vertical shaded area) (Voous 1960, Snow & Perrins 1998), and southern boundary of arctic mammoth faunal assemblage in the Late Valdai (Baryshnikov & Markova 1992). **1**-Gorham's cave, **2** – Arene Candide cave, **3** – grotto Colombi, **4** – Covolo di Trene site, **5** – Cardamone site, **6** – grotto Romanelli, **7** – Kozarnika & Devetashka caves, **8** – Chokurcha cave & Prolom site II, **9** – Adzhi-Koba cave, **10** – Binagady site, **11** – Ignatievskaya cave, **12** – Okladnikova cave, **13** – Denisova cave. Circlets – Early and Middle Valdai, and diamonds – Late Valdai sites. Dashed line – reconstructed southern limits of breeding range of snowy owl in the Late Valdai.

humus deposits or 'red layer' (horizon V) yielded a radiocarbon date of 10,607 ± 158 yBP, corresponding to the boundary of Late Dryas and Preboreal (Smirnov 1993, 1995). However, the radiocarbon date run on reindeer bones from horizon IV yielded a result of 15,560 ± 130 yBP (LU-4487) (Vartanian, pers. comm. 2000). There are two radiocarbon dates from the lower horizon IX or cultural layer 6. The date for the upper part of horizon IX has indicated an age greater than 33,900 yBP. (LE-4201; Guslitzer & Pavlov 1993), and the other was as 38,200 ± y900 BP (GIN-8404). Dr. L. Sulerzhitsky (Geological Institute, Moscow) ran the second radiocarbon date on a sample of heavily fragmented cave bear bones, which was submitted for analyses by the author in 1996. Assigning this radiocarbon date to layer VI by Sinitsin & Praslov (1997) was probably a misprint or mistake.

There are nine species of megafauna in horizon VI and 15 species in horizon VII in Grotto Bolshoi Glukhoi. Species composition from those horizons have very slight difference from each other and consist of the same dominant species: cave bear, *Spelaearctos spelaeus*, Pleistocene hare *Lepus tanaiticus*, reindeer *Rangifer tarandus*, arctic fox *Alopex lagopus*, wolf *Canis lupus*, Ural's horse *Equus uralensis*, bison *Bison priscus*, and mammoth *Mammuthus primigenius*. (Kuzmina & Sablin 1991).

Chronological correlation of the sites

Artefacts recovered from horizon 5, of which sub-horizons were not divided in 1960-1962 (see Fig. 1 Column A and B) in Medvezhya Cave were believed to have the cultural affinities to artefacts in the fifth cultural layer of Grotto Bolshoi Glukhoi. They were classified as belonging to the middle Ural variant of upper Paleolithic cultures of northeastern Europe (Guslitzer & Pavlov 1993). Microfaunal analyses and the morphology of collared lemming show the correspondence of the horizons VI and VII in Grotto Bolshoi Glukhoi to the layer 5 (brown loamy clay) of Medvezhya cave (Guslitzer & Pavlov 1987). Analyses of avifauna assemblages support this conclusion (see Potapova 1990, 1991; Potapova unpublished data).

Lower humus horizons in Medvezhya cave (layer 4) and Grotto Bolshoi Glukhoi (horizon V) probably correspond to each other, and were formed in relatively temperate condition in a terminal phase of the Late Pleistocene. However, the conditions and rate of deposits and bone accumulations were different in these caves. In the high latitude of Ural Mountains the humus loam layer was very thin and therefore yielded a small amount of microfauna, while in the Sredniy Urals it was thicker and contained numerous rodents and bird bones (see Sukhov 1976, Guslitzer & Pavlov 1987, Smirnov 1995). On the basis of avifauna analyses, horizon IV of Grotto Bolshoi Glukhoi corresponds to layer 3 in Medvezhya cave (Potapova 1990, Potapova unpublished data), which was recently confirmed by newly received radiocarbon date from Grotto Bolshoi Glukhoi. However, the only radiocarbon date received for the humus layer in Grotto Bolshoi Glukhoi contradicts the ages of deposit sequences and microfaunal analyses in comparable caves. According to the radiocarbon date the humus horizon is younger than not only the humus horizon 4 of Medvezhya cave, but also younger than its overlaying grey clay horizon 3. Probably the radiocarbon sample was taken from mixed layer between horizon V and horizon III, where these horizons are in touch (see Guslitzer & Pavlov 1987, Fig. 3). More radiocarbon dates are needed to confirm the results of faunal analyses.

MATERIAL AND METHODS

Remains of *Nyctea scandiaca* from Medvezhya cave and Grotto Bolshoi Glukhoi are stored in the Zoological Institute in St. Petersburg, Russia. Comparative collections of skeletons in the Zoological Institute, St.

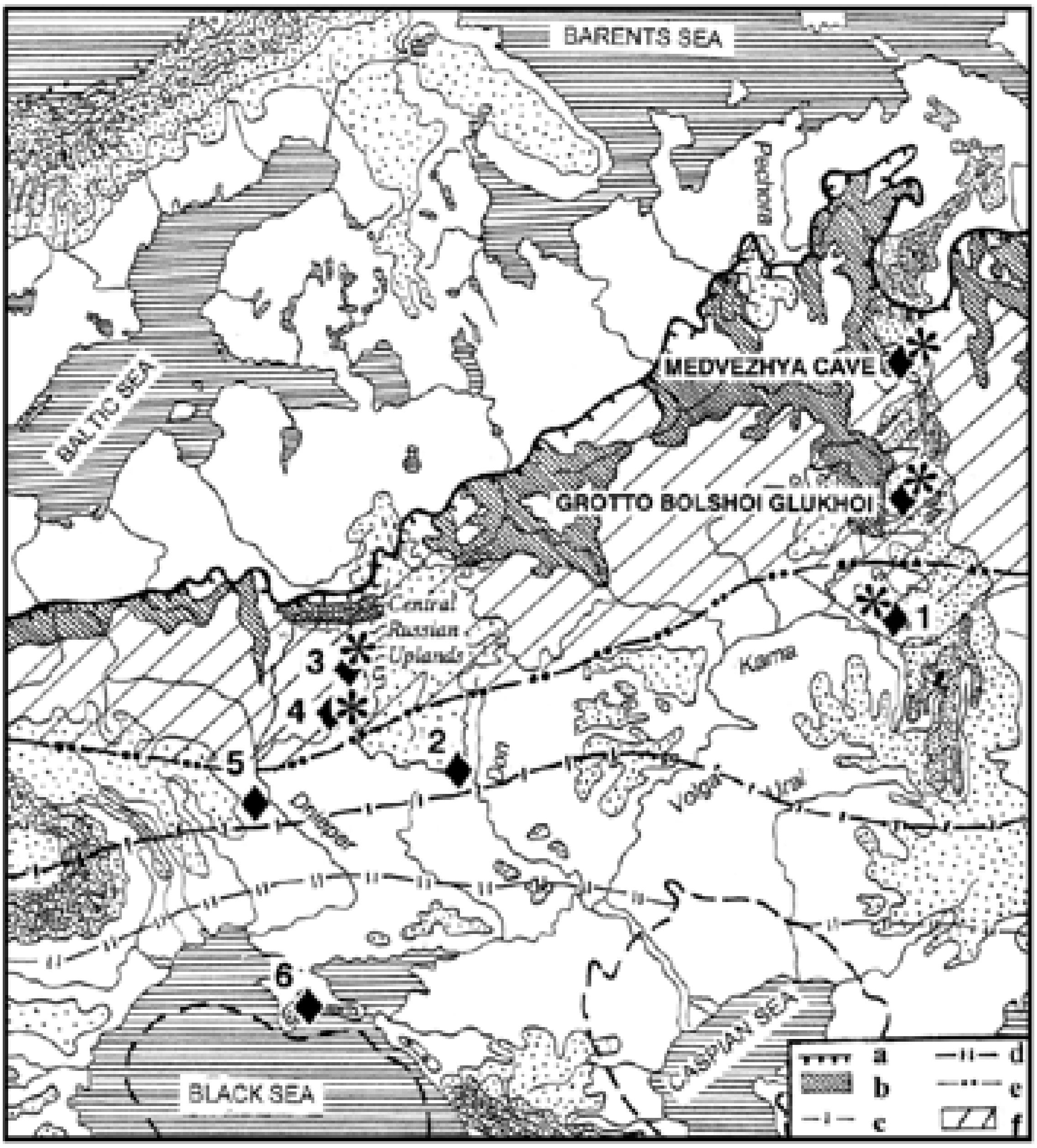

Figure 5 Late Valdai (Würm) sites containing remains of snowy owl *Nyctea scandiaca* (diamonds) and lemmings (asterisks). **1** – Ignatievskaya cave, **2** – Kostenki I (layer 1) and Kostenki XIV (layer 3) sites, **3** – Yudinovo site, **4** – Mezin site, **5** – Mezhirich site, **6** – Adzhi-Koba cave. **a** – boundary of ice sheet (Velichko et al. 1984), **b** – pro-glacial basins (Grosswald 1980, Velichko *et al.* 1984), **c** – boundary of continuous permafrost, **d** – boundary of discontinuous permafrost (Baulin & Danilova 1984), **e** – southern boundary of the lemming range and arctic sub-assemblage of mammoth faunal assemblage (Baryshnikov & Markova 1992), **f** – reconstructed breeding range of snowy owl in the Late Valdai. Dotted areas show uplands and mountains.

Petersburg, in the Paleontological Institute, Moscow, Russia, and in the Smithsonian Institution, Washington D.C., USA were used for identifications. Measurements of bones were taken using the guides of Von den Driesch (1976) and Mourer-Chauviré (1975). Anatomical terms and their abbreviations are given in accordance with Baumel & Witmer (1993) and Weesie (1988). Locations of the sites on the maps follow Beregovaya (1960), Markova *et al.* (1995), and Smirnov *et al.* (1999). Names of geographical localities were used in accordance with the Times Atlas of the World (1993) and adopted spelling was made from Atlas Mira (Sergeeva 1982). The boundaries of ice sheets, proglacial basins, permafrost and coastlines follow Grosswald (1980), Velichko *et al.* (1984) Faustova (1984) and Baulin & Danilova (1984).

RESULTS

Taphonomy

Snowy owl never uses shelters or caves for roosts or nests (Mikkola 1983; Snow & Perrins 1998) and must have been brought to the caves by predators. Excavated bones of snowy owl did not show signs of butchering, burning or other signs of human activity. Among more than 6774 diverse bird remains from Medvezhya cave, no tooth punctures, fractures and other damage by carnivores (Bickart 1984) were observed. One whooper swan (*Cygnus cygnus*) distal tibia had cut marks due to probable butchering by man (Potapova, unpublished data).

Bones of eagle owl were not recovered from both caves. Indirect indication at eagle owl nesting or resting in the caves gives the faunal composition of birds and small mammals. There were found numerous specimen remains of large (Anseriformes -Anserinae) and especially middle sized (Anseriformes - Anatinae, Galliformes - small Tetraonidae, Falconiformes, Strigiformes) birds, among which the specimens of willow grouse (*Lagopus lagopus*) and rock ptarmigan (*Lagopus mutus*) were predominant (Potapova 1990, 1991). The two latter formed up to 79% (Grotto Bolshoi Glukhoi, horizon VII) to 99% (Medvezhya cave, hor. 5) of Galliformes specimens recovered from the deposits (Fig. 1). Large and middle-sized birds are common in eagle owl diet including diurnal (Falconiformes) and nocturnal (Strigiformes) birds of prey and a large variety of the latter is very characteristic prey of particularly eagle owl (Mikkola 1976, 1983). Species of grouse form the major bird food of the eagle owl in winter in northern taiga of Ural, and their proportions in owl's pellets corresponds to their availability in the area (Teplov 1948). Nowadays, the northern Ural's taiga species hunts predominantly capercaillar (Teplov 1948), but in the Late Valdai, approximately between 19,000 - 12,000 yBP, it fed mostly on numerous willow grouse on the vast open territory adjacent to the wooded western slope of Severnyy Ural and Upper Pechora basin.

Other species of owls, particularly tawny owl (*Strix aluco*) might have used the cave contributing to accumulation of passerines in the deposits and thus, reducing the proportion of large sized bird's specimens. This may explain the relatively low ratio of raptors (from 2% to 13% of Falconiformes and Strigiformes together) in avifaunal compositions of Medvezhya cave and Grotto Bolshoi Glukhoi coming from eagle owl pellets. Predators normally form as much as 23-36% of the total bird food of eagle owl. This is considerably greater than their record of bird populations, because eagle owls do not tolerate other predator birds in their territory and have a greater hunting pressure on them (Mikkola 1983).

Hare (*Lepus tanaiticus*) was predominantly represented in both caves (Kuzmina 1971; Kuzmina & Sablin 1991) and by fore limb bones, with a low ratio of hind limbs, and lacking skulls and mandibles (Potapova unpublished data). It is known that eagle owl hunts hare and eats it on the spot, leaving behind the uneaten head and distal hind limbs (Teplov 1948). However, an entire killed hare can be brought to the nest (Egorov & Labutin 1959).

At Medvezhya cave, the clustered distribution of bird remains matched the places with high density of rodents. It is accounted for disintegration of owl's pellets in particular roosting or nesting places. It probably was a coincidence that microfaunal remains were also associated with megafauna bones brought to the cave by man, concentrating around a former drip line of the cave's roof (Potapova 1990). It is not surprising that bones of eagle owl were not found in the cave's deposits. In many sites of Europe, where records of eagle owl were absent, snowy owl remains were found together with willow grouse and ptarmigan, which were proved to have been accumulated by eagle owl (Mourer-Chauviré 1975; Brodkorb 1971; Cassoli 1980; Baales 1992).

As it can be seen from Figure 1, the eagle owl primarily hunted willow grouse and ptarmigan which were the most abundant species in both site areas (Potapova 1990). The overrepresentation of distal extremity bones (carpometacarpals, tarsometatarsals) over bones from proximal extremities (humerus, femur) and underrepresentation of pelvic girdle, cranium and mandibles in grouse are indicators to non-human, but owl activities in caves in the Pleistocene (Brain 1982; Mourer-Chauviré 1979, 1983; Baales 1992). Patterns of grouse bone fragmentation (Bochenski 1993) revealed the different activity of eagle owl. It used Medvezhya cave primarily for nests, while Grotto Bolshoi Glukhoi mostly served as a roosting shelter (Potapova, unpublished data).

SYSTEMATICS

Nyctea scandiaca (LINNAEUS, 1758)

Material:
Medvezhya cave
Layer 5 - 1 dex. prox. cor.; 1 dex. dist., 1 prox. ulna; 2 sin. dist. tibia; 1 whole sin. and 1 prox. and 1 dist. sin. tmt. Total - 8/2.
Layer 3 - 1 dex. dist. tibia. Total - 1/1.
Mixed layers 5 and 3 - 1 sin. cor. with broken ends. Total - 1/1.

Grotto Bolshoi Glukhoi
Horizon IV - 1 dex. 1phal. III dig. Total - 1/1.

The bone measurements are given in Table 1. Bones of snowy owl differ from eagle owl by smaller sizes (Mourer-Chauviré 1975: tables 21, 22) and less bulkiness. Except for the width of the tarsometatarsal diaphysis, other non-broken bones of snowy owl from Medvezhya cave match females of the modern subspecies from Europe and North America and are smaller than the Middle Pleistocene *N. scandiaca gallica* MOURER-CHAUVIRÉ (Table 1).

Current distribution range and biology
The breeding range is circumpolar and lies within the tundra zone in open biotope habitats from sea level to uplands from Scandinavia to Eastern Siberia and Northern America. During breeding time in years when lemmings are abundant, a hunting territory can be as small as 0.75 km^2 (Mikkola 1983). Being a predominantly sedentary species, snowy owl often makes nomadic fall-winter migrations to the south, normally far down as 60° N, depending on food availability (Snow & Perrins 1998). In some winters it reaches Crimea, Caucasus, and the Kazakhstan steppes in Russia and even the southern Russian Far East, the Mongolian steppes and northern China (Pukinskii 1977; Mikkola 1983; Snow & Perrins 1998).

Table 1 Measurements of the Pleistocene and recent bones of snowy owl *Nyctea scandiaca*. Symbol * = data from Mourer-Chauviré (1975). Some fossil bones have damaged epiphysis and symbol > means that the actual size of the bone is larger. Abbreviations of measurements follow Von den Driesch (1976).

Ulna			Tibia			Tarsometatarsus	
Did	4	5	Bd	Dd	Sc	Bp	SC
Medvezhya Cave, *Nyctea scandiaca*							
n=1			n=2			n=1	n=2
13.7	>12.1	>12.8	>16.6, >16.2	>11.3, >12.7	7.2, -	17.3	10.1, 10.6
Saint-Esteve, *Nyctea scandiaca gallica**							
means							
-	n=6		n=4	n=4	n=6	n=2	n=7
-	13.6	13.6	18.0	14.4	8.1	18.3	10.1
Modern *Nyctea scandiaca*, females*							
-	n=8		n=8			n=7	
-	13.4	12.8	16.8	14.3	7.3	17.9	9.9
Modern *Nyctea scandiaca*, North America, n=3							
means							
14.3	12.1	13.2	17.0	14.3	9.5	18.0	9.9
limits							
14.2-14.7	11.5-13.1	12.9-13.8	16.5-17.3	14.0-14.7	9.2-9.8	17.6-18.4	9.7-10.4

In modern times snowy owl is a rare visitor at Pechoro-Ilych State Reserve, located just north of Medvezhya cave. Single, exhausted, males were observed and hunted in fall-winter in the Ilych River valley in Pechoro-Ilych State Reserve in the 1930ies and 1940ies (Teplova 1957). Remains of snowy owl bones never have been reported from eagle owl pellets on the territory of the Reserve (Teplov 1948).

Records in the Pleistocene

The earliest findings of snowy owl come from a Günz site in Bourgade (MNQ 20), in France. Other remains are known from Mindel (grotto L'Escale), Mindel-Riss (Orgnac 3), Riss (L'Aven 1 des Abimes de la Fage, grotto Lazaret), early Riss-Würm (grottos de la Carrière, Lherm and Tuteil) and early Würm (grotto Malarnaud) sites in southern France and the French Pyrenees (Mourer-Chauviré 1975, 1980a, Vilette 1983, Clot & Mourer-Chauviré 1986). Snowy owl remains were also recorded in Starun' tar pit (Early Würm), Poland (Burchak-Abramovich 1975). The larger-sized subspecies *Nyctea scandiaca gallica* MOURER-CHAUVIRÉ, 1975 was described from the Mindel deposits of grotto de Escale à Saint-Esteve-Janson, in France (Mourer-Chauviré 1975). Identified as *N. scandiaca* aff. *gallica* in Le Morin à Pessac-sur-Dordogne, this subspecies presumably locally survived through the maximum Würm glacial in France (Mourer-Chauviré 1975).

Middle Pleistocene (Acheulean) records of the species are absent in Spain, but known there from Late Würm (Magdalenian) fauna in Erralla cave (Mourer-Chauviré 1980b, Eastham 1985). In Central Europe, Middle Pleistocene findings of snowy owl bones are known from the Hunas site (late Middle Pleistocene) in Germany (Janossy 1983).

There are few Early Würm (I-II) sites containing *N. scandiaca* remains (Mourer-Chauviré 1975; Janossy 1986). However, there are numerous Late Würm (about 30,000 - 10,000 yBP) localities in West, Central and East Europe with recorded snowy owl remains (Brodkorb 1971; Mourer-Chauviré 1975, 1977, Heinrich 1977, Cassoli 1980, 1992; Delpech 1983; Vilette 1983, 1984; Clot & Mourer-Chauviré 1986; Janossy 1963, 1986; Bochenski & Tomek 1994; see also brief review of Pleistocene sites with snowy owls remains: Boev 1998). Recovered bones of *Nyctea scandiaca* were abundant only in southwestern France (Le Morin and some other localities; Mourer-Chauviré 1975, 1983; Tyrberg 1998).

There are no Pleistocene records of snowy owl in Scandinavia (Tyrberg 1998). Species remains are scarce in the Pyrenean Peninsula and very rare in the British Islands in the Late Pleistocene (Bouchud 1952; Eastham 1985; Elorza 1990, 1993). There is only one record reported from the Devensian Glaciation deposits in Kent's cavern, south Devon in southwest Britain (Harrison 1987). There are unconfirmed records (Sardinia: Milne-Edwards 1871; Brodkorb 1971) or reports on snowy owl remains in the Pleistocene deposits of Mediterranean Islands (Weesie 1984, 1988; Florit *et al.* 1989; Salotti et al. 1997; Segui *et al.* 1998; Alcover *et al.* 1992; Bonifay *et al.* 1998; Lax 1999).

The most southern findings of snowy owl in Europe, excluding Russia, were in Gorham's cave at Gibraltar (Fig. 4 no. 1) (Mousterian: Eastman 1968), the Cardamone site and grotto Romanelli in Puglia, south Italy (Fig. 4 no. 5 and 6) (Late Pleistocene) (Cassoli 1980) and Devetashka and Kozarnika caves (Fig. 4 no. 7) in Bulgaria (Boev 1999). The date of the latter was widely estimated as 80,000 - 16,000 yBP (Boev 1998).

Pleistocene findings of snowy owl in European Russia and adjacent territories were recorded in several Late Paleolithic localities. These remains were found in Kostenki – 1 (loess layer 18,230 - 24,100 yBP), Kostenki XII (layer 1: 23,600 - 26,300 yBP), Kostenki XIV (layer 3: 14,300 yBP) (Potapova, unpublished data) on the Don River, in Yudinovo (Fig. 5 no. 3), Mezin and Mezhirich sites (Fig. 5 no. 4 and 5) in Dnieper River basin (Zubareva 1950 Umanskaya 1975, 1978, Korniets et al. 1981), and Adzhi-Koba cave (Fig 4, no. 9, Fig. 5 no. 6) in the Crimea Peninsula (A.V. Panteleev, pers. comm. 1999). Other Late Pleistocene remains were previously reported from Medvezhya cave in Severnyy Ural (Potapova 1990) and in Ignatievskaya cave (Fig. 3 no. 1, Fig. 4 no. 11, Fig. 5 no. 1) in Yuzhnyy Ural (excavation area I, layer 2, Potapova unpublished data). In Eliseevichi and Berdysh sites, located in the north Dniepr basin, single bones of *Bubo bubo* were identified (Vereshchagin & Kuzmina 1977; Umanskaya 1975, 1978; Soffer 1985). It is unlikely that eagle owl was recovered along with remains of predominantly arctic and open biotope mammals in these sites. There is a possibility that these bones belonged to snowy owl.

Records of snowy owl in the Early and Middle Würm (Mousterian) are rare and known only from archeological sites in Ignatievskaya cave (Fig. 3 no. 1, Fig. 4 no. 11, Fig 5 no. 1) in Yuzhnyy Ural (test unit V, layer 8; Potapova, unpublished data), grotto Prolom II and Chokurcha cave (Fig. 3, no. 2 and 3) in Crimea Peninsula (Baryshnikov & Potapova 1988, 1992). The coracoideum from Chokurcha cave was believed to be of an eagle owl, *Bubo bubo* (Voinstvenskii 1967; Baryshnikov & Potapova 1988, 1992). Another Middle Pleistocene and the most southern finding of *Nyctea scandiaca* was reported from the Binagady site (Fig. 4, no. 10) (Early Würm) in Eastern Transcaucasia (Burchak-Abramovich 1975). This is the only Pleistocene record of snowy owl recorded in the Caucasus.

In south Siberia the remains of snowy owl in the Pleistocene are scarce. Few bones were found in the Late Pleistocene layer 3 (galley 1) in Okladnikov's cave (Fig. 4, no. 12, 51°57'N; 84°82'E), and one bone in layer 9 (section IV, Sartanian stage) of Denisova cave (Fig. 4 no. 13, 51°23'N; 85°05'E) in the northern foothills of the Altai Mountains

(Martinovich 1990; Panteleyev 2000). *Nyctea scandiaca* was also identified from Late Pleistocene (about 13,500 yBP) deposits in Tonnelnaya cave, vicinity of Krasnoyarsk (Ovodov & Martynovich 1999). Snowy owl remains have never been found in other Mousterian and Late Paleolithic faunal assemblages in the upper Yenisey and Angara River Valleys (Afontova Gora I-IV, Malta, Pereselencheskii Punkt, Kashtanka cave I, Aidashinskaya cave, Kokorevo II, Tashtyk I, grotto Dvuglazka and Krasnyi Yar sites), upper Lena River valley (Bolshoi Yakor 1) and Transbaikalia (Ust-Kyakhta 17, Zasukhino, Khariyaska 2 and others) (Gromov 1948; Tugarinov 1932; Martinovich 1990, 1991; Ovodov & Martinovich 1992, 1999; Derevyanko *et al.* 1998).

RESULTS AND DISCUSSION

Distribution range and migrations

Bone morphology of the Late Pleistocene snowy owl is similar to that of the recent owl, which lets us assume that the fossil species might have had quite similar biology, behaviour and hunting strategy. Today, the breeding range of the snowy owl lies in the vast open biotopes of the northwestern arctic coast of Scandinavian Peninsula, northern European Russia and arctic Siberia in the Palearctic. In low lemming winters, snowy owl migrates to the south reaching middle latitudes (53º-55º N) of European Russia (Fig. 2d), and rarely gets to northern Poland, open plains in Germany, Southeast Russia and northern China and Mongolia (Pukinskii 1977; Snow & Perrins 1998). Generally, the species breeding area (Fig. 2c) matches the range of lemmings (*Lemmus lemmus*, *Lemmus sibiricus* and *Dicrostonyx torquatus*) (Figs. 2a, b), which form the basic food of the snowy owl in the Northern Palearctic. The ranges of two latter species extends southward beyond the snowy owl breeding range, matching the range of few major plants, among which are *Alnaster fruticosus* (for *Dicrostonyx torquatus*), *Selaginella selaginoides* (for *Lemmus sibiricus*) and *Betula nana* (Markova *et al.* 1995), pertaining in their turn to and laying within the permafrost boundaries (Fig. 2e). In the Palearctic mainland, and particularly in Siberia, where the population is flourishing, the species breeding success is heavily dependent on lemmings (Osmolovskya 1948; Pitelka *et al.* 1955; Watson 1957; Dorogoy 1981, 1983, 1987, 1995; Hume 1997). Lemmings are easily hunted under tussock and moss vegetation in tundra, and are preferably taken instead of reticent burrowing rodents (i.e. genus *Microtus*), in areas where the permafrost does not reach the surface. In northern Europe, where the range of lemmings is small (Norway), or where lemmings are absent (Iceland, Fetlar Island), the snowy owl is more dependent on other voles, rabbits and birds (Mikkola 1983; Hume 1997).

Snowy owl population density depends on the landscape type and development of grass vegetation (Egorov 1971). It is low in lowlands with marshy polygonal and tetragonal moss tundra - the biotopes preferred by the Siberian lemming. The density of snowy owl in well drained territory and in complex dry landscapes with ridges, mounds, hillocks and hills with short vegetation, where the species has a good view over the surrounding countryside can be twice as high (Egorov 1971; Mikkola 1983). The latter biotopes are preferred by the collared lemming. This could be the factor explaining why collared lemming occurs more frequent in modern snowy owls diet than Siberian lemming (see Krechmar & Dorogoy 1981; Pukinskii 1977).

In winters with low lemming density snowy owl moves to the south, switching its diet to open biotopes voles (*Microtus* and *Clethrionomys* in Scandinavia: Mikkola 1983) and birds. The latter increase significantly compared to the owl's summer diet (Mikkola 1983). Willow grouse and ptarmigan are the primary food for snowy owl in the northern taiga of Siberia during late fall and winter. During this season snowy owls follow tundra grouse, making seasonal movements towards the south (Krechmar 1966; Skrobov 1975; Pavlov 1975; Perfiliev 1975; Pukinskii 1977; Voronin 1978). The same pattern of year-round snowy owl life style probably occurred at least in the Late Pleistocene.

The southern ranges of snowy owl were considerably shifted to the south in the Early and Middle Pleistocene in Western Europe. The Mindel site l'Escal is known to have yielded sub-adult bones of snowy owl, thus directly giving evidence of nesting as far south as the Durance Valley (Mourer-Chauviré 1975, 1983).

However, there are no records of snowy owl on the Russian Plain, Crimea Peninsula, Ural Mountains, or Siberia earlier than the Valdai glaciation. The facts that remains of snowy owl were absent from the rich late Valdai fauna of Afontova Gora on Upper Enissei (numerous *Lagopus lagopus* remains), and were not recovered either among bird remains in the Denisova cave in the Northern Altai mountains (dated Würm 282000 ± 56 KA yBP; *L. lagopus* remains are dominant), indicate that snowy owl penetrated to those regions from the West through Central Europe after the Mikulino (Eemian) interglacial, or that it was a possibly extremely rare species in south Siberia during the preceding Riss glaciation. In the Russian Plain, however, deposits yielded earliest tundra-dwelling rodents - *Dicrostonyx simplicior*, *Lemmus sibiricus*, *Microtus gregalis* (Markova 1998), and the potential findings of snowy owl could still be expected as early as the Dnieper (Riss) glacial.

In the Middle and Late Valdai the southern ranges of lemmings were shifted south as far as 48°N to 52°N in the Russian Plain, embracing the valleys and divides of Upper Ural, Kama, and Dnieper Rivers (Agadjanian 1973, 1976: Markova 1984, Markova *et al.* 1995; Markova 1998). In the Early Würm the snowy owl most likely bred in the northern Carpathian foothills (found in Raj cave Fig. 3 no. 4, Poland; Bochenski 1974). It was migratory to the Bukk Hills area in the Carpathian basin, the southern foothills of the Carpathians north range, where remains of *Nyctea scandiaca* were recovered at Lambrecht cave, but lemming remains were not recorded (Janossy 1963, 1986). In the Early Würm snowy owl obviously was a seasonal visitor in the Pyrenees Peninsula, west of the Pyrenees range (Gorham's cave, Fig. 4 no. 1), southern France sites (i.e. le Lazaret) and in the Balkans (Kozarnika and Devetashka caves, Fig. 4 no. 7).

In the Middle Valdai stage, the only sites containing both snowy owl and lemming remains were Ignatievskaya cave (Fig. 3 no. 1, Fig. 4 no. 11, Fig. 5 no. 1) in Yuzhnyy Ural. The low ratio of *Dicrostonyx* in the latter, where, however, narrow-skulled voles *Microtus gregalis* predominated (Smirnov *et al.* 1990), makes the site to be the most southern boundary of the snowy owl breeding range, which was, probably sporadic or rare, in the western foothills of Ural Mountains (Fig. 3). The findings of *Nyctea scandiaca* in Mousterian sites of Crimea Peninsula (Prolom II, Chokurcha, Fig. 3 no. 2 and 3), and Transcaucasia (Binagady tar site, Fig. 4 no. 10), far south off the 'lemming remains' boundary, is evidence that the species was migratory on those territories, and presumably bred in the northern part of Russian Plain. The Raj and Starun' sites (Figs. 3, 4, 5) in Poland, located far north from the southern 'lemming boundary', were areas where the snowy owl might have bred.

During the Late Valdai (Würm) stage the southern range of lemmings followed the southern boundary of the arctic sub-assemblage belt of Mammoth tundra-steppe mammals (Baryshnikov & Markova 1992). The southern limits of the snowy owl's breeding range in the Upper Pleniglacial of the Last Glaciation could not go further south than the southern boundary of the arctic sub-assemblage. It roughly went from the northeastern foothills of the Pyrenees Mountains through the southern Massif Central in France, north of the Alps and Carpathians, and through the Central Russian Uplands to Sredniy Ural. In Siberia the boundary might have closely followed latitude 56°N - 60°N (Fig. 4).

The remains of species found beyond the southern 'lemming boundary' in Gorham's cave in Spain, Arene Candide, grotto Colombi and Romanelli, Covolo di Trene and Cardamone sites in Italy (Fig. 4, 1-6) obviously belonged to migrant birds.

Surprisingly, there were no records of *Nyctea scandiaca* in the Late Würm of Poland (Bochenski 1974, 1993). This may indicate very low population density or even absence of the species in Upper Visla River Basin north of the Carpathians. At that time the species range could have been shifted to south by the last ice Eurasian sheet and related proglacial drainage system, with ice-dammed fresh water basins (particularly Warsaw-Berlin or Elbe ancient Gulf: see Grosswald 1980). Severe conditions in south Poland are reflected in the avifauna composition of Mamutova cave (15,000 - 29,000 yBP), where willow grouse and ptarmigan were predominant (Bochenski 1974). The presence of severe conditions in Mamutova cave area is confirmed by the absence of reliable Late Paleolithic archaeological sites in the North European Plain (Germany, Poland), where ice sheet advanced far to the south (Markova 1982). The remains of *Nyctea scandiaca* and predominant remains of *Dicrostonyx torquatus*, in Pilisszanto and Remethedy rock shelters in northern Hungary (Janossy 1986) give an indication that snowy owl could breed in a narrow belt just south of the northern range of the Carpathians.

In the Russian Plain, sites with findings of snowy owl and lemming remains are located to the south of the arctic sub-assemblage boundary (Fig. 5). Apparently, snowy owl was a regular seasonal visitor to the areas (Mezhirich and Kostenki) just south from the breeding range and nomadic or eruptive to Adzhi-Koba (Fig. 4 no. 9, Fig. 5 no. 6) in the Late Valdai.

In European Russia, the snowy owl might have bred in the latitudes 51°45' N in Desna River basin (Mesin site) and 55°07' N in the western foothills of the northern part of Yuzhnyy Ural (Ignatievskyaya cave, Fig. 3, no. 1, Fig. 4 no. 11, Fig. 5 no. 1). In the late Valdai these areas were tundra-steppes and northern periglacial steppes. The low ratio of lemmings in the rodent fauna in Ignatievskaya cave (Fig. 3 no. 1, Fig. 4 no. 11, Fig. 5 no. 1) (Smirnov *et al.* 1990) indicates that the species might have been a sporadic breeder, or its breeding range was located just north of the cave area.

At Kostenki sites (Fig. 5 no. 2) very few species of birds were recovered, including snowy owl (Potapova, unpublished data). Most of snowy owl remains were tarsals (tarsometatarsus), among which one talon had all phalanxes attached, supported together by hard clay conglomerate (Potapova, unpublished data). This find is very interesting, because in Europe there are few known Magdalenian sites containing talons of snowy owl, which proved to be hunted by man (Mourer-Chauviré 1979). The snowy owl from Kostenki might have been also selectively hunted by man and used for certain purposes. Feathered talons of diurnal and nocturnal birds of prey are known to be very popular amulets among aboriginal tribes of Siberia and Northern America. High proportions of snowy owl remains among avifauna in Kostenki sites (Fig. 5 no. 2) indicate frequent visits of the species to the Middle Don River basin. Snowy owl also may have played a significant role in cosmology of the Kostenki inhabitants.

The sites containing snowy owl remains reported for Siberia (Okladnikov's cave, Fig. 5 no. 12, and Tonnelnaya and Denisova caves, Fig. 4 no. 13) are located beyond the southern arctic sub-assemblage's boundary, and the latter has scarce remains of Lemmini (Derevyanko *et al.* 1998). Obviously, snowy owl was a seasonal visitor to South Siberia. The fact that none of the snowy owl remains were found at numerous sites within the southern boundary of arctic sub-assemblage, tells us that the range of snowy owl lied far north of 60°N in West and Central Siberia. Probably, in the Late Valdai the range of snowy owl was significantly shifted far to the north in Siberia, in comparison to its location in Europe. The species may have occupied the vast arctic shelf area in northern Siberia, which was totally open about 13,000 – 15,000 years ago (Sher 1997a).

Ecological remarks

In Siberia the snowy owl prefers to take collared lemmings, when they are available. The snowy owl selectively hunts *Dicrostonyx torquatus*, even if the population of the latter is lower than that of Siberian lemming *Lemmus sibiricus* (Krechmar & Dorogoy 1981; Dorogoy 1987; Potapov pers. comm. 1999). Remains of *Dicrostonyx* were dominant over Siberian lemming in the Late Valdai sites (about 90%), but they had a lower ratio in the Early and Middle Valdai (Kochev 1993; Smirnov 1999a; Smirnov & Golovachev 1999). The sites yielding snowy owl remains were more numerous in the Late Valdai than in the Early and Middle Valdai. In the Pleistocene, snowy owl flourished, hunting lemmings of the genus *Dicrostonyx*, and was obviously more abundant in places where populations of these lemmings were high. It is hard to consider this correlation as a coincidence.
In the Ural Mountains snowy owl hunted extinct *Dicrostonyx simplicior* FEJFAR (form 1, 2 and 3; Middle Pleistocene), that inhabited tundra and temperate forest-steppes, and *D. guilielmi* (form 3 in Ural; Late Valdai, 24,000 - 14,000 yBP), that lived in cold steppes with occasional trees. These lemmings existed within the range of zonal faunas in quite severe conditions, to highly disharmonic faunas in temperate conditions. Since the Middle Pleistocene collared lemming was represented by quite a few forms and transitional forms - *D. simplicior-guilielmi*, *D. guilielmi-simplicior*, *D. torquatus-guilielmi* etc., reflecting the rapid evolutionary rate of molar morphology (Smirnov *et al.* 1997, Smirnov 1999a, Smirnov & Golovachev 1999), changes in diet preferences and ecology (Smirnov 1990). These forms were chronologically isolated in the northeast of Europe during the second half of the Pleistocene (Kochev 1993), and sometimes were represented by different forms in different locations in certain period of times (Smirnov 1999b). During the second half of the Pleistocene and the Holocene the high ecological flexibility of collared lemming was gradually narrowing towards the specialisation to arctic conditions (Smirnov 1990). It can be only assumed that being dependent on a wide variety of prey species, snowy owl had a more flexible hunting strategy in the Late Pleistocene when compared to modern owls.

It is still unclear if snowy owl was migrant or breeding in the Mediterranean shore in the Günz (MNQ 20, Bourgade) and what bird species were hunted by snowy owl in the Early Middle Pleistocene. The genus *Nyctea*, and particularly the species *Nyctea scandiaca*, appeared in the Early Pleistocene without any transitional forms (Bochenski 1992) from other known genera, and it was already a specialised form and distinct from other owls. Since snowy owl originated, it must have had its own specialisation to hunt rodents - the strategy in which snowy owl differs from the other species of Buboninae, characterised by perching in open biotopes for long periods on hummocks, waiting for prey to move. However, snowy owl diet composition during the Günz and Mindel epochs still remains enigmatic. It definitely hunted lemmings, since earliest lemmings remains are dated back to Early Biharian (*Dicrostonyx*; MNQ19, Early Pleistocene), and the earliest part of late Villányian (*Lemmus*; MN 17, Pliocene; Fejfar & Heinrich 1989) in Western Europe. Due to a scarcity of lemmings in the fauna, it is most likely that snowy owl hunted a large variety of extinct voles, which were apparently easier to hunt using a 'waiting' strategy. Probably, these must have been species ancestral to lagurids, inhabiting open biotopes - *Lagurodon*, *Borsodia*, *Prolagurus*, and extinct narrow skulled vole, *Microtus (Stenocranius) hintoni*, as well as other extinct species - *Allophaiomys*, *Mimomys*, *Pliomys*, *Allocricetus*.

Due to findings of subadult bones among the numerous remains of the species in l'Escal in southern France, it was shown that snowy owl bred in southern France in the Middle Pleistocene (Mindel, MNQ 22; Mourer-Chauviré 1975, 1983). Remains of willow grouse and ptarmigan were not recorded there. Probably, the birds in the winter diet of snowy owl played a lesser role than nowadays, when rodent fluctuation, typical for arctic tundra was not so significant. The large size of snowy owl *Nyctea scandiaca gallica* from the Middle Pleistocene (Mindel) indirectly indicates the adaptation to hunt larger size animals (and birds?). These could have been rabbits, hares and large rodents - the size category of animals preferred by eagle owl. In its turn, eagle owl could compensate the lack of willow grouse and ptarmigan by hunting birds of the same size category - different species of pigeons, extinct grey partridge *Perdix paleoperdix*, and grey partridge *Perdix perdix*, which remains were found in numerous cave sites in France. Pigeons and grey partridge are still preferred by eagle owl in many places of Western, Central and Eastern Europe (Brain 1981; Jaksic & Marti 1984; Donazar & Ceballos 1989; Darolova 1990; Boev 1993). According to fossil records, willow grouse and ptarmigan were definitely widely hunted by these two large owls in Europe during the Riss - Würm and in Siberia during the Würm glacial stages.

The relict strategy to hunt rabbits and birds and even fish (!) (absence of lemmings in its diet) is now preserved and demonstrated by the population of *Nyctea scandiaca* in the west of its range – in Iceland and Fetlar (Shetland Islands).

Numerous (cave) sites in Europe with the remains of snowy owl provide substantial evidence that the eagle owl hunted snowy owl on a regular basis and that during the glacial and interglacial epochs the ranges of *Nyctea scandiaca* and *Bubo bubo* largely overlapped. Eagle owl hunts only by dark nights, snowy owl does not limit hunting activity only to nights: it is directly regulated by the activity of the main prey species i.c. lemmings (Portenko 1972). In the Pleistocene, regular eagle owl predation on snowy owl might have occurred only in places where 'dark nights' coincided with the range of snowy owl. Also, the area inhabited by eagle owl must have had at least some forests. Even considering the fact that about 80% of owl's food comes from open areas, woods must form in average 60% of eagle owl biotopes in inland habitats (Mikkola 1983). For snowy owl the predominantly open biotopes suitable for breeding must have been inhabited by lemmings. It comes as no surprise that the southern boundary of snowy owl biotope limits closely follows the southern border of periglacial forest-steppe reconstructed for the maximum Valdai cooling on the Russian Plain (Grichuk 1973 by: Praslov 1984). Periglacial forest-steppes were probably the characteristic areas where ranges of snowy and eagle owl overlapped and where snowy owl had strong competition for food and high predation pressure from eagle owl.

During the Valdai glaciation snowy owl predominantly occupied open landscapes in the north (periglacial tundra-steppes and periglacial forest-steppes), while the eagle owl inhabited open and semi-open biotopes in the south (periglacial forest-steppes, southern periglacial forest-steppes, steppes and desert areas). According to huge accumulations of lemming remains in cave sites, it is obvious that eagle owl hunted both species of lemmings dispersed north of the southern periglacial forest-steppe boundary. However, the territory along the ice sheet or coastal line of pro-glacial basins in Europe was most likely out of the eagle owl's reach, and occupied by snowy owl. That was the only area where the snowy owl did not experience hunting pressure from the eagle owl.

With the gradual degradation of the ice sheet in Europe and retreating lemming ranges, the ranges of snowy and eagle owl moved to the north. The eagle owl was expanding its range, following the expansion of the forests to the north in Europe and Siberia, while snowy owl was retreating. As a result, significant irreversible environmental changes and destruction of tundra-steppe communities during the Pleistocene-Holocene transition in the Northern Palearctic (Sher 1997a,b) removed snowy owl from vast territories in Europe and Asia into narrow zonal habitats of arctic tundra. The ranges of snowy and eagle owl became almost separated. Overlapping ranges of snowy and eagle owls can be found today in the mountain area of southern and central Norway. This is a relict, probably of the Pleistocene-Holocene age.

Plumage

The white plumage of snowy owl is an adaptation to life in the arctic tundra, where winter prevails considerably over summer months. Daylight hunting activity of the species is also the adaptation to life in high latitudes. Occupying mostly middle latitudes of Western, Central and Eastern Europe, the snowy owl must have had definitely dark (brownish) plumage and was predominantly a crepuscular or night hunter during the Pleistocene. If it had white plumage, the snowy owl would have been easy prey for mammal predators (white plumage is seen by birds as a grey color; Potapov, pers. comm. 2000) and would not have survived through the Pleistocene interglacials. Snow in northern Europe and Siberia must have played a most important role in the development of white plumage of the species. The full transformation from brown to white plumage might have happened after the Late Valdai glacial maximum, when continental winters with low snowfall changed to a climate with high snowfall. These climatic changes probably began in the terminal Pleistocene - Early Holocene. This is the period when snowy owl appearance dramatically changed.

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