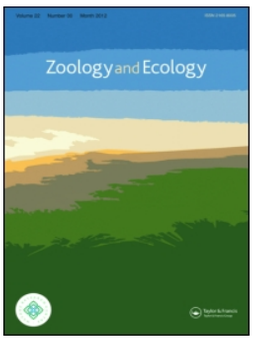

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Mammals of Valdai Lakeland – 80 years later

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ABSTRACT

The article presents a complete species list of the modern mammal fauna and the zoogeographical analysis of the Valdai Lakeland (north-west of European Russia). The current state of the fauna therein is compared to the data reported by S.U. Stroganov in 1936. Results of the recently conducted genetic and ecological research are presented. New data on sibling species and intraspecific forms of Eulipotyphla and Rodentia are analysed. The current increase in the Valdai Lakeland forest cover accounts for the prevalence of forest fauna and, especially, for that of southern taiga species. Due to alien species the ecosystem role of semi-aquatic mammals has significantly increased.

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Sibling species; mammal; fauna; zoogeography; karyotyping; biological invasions

Introduction

Until a few decades ago it was assumed that faunal diversity of any particular region remains relatively stable over historical time and that only detailed studies of the region can reveal any significant changes in it. Based on the example of the Valdai Lakeland in the north-west of European Russia we would like to demonstrate temporal changes in theriofauna.

The Valdai Lakeland is one of the territories that, due to their biodiversity, attract many zoologists and are therefore theriologically well-studied (Kuznetsov and Tishkov 2012). During the most recent glaciation of the Russian Plain, the Valdai Lakeland area was at the glacier's margin, which accounts for the present glacial landforms (terminal moraine ridges and mounds, kames, eskers, outwash plains, etc.) as well as for specific conditions for biota development (possibilities for maintaining wildlife refuges, mixing faunas, etc.). At the present time, the Valdai Lakeland is part of the Valdai Upland and is a transition zone between southern taiga and coniferous-broadleaf forests (Morozov 1992). Forests of this region include nemoral communities, making them similar to forests of Belarus and Poland (Matuszkevicz et al. 2014). In addition, traces of centuries-long human activities in the Valdai region, such as vast forest clearances, extensive ploughing and habitat fragmentation, have led to the formation of a unique landscape that combines woodlands, meadows and fields (Belonovskaya, Krenke, and Tsarevskaya 2014). Recently, due to the decreasing intensity of economic development, depressed agriculture and continuous depopulation of the region, there have appeared indications of an opposite trend: an increase in the extent of wooded areas through natural reforestation of arable lands and meadows, which is accompanied by increasing recreational pressure on the banks of large lakes and surroundings of Valdai town. Such opposing trends of natural and human-induced processes inevitably affect the fauna and populations of mammals within the region.

An overview of the thousand-year long history of mammal fauna development in the Valdai Lakeland has been published very recently (Tishkov 2013). For this paper, a more detailed analysis of a much shorter period in the recent history of this region has been carried out. The period analysis starts with Stroganov's (1936a, 1936b) research data published in the Zoologicheskii Zhurnal ('Russian Journal of Zoology') in 1936. The two articles by S. U. Stroganov comprise the first complete species list of the Valdai Upland mammal fauna together with short descriptive notes on 55 mammal species containing information on their systematics (often personally suggested by the author) and morphological features, characteristics of species distribution over the study region, population sizes and habitats as well as the zoogeographical analysis of the fauna.

Eighty years have elapsed since the publication of S.U. Stroganov's important works (1936a, 1936b). Over the period spanning the end of the twentieth and the

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beginning of the twenty-first centuries, large-scale theriological research has been conducted within the Valdai Lakeland. Moreover, over the last 80 years, concepts of species composition and structure of some groups of mammals have developed with the discovery of sibling species and/or genetically discrete intraspecific forms, i.e. the state of animal populations has changed and our knowledge about them has deepened.

The goal of the present study was to evaluate changes in systematics, faunal composition and mammal populations within the Valdai Lakeland over the past 80 years. The specific objectives of the study were to update the list of mammal species in the study region, to characterise the abundance and population dynamics of natural and alien species and to conduct zoogeographical analysis, enabling a better understanding of modern trends of change in theriofauna of the Valdai Lakeland.

Materials and methods

The Valdai Lakeland is considered to encompass a wide belt of land with numerous lakes (Velie, Valdai, Uzhin, etc.) between Lake Seliger in the south and Lake Borovno in the north. Specific landscapes, wildlife and history of this region predetermined the establishment of the Valdai National Park covering an area of 158,000 ha (Figure 1). At present, most of its area (83.9%) is occupied by forests, among which spruce, birch and pine woodlands predominate. Meadows and shrubs occupy 15.2% and lakes and water courses 5.6% of the total park area. The area of the park is characterised by specific mosaic distribution patterns and close proximity of different types of biotopes. Separate small areas of pure spruce woodlands occupy 2.7 ha and pine woodlands – 2.3 ha on average.

The data presented in this paper were collected by the authors in the course of many years (since 1973 up to now) of studies that were mainly carried out within the area of the Valdai National Park, particularly, near the Research Station of the Institute of Geography of the Russian Academy of Sciences (IGRAS Research Station, Figure 1), where long-term research into various components of biota was conducted (Shvarts, Demin, and Zamolodchikov 1992; Glazov 2004; Kuznetsov and Tishkov 2012 and others). The Valdai National Park was established in 1990 and in 2004 it was included into the World Network of Biosphere Reserves. This status facilitated scientific research within the study area. Findings available in other literature sources were also used in this paper.

The authors took part in small mammal surveys that were carried out between 1974 and 1987. During these surveys, 2888 and 1620 small mammals were caught using steel spring traps and pitfall traps, respectively. More detailed information on the scale of surveys and positioning of traps in that period is presented in the report (Shvarts, Demin, and Zamolodchikov 1992). During the further surveys of 2011 and 2013, 163 small mammals representing 12 species were caught using live traps and cone traps mainly at the sites of the previous long-term research: the IGRAS Research Station, villages of Novotroitsy, Sokolovo and Lake Krenie (Figure 1). During those two years, species identity and intraspecific structure of small mammals belonging to the orders of Eulipotyphla and Rodentia were verified by chromosome analyses, which involved preparation of air-dry samples and their subsequent treatment using different chromosome banding techniques (standard, G- and C-banding) (Seabright 1971; Sumner 1972). Karyotyping was carried out on 6 Eurasian Common Shrews (*Sorex araneus* L., 1758), 5 Northern Birch Mice *Sicista betulina* (Pall., 1779), 3 European Pine Voles *Microtus subterraneus* (Selys-Longchamps, 1838), 8 Root (Tundra) Voles *Microtus oeconomus* (Pall., 1776), 1 Vole of the superspecies complex *M. arvalis*, 2 Herb Field Mice *Apodemus uralensis* (Pall., 1811) and 4 Yellow-necked Field Mice *Apodemus flavicollis* (Melch., 1834).

Data on large and medium-sized non-hibernating mammals (*Sciurus vulgaris*, Lagomorpha, Artiodactyla and Carnivora except *Nyctereutes procyonoides*, *Ursus arctos* and *Meles meles*) were collected along transects of the annually undertaken winter monitoring, which is widely used in Russia. One of the authors of this paper (V. I. Nikolaev) took part in those surveys. The latest revision of the methodology for winter mammal surveys was approved in 2009: 'Methodological Recommendations for Organizing, Conducting and Data Processing of Winter Transect Surveys of Game Species of Russia' (Science and Technical Council of the Ministry of Agriculture of Russia, Protocol No. 15, 28 May 2009). The winter monitoring data used in this paper were not published earlier. They were obtained from the monitoring conducted along the permanent 211 km long transect No. 21, the greater part of which (198 km) runs through woodlands and the minor (13 km) through fields. This transect characterises the territory of the Valdai National Park covering an area of 122.6 thousand hectares. The number of Brown Bear (*Ursus arctos* L., 1758) individuals was estimated according Gubar (1990) and Kuzyakin and Chelintsev (2005), using the results of the observations at special feeding sites and oat fields in August–September. The number of bear footprints and sightings during the summer–autumn period were used also. Numbers of other large hibernating mammals were obtained from visual observations during long-term field work in different parts of the National Park.

To describe the population size, we used the following estimates: Very Rare, Rare, Common, Numerous. Species were categorised as numerous, if their number was at least twice as high as that of other species. Species were graded rare if their occurrence was sporadic or they were observed once. Endangered species were classified as very rare. Other species were considered as common.

Figure 1. Valdai Lakeland. Showing boundaries of the Valdai National Park and its buffer zone, primary long-term study sites including sites of the 2011 and 2013 studies, hydrographic network, roads and the boundary between administrative regions.

The data reported by Stroganov (1936a, 1936b) are presented according to the author's personal interpretation.

The nomenclature used generally follows Wilson and Reeder (2005), taking into account the new treatment of mammal taxonomy used in the IUCN Red List (IUCN 2016). For example, experts of the IUCN Red List confirm the Eulipotyphla concept (Douady et al. 2002 and other) and do not consider Erinaceomorpha and Soricomorpha as orders.

Results

Eulipotyphla

Disappeared species

Stroganov (1936a) recorded 10 species of the order Eulipotyphla (Table 1). The presence of two of those species has not been confirmed by recent surveys within the Valdai Lakeland. One of them is the Tundra Shrew (*Sorex tundrensis* Merriam, 1900), which is reliably registered

Table 1. Eulipotyphla of Valdai Lakeland.

No	English and scientific names	By Stroganov (1936a)	Late 20th – early 21st centuries	
			Abundance estimate	Comments
1.	Western European Hedgehog *Erinaceus europaeus* L., 1758	Common	Rare	Confirmed by genotyping
2.	European Mole *Talpa europaea* L., 1758	Everywhere	Common	
3.	Russian Desman *Desmana moschata* (L., 1758)	Rare	Disappeared	In the Red Data Book of Tver Region
4.	Eurasian Pygmy Shrew *Sorex minutus* L., 1766	Common	Common	
5.	Laxmann's Shrew *Sorex caecutiens* Laxmann, 1788	Common	Common	
6.	Even-toothed Shrew *Sorex isodon* Turov, 1924	Rare	Rare	
7.	Eurasian Common Shrew *Sorex araneus* L., 1759	Numerous	Numerous	
8.	Eurasian Least Shrew *Sorex minutissimus* Zimmermann, 1780	Very Rare	Rare	In the Red Data Book of Tver Region
–	Tundra Shrew *Sorex tundrensis* Merriam, 1900	Single	Presence is not confirmed	
9.	Eurasian Water Shrew *Neomys fodiens* (Pennant, 1771)	Common	Common	

in Europe no further west than the middle reaches of the Mezen River in the Arkhangelsk Region (Bobretsov et al. 2008). The other species is the Russian Desman *Desmana moschata* (L., 1758) recorded only in the Tver Region, only rarely and only within the upper Volga River basin, with the last reliable species occurrence recorded in 1955 (Viktorov and Istomin 2002). Therefore, the modern Eulipotyphla fauna of the Valdai Lakeland consists of 8 species.

Taxonomy changes and clarifications

Microsataellite genotyping of the tissue sample from the Hedgehog trapped in 2011 at the edge of Novotroitsy village confirmed the species identity as *Erinaceus europaeus* (L., 1758) (Matveeva et al. 2016). The number of Western European hedgehogs has decreased (Table 1).

Over the past 80 years there has been an important breakthrough made in the understanding of the intraspecific structure of the Eurasian Common Shrew. To date, a total of 74 valid chromosome races of this species have been discovered (Shchipanov and Pavlova 2016), with differences among them determined by Robertsonian (Rb) translocations of 10 acrocentric chromosomes: *g, h, i, k, m, n, o, p, q,* and *r* (Searle et al. 1991; Searle and Wójcik 1998). Rb translocations and the resultant metacentrics are designated as race-specific Rb-translocations and race specific-metacentrics (Searle and Wójcik 1998). There are 26 chromosome races of this species known in Russia (Shchipanov and Pavlova 2016), many of which are concentrated within the area of the Valdai glaciation, particularly, near the southern boundary of the glacier (Orlov and Kozlovsky 2002; Orlov et al. 2007). The chromosome races Seliger, St. Petersburg and Moscow are known within the Valdai Lakeland and its nearest surroundings (Shchipanov and Pavlova 2016). The Seliger race was first found at the southern end of the Valdai Lakeland between Lakes Seliger and Sterzh (Bulatova et al. 2000). Later a hybrid zone between races Seliger and Moscow was discovered in the same locality (Bulatova, Shchipanov, and Searle 2007) and a contact zone between three chromosome races (Seliger, Western Dvina and Moscow) was identified 50 km southwest (at Lake Luchanskoe, Tver Region) (Orlov and Borisov 2007; Orlov et al. 2010; Bulatova et al. 2011). Races Seliger and St. Petersburg were recorded in the surroundings of Lake Valdai (Bulatova, Shchipanov, and Searle 2007; Orlov et al. 2008). The race Pskov occurs west of and the race Mologa – northeast of the Valdai Lakeland and diffusion of these races into the Valdai Lakeland is not excluded.

We conducted karyotyping (G-banded chromosomes) of six female Eurasian Common Shrews captured in 2013 near Lake Krenie (57.98° N, 33.37° E, see Figure 1) and established that they belong to the Seliger chromosome race (Figure 2). It is characterised by the formula: *af, bc, g, hn, ik, jl, m/q, pr, o, tu,* XX/XY1Y2, with specific metacentrics *hn, ik, mq,* and *pr* (Bulatova et al. 2000). Polymorphism for three chromosome fusions (Robertsonian translocations) (1) *go/g, o*; (2) *mq/m, q*; (3) *pr/p, r* – is known for the Seliger race (Bulatova, Shchipanov, and Searle 2007; Pavlova, Bulatova, and Shchipanov 2007). In the studied set we revealed chromosomal polymorphism connected with Robertsonian translocations *pr* and *jl*. Three of the six individuals studied were heterozygous only for Rb translocation pr with the chromosome formula (*g, hn, ik, jl, mq, o, p/r*) and diploid number of chromosomes $2n = 23$. In three of the six individuals studied, only the Rb translocation *pr* was found to be heterozygous with the chromosome formula (*g, hn, ik, jl, mq, o, p/r*) and diploid number of chromosomes $2n = 23$. The fourth female was heterozygous for *pr* and *jl* translocations with the chromosome formula (*g, hn, ik, j/l, mq, o, p/r*) and $2n = 24$ (Figure 2). The remaining two individuals had a 22-chromosome karyotype and the chromosome formula (*g, hn, ik, jl, mq, o, pr*).

Figure 2. G-banded karyotype of the 24-chromosomal female Eurasian Common Shrew (*Sorex araneus*) of the Seliger race from the Lake Krenie area, heterozygous for the *pr* and *jl* translocations with the chromosomal formula (*g, hn,ik, j/l, mq, o, p/r*).

Number of some species

The European Mole (*Talpa europaea* L., 1758) is common. Its average population densities are 3–4 individuals per hectare in *Oxalis acetosella – Picea abies* forests and nemoral spruce forests and much lower in other types of spruce forests. Mole populations abruptly decrease due to summer droughts, recovery of their population size taking 2–3 years (Glazov 2004).

Among the 1620 small mammals caught in pitfall traps near the IGRAS Research Station during the 1974–1987 period, there were 1082 shrews of the genus *Sorex* and 103 Eurasian Water Shrews *Neomys fodiens* (Pennant, 1771). The Eurasian Common Shrew was the most numerous species representing 39% of the total number of trapped small mammals and 58.4% of the total number of trapped *Sorex* individuals. The Laxmann's Shrew (*Sorex caecutiens* Laxmann, 1788) was common, accounting for 23.8% of the total number of trapped *Sorex* individuals. The other shrew species were characterised by the following percentages of the total number of trapped *Sorex* individuals: the Eurasian Pygmy Shrew (*Sorex minutus* L., 1766) – 13.9%, the Even-toothed Shrew (*Sorex isodon* Turov, 1924) – 3.9% and the Eurasian Least Shrew (*Sorex minutissimus* Zimmermann, 1780) – 0.5% (Shvarts, Demin, and Zamolodchikov 1992).

Diversity and ecological significance of shrews

The data obtained and the multifaceted analysis of *Sorex* distribution throughout different biotopes within the Valdai Upland, their scull morphometry, feeding habits and prey distribution showed significant differences in jaw sizes of various shrew species that share the same territories, which explains formation processes of multispecies shrew communities in Valdai, including faunal mixing. For example, the Laxmann's Shrew shares habitats with the Eurasian Common Shrew and the Eurasian Pygmy Shrew. The distribution range of the Eurasian Common Shrew is larger than that of the Laxmann's Shrew, while the distribution range of the Eurasian Pygmy Shrew is smaller than that of the Laxmann's Shrew (for more detail see Shvarts and Demin 1986; Shvarts, Demin, and Zamolodchikov 1992; Shvarts et al. 1992; Shvarts and Demin 1994; Shvarts 2004). The evolutionary, zoogeographic and biocenotic significance of differences in sizes of co-existing shrew species is demonstrated for other regions also (Sheftel 1990, 1994; Kirkland 1991; Fox and Kirkland 1992; Hanski 1994; Whitaker and French 1994; Churchfield et al. 1997; Churchfield, Nesterenko, and Shvarts 1999; and other works).

The multifaceted analysis that we have performed shows that the rate of food consumption by shrews in different Valdai forest biocenoses varies from 24 to 245 kg per year, which accounts for 32–240% of the summertime mass of soil invertebrates, not including reproduction inputs (Shvarts, Chernyshev, and Popov 1997; Shvarts 2004). Throughout a year shrews consume a significant proportion of invertebrates and stimulate invertebrate reproduction, which together with other factors (Shchipanov, Alexandrov, and Alexandrova 2006) allows considering *Sorex* shrews as powerful biological catalysers of forest litter decomposition processes in boreal forests.

Chiroptera

Newly emerged species

Stroganov (1936a) specified 9 species of bats (Table 2). This species list has remained practically unchanged over the past 80 years. One species has been added: the Natterer's Bat *Myotis nattereri* (Kuhl, 1817) that has recently been found near Borovichi town and listed in the Red Data Book of the Novgorod Region (Doynikova et al. 2015). The Northern Bat *Eptesicus nilssonii* (Keyserling et Blasius, 1839), Daubenton's Myotis *Myotis daubentonii* (Kuhl, 1817), Pond Myotis *Myotis dasycneme* (Boie, 1825) and, supposedly, the Whiskered Myotis (*Myotis mystacinus* Kuhl, 1817) have been detected within the Valdai National Park recently (Popov 2012; Shauro 2012). It is possible that other bat species inhabit this area.

Changes in taxonomy and clarifications

Systematics of some species has been changed: the Brandt's Myotis was considered as a subspecies of the Whiskered Myotis by Stroganov (1936a), who mentioned that it was difficult for him to identify the *Myotis* subspecies and that it was their forearm size that allowed an approximate identification of it as *Myotis mystacinus brandti*. However, at present the Whiskered Myotis *Myotis mystacinus* (Kuhl, 1817) and the Brandt's Myotis *Myotis brandtii* (Eversmann, 1845) are considered to be two independent species (Strelkov and Buntova 1982; Strelkov 1983; Kruskop 2012), although their identification is complicated. The Brandt's Myotis is known in the Novgorod Region from a single find near Novgorod city (Doynikova et al. 2015). There are no reliable confirmations of *M. mystacinus* s. str. presence in the Valdai

Table 2. Chiroptera and Lagomorpha of Valdai Lakeland.

No	English and scientific names	By Stroganov (1936a, 1936b)	Late 20th – early 21st centuries	
			Abundance estimate	Comments
Chiroptera				
10.	Natterer's Bat *Myotis nattereri* (Kuhl, 1817)	Not mentioned	Rare	In the Red Data Book of Novgorod Region
11.	Whiskered Myotis *Myotis mystacinus* (Kuhl, 1817)	Common	Rare?	Needs confirmation
12.	Brandt's Myotis *Myotis brandtii* (Eversmann, 1845)		Rare	In the Red Data Book of Novgorod Region
13.	Daubenton's Myotis *Myotis daubentonii* (Kuhl, 1817)	The number not estimated	The number not estimated	
14.	Pond Myotis *Myotis dasycneme* (Boie, 1825)	The number not estimated	Rare	In the Red Data Book of Novgorod Region
15.	Brown Long-eared Bat *Plecotus auritus* L., 1758	Common	The number not estimated	
16.	Noctule *Nyctalus noctula* (Schreber, 1774)	Common	Rare	In the Red Data Book of Novgorod Region
17.	Nathusius' Pipistrelle *Pipistrellus nathusii* (Keyserling et Blasius, 1839)	Common	The number not estimated	
18.	Common Pipistrelle *Pipistrellus pipistrellus* (Schr., 1774)	The number not estimated	Rare?	Needs confirmation
19.	Northern Bat *Eptesicus nilssonii* (Keyserling et Blasius, 1839)	The number not estimated	Rare	In the Red Data Book of Novgorod Region
20.	Parti-coloured Bat *Vespertilio murinus* L., 1758	Common	Rare?	Needs confirmation
Lagomorpha				
21.	European Hare *Lepus europaeus* Pall., 1778	Common	Common	
22.	Mountain Hare *Lepus timidus* L., 1758	Common	Common	

Lakeland, but, judging from the data from the neighbouring regions, the occurrence of both species is possible. Chiroptera remains the least studied order of mammals in the fauna of the Valdai Lakeland to date (Popov 2012).

Lagomorpha

Number of species

Stroganov (1936b) recorded two species of hares (Table 2), which are still present, although Leporidae were formerly attributed to the order Rodentia. The Valdai and Demyansk districts are known for their European Hare (*Lepus europaeus* Pallas, 1778) hunting traditions (Stroganov 1936b). Recently the European Hare population has significantly declined due to the decrease in the total area of meadows, and its importance as a game species has been lost. European hare tracks were found in 2003 (32 individuals) and in 2008 (15 individuals), but they have not been recorded in 2002, 2004–2007 and 2009–2015.

The Mountain Hare (*Lepus timidus* L., 1758) is common. The 1990–2015 winter surveys in the Valdai National Park revealed that the Mountain Hare population size was fluctuating and generally tended to decrease. There were over 2000 individuals until 2006 with peaks (over 4000, maximum 4580 individuals) observed in 1992, 1996, 2001 and 2002. However, after 2007 there were no more than 1703 individuals recorded, their number reaching a low point of 669 in 2011.

Rodentia

Disappeared and newly emerged species

Stroganov (1936b) mentioned 20 rodent species including the Brown Rat *Rattus norvegicus* (Berk., 1769), although its distribution range was just approaching the Valdai Lakeland at the time when it was registered in the Rzhev District of the Tver Region. Over the past 80 years, this species list has changed (Table 3). The Forest Dormouse *Dryomys nitedula* (Pall., 1778) used to be a rare species found only in the Tver Region, but now it has probably disappeared (Viktorov and Istomin 2002). The Garden Dormouse *Eliomys quercinus* (L., 1766) has probably also disappeared from the Tver Region (Viktorov and Istomin 2002), but it is still, although rarely, found in the Novgorod Region (Doynikova et al. 2015). The Siberian Flying Squirrel *Pteromys volans* (L., 1758) is very rare, with the last reliable occurrences recorded in 2004 in a coniferous forest near the Ostashevo village, the Moshenskoe District of the Novgorov Region (Doynikova et al. 2015) and in 2012–2013 in Selizharovo and Andreapol Districts of the Tver Region (two individuals caught in marten traps) (Komarova, Palkova, and Schmitov 2015). Numbers of the Black Rat *Rattus rattus* (L., 1758) have significantly decreased, with the last capture reported in 1979, and no occurrence recorded in recent years.

It is interesting that S.U. Stroganov found the Black-bellied Hamster *Cricetus cricetus* (L., 1758). This forest-steppe species started to spread into the Valdai Upland from the southeast in the early 1930s following forest clearances. Approximately 10 individuals of the

Table 3. Rodentia of Valdai Lakeland.

No	English and scientific names	By Stroganov (1936b)	Late 20th – early 21st centuries	
			Abundance estimate	Comments
23.	Siberian Flying Squirrel *Pteromys volans* (L., 1758)	The number not estimated	Rare	In the Red Data Books of Tver and Novgorod Regions
24.	Eurasian Red Squirrel *Sciurus vulgaris* L., 1758	Common	Common	
25.	Forest Dormouse *Dryomys nitedula* (Pall., 1778)	Very rare	Disappeared	In the Red Data Book of Tver Region
26.	Garden Dormouse *Eliomys quercinus* (L., 1766)	Rare	Rare	In the Red Data Books of Tver and Novgorod Regions
27.	Eurasian Beaver *Castor fiber* L., 1758	Was absent	Common	Reintroduced since 1949
28.	Northern Birch Mouse *Sicista betulina* (Pall., 1779)	The number not estimated	Common	Karyotyping
29.	Black-bellied Hamster *Cricetus cricetus* (L., 1758)	Rare	Disappeared	In the Red Data Book of Tver Region
30.	Wood Lemming, *Myopus schisticolor* (Lilljeborg, 1844)	Not mentioned	Rare	In the Red Data Books of Tver and Novgorod Regions
31.	Bank Vole *Myodes glareolus* (Schr., 1780)	Numerous	Numerous	
32.	Northern Red-backed Vole *Myodes rutilus* (Pall., 1779)	Rare	Common	
33.	Muskrat *Ondatra zibethicus* (L., 1766)	Was absent	Common	Introduced in 1931
34.	European Water Vole *Arvicola amphibius* (L., 1758)	Common	Common	
35.	European Pine Vole *Microtus subterraneus* de (Selys-Longchamps, 1838)	Not mentioned	Rare	In the Red Data Books of Tver and Novgorod Regions, karyotyping
36.	Root Vole *Microtus oeconomus* (Pall., 1776)	Common	Common	Karyotyping
37.	Field Vole *Microtus agrestis* (L., 1761)	Rare	Rare	
38.	Common Vole *Microtus arvalis* (Pall., 1778)	Numerous	Common?	Needs confirmation
39.	East European Vole *Microtus levis* Miller, 1994		Rare?	Karyotyping
40.	Eurasian Harvest Mouse *Micromys minutus* (Pall., 1771)	Rare	Rare	
41.	Striped Field Mouse *Apodemus agrarius* (Pall., 1771)	Very rare	Rare	
42.	Herb Field Mouse *Apodemus uralensis* (Pall., 1811)	Very rare	Common	
43.	Yellow-necked Field Mouse *Apodemus flavicollis* (Melch., 1834)	Common	Rare/Common	
44.	House Mouse *Mus musculus* L., 1758	Common	Common	
45.	Brown Rat *Rattus norvegicus* (Berk., 1769)	Was absent	Common	
46.	Black Rat *Rattus rattus* (L., 1758)	Common	Rare?	Needs confirmation

Black-bellied Hamster were detected in the August of 1932 in a barley field near the Shiblino village of the Lukovnitsa District of the Tver Region (Stroganov 1936b). This species has apparently not spread into the Novgorod Region. No finds of the Black-bellied Hamster have been reported recently. It is listed in the Red Data Book of the Tver Region (Viktorov and Istomin 2002).

Over the past 80 years there have been five new species added to the list of the Valdai rodent fauna. The introduced Muskrat *Ondatra zibethicus* (L., 1766) and the reintroduced Eurasian Beaver (*Castor fiber* L., 1758) have become common. The population of the Eurasian Beaver has reached, apparently, its maximal density within the Valdai National Park: there were 500–600 individuals reported in surveys during the last 20 years. Information on occurrence of the North American beaver (*Castor canadensis* Kuhl, 1820) within the Valdai National Park (Bobrov, Warshavsky, and Khlyap 2008) has not been reliably confirmed.

S. U. Stroganov did not mention the Wood Lemming *Myopus schisticolor* (Lilljeborg, 1844), although it had been already reported in the Novgorod Region in 1931; it was also found in forests of the Valdai National Park later in 2004 (Doynikova 2005; Doynikova et al. 2015).

The population of the Brown Rat (*Rattus norvegicus*) has grown. In the 1930s, its occurrence was limited to the Rzhev District of the Tver Region (far more to the south than the Valdai Lakeland), but in the 1950s it started spreading into the Novgorod Region and, by the late twentieth century, it had become widespread throughout the Novgorod Region (Kucheruk 1990). According to our observations, the Brown Rat is common in Valdai city, in Novotroitsy and some other villages nowadays (Table 3).

Changes in taxonomy and clarifications

S. U. Stroganov did not suspect the existence of two sibling species of the super species complex *Microtus arvalis*. In 1930 these voles (it is not known whether one or both sibling species) inhabited fields in spring–summer and at harvest time moved to barns, straw stacks and buildings to overwinter. Like the Bank Vole *Myodes glareolus* (Schreber, 1780), they were the most widespread rodents in Valdai (Stroganov 1936b). Their numbers have recently decreased, as was revealed during the 1974–1987 surveys: there were only 12 individuals of *M. arvalis* s. l. (0.27% of all small mammals trapped during that period) caught in the northern forest-dominated part of the Valdai Lakeland. Five of them were trapped in agricultural lands and the rest – in spruce (*Picea abies*) forests of different types (with dominant ground vegetation of wood sorrel (*Oxalis acetosella*),

green mosses (*Bryophyta* spp.) and false lily of the valley (*Maianthemum bifolium*) and mountain cranberry-pine forest (*Vaccinium vitis-idaea – Pinus sylvestris*) (Shvarts, Demin, and Zamolodchikov 1992). In 2011 one vole of *M. arvalis* s. l. (0.67% of the total number of small mammals) was trapped in the vicinity of the Sokolovo village in the open part of the regenerating formerly cut oak forest. Karyotyping of this vole revealed that it belongs to 54-chromosome *M. levis* Miller, 1994 (syn. *M. rossiaemeridionalis* Ognev, 1924). It is possible that 46-chromosome *M. arvalis* (Pall., 1778) also inhabits the Valdai Lakeland. The nearest reliably recorded occurrence of *M. arvalis* s. str. is in the Staritsa District of the Tver Region (Bulatova et al. 2010; Shchipanov et al. 2010).

Prognosis based on the concept of the 'combined system of ecological niches of small mammals' and subsequent evidence of the European Pine Vole's (*Microtus subterraneus*) occurrence in Valdai, i.e. hundreds of kilometres north-east of the previously known distribution range of this species (Shvarts 1985, 2004; Shvarts and Zamolodchikov 1991; Shvarts, Demin, and Zamolodchikov 1992) are of great importance for the understanding of theriofauna dynamics. The existence of this previously unknown part of the European Pine Vole's distribution range was confirmed by records in Estonia and in regions of St. Petersburg, Pskov, Novgorod, Tver and Bryansk in Russia (Shvarts 1985; Zagorodnyuk 1992; Shvarts et al. 1997; Baskevich et al. 2007 and other). According to Zagorodnyuk (1992), the spread of the European Pine Vole into these East European regions could have originated from Balkans refuges and could have been accompanied by specific changes in the ecology of this species. In Valdai it is a typical inhabitant of nemoral grass-shrub communities developed under the canopy of spruce forests (Shvarts 1985). Populations of the European Pine Vole from the north-western part of its distribution range, including Valdai, were found to be characterised by the 54-chromosome karyotype and were attributed to the *transvolgensis* subspecies. The populations that spread south of that area were characterised by the 52-chromosome karyotype. It was suggested to provisionally consider these 54- and 52-chromosome karyotypes as geographic vicarious races named *subterraneus* and *dacius*, respectively (Zagorodnyuk 1989). Later Zagorodnyuk (1992) suggested raising the rank of 54- and 52-chromosome forms of *Microtus subterraneus* to geographic vicarious species. However, research by Baskevich et al. (2015) revealed that differences between the two karyotypes are limited to only one chromosomal rearrangement – Robertsonian translocation, which is insufficient for isolating these 54- and 52-chromosome varieties.

There are interesting data on genetics of the Root Vole (*Microtus oeconomus*) in Valdai (Baskevich, Khlyap, and Shvarts 2014; Baskevich et al. 2016). Karyotyping of eight individuals of *Microtus oeconomus* from the Valdai National Park revealed the chromosomal polymorphism for Robertsonian translocation: two individuals had a 31-chromosome karyotype and six individuals had a standard 30-chromosome karyotype, with the latter known practically at all the locations, where research into cytogenetics of this species was conducted (see Vorontsov et al. 1986; Baskevich et al. 2016). The use of G-banding of chromosomes of Root Voles from the Valdai National Park demonstrated polymorphism connected with Robertsonian fission of chromosome no. 8 found only in the heterozygous state. Previously, cases of Robertsonian polymorphism ($2n$ = 32, 31 and more rarely 30) were reported for isolated populations in Fennoskandia (Fredga, Persson, and Stenseth 1980), but there were both heterozygous and homozygous carriers of this chromosomal rearrangement. This can serve as the evidence of refuge existence within the glacial area of the Scandinavian Shield, from which the descendants of Root Voles have spread into the present-day Valdai (Baskevich, Khlyap, and Shvarts 2014; Baskevich et al. 2016). The molecular genetics of *Microtus oeconomus* in Valdai have not been analysed yet. Presumably, they can be attributed to the northern European phylogroup, which was distinguished based on the data from other regions (Brunhoff et al. 2003; Abramson and Tikhonova 2005).

Cytogenetic testing of the birch mice from the group *betulina* (5 individuals) captured in the vicinity of Lake Krenie was carried out. The use of chromosome markers confirmed that they belong to a 32-chromosome sibling species of the Northern Birch Mouse (Baskevich, Khlyap, and Shvarts 2012). Patterns of *C*-banded chromosomes of *Sicista betulina* from the Valdai National Park slightly differ from those of specimens from the Moscow Region and the Eastern Carpathians, which shows the chromosome-scale structure of species within the European part of its distribution range (Baskevich, Khlyap, and Shvarts 2012).

In the Valdai Lakeland, the Northern Birch Mouse inhabits biotopes of the nemoral type with a rich grass cover as well as birch forests. In the second half of August, youngsters can also be caught in pine forests (Shvarts, Demin, and Zamolodchikov 1992). The Northern Birch Mouse prefers those spruce forests of Valdai that have herb-rich ground vegetation and practically never occurs in green moss (*Bryophyta*) or false lily of the valley (*Maianthemum bifolium*) spruce forest communities (Shvarts, Demin, and Zamolodchikov 1992; Glazov 2004). In spring, *Sicista betulina* males are very active in spruce forests with nemoral ground vegetation as well as in forest-meadow floodplain communities, where they were caught in significant numbers using pitfall traps (Shvarts, Demin, and Zamolodchikov 1992). From 1974 to 1987, in the area of the IGRAS Research Station, there were 37 individuals *Sicista betulina* caught with steel spring traps (1.3% of the total number of small mammals

trapped) and 110 individuals – with pitfall traps (9.3% of the total number of small mammals trapped by this method). In a nemoral-type wood sorrel spruce forest (*Oxalis acetosella – Picea abies*) the Northern Birch Mouse was irregularly captured during trapping surveys, with its numbers varying from 0.2 to 2 individuals per 100 traps (Shvarts, Demin, and Zamolodchikov 1992). In surveys of 2011–2013, there were about 2% of the Northern Birch Mouse among the trapped small mammals.

In the Valdai Lakeland, the genus *Apodemus* (also referred to as *Sylvaemus* – see Pavlinov and Khlyap 2012) is represented by the Herb Field Mouse (*Apodemus uralensis*) and the Yellow-necked Field Mouse (*Apodemus flavicollis*). Karyotyping of two Herb Field Mouse individuals captured near Lake Krenie revealed (using C-banding) chromosome characteristics (Baskevich, Khlyap, and Shvarts 2012) similar to those of *A. uralensis mosquensis* (Orlov et al. 1996; Bogdanov 2001). The population size of the Herb Field Mouse has increased since the time described by Stroganov (1936b), who studied only one specimen of this species. During the 1974–1987 surveys, Herb Field Mice constituted 4.4% of the total number of trapped small mammals and reached the highest densities in nemoral spruce forests (up to 7 individuals per 100 traps in August 1985). At present, this species is also common (8% of the total number of rodents trapped in 2011).

The chromosome study of four Yellow-necked Field Mouse individuals captured in the areas of Sokolovo ($n = 3$) and Lake Krenie ($n = 1$) (see locations in Figure 1) revealed that all of them have a standard 48-chromosome karyotype (Baskevich, Khlyap, and Shvarts 2012) typical of most of the studied populations of this species (Kartavtseva 2002). The Yellow-necked Field Mouse from the Soltsy District of the Novgorod Region ($n = 1$) belongs to the northern group of the *A. flavicollis* intraspecific structure that is distinguished for the mitochondrial gene of the first subunit of cytochrome oxidase (*COI*) (Bogdanov et al. 2014). Despite the fact that the distribution area of this group is only very generally outlined (Bogdanov et al. 2014), it is possible to suggest that it includes the Valdai Lakeland. In the 1970s, the number of Yellow-necked Field Mice decreased to single finds (1.3% of the total number of trapped rodents), i.e. this rodent species was rarer than at the time described by Stroganov (1936b). Recently, its population has increased, and this species was common in 2011 (19.4% of the total number of trapped rodents).

Number of some species

The Eurasian Red Squirrel (*Sciurus vulgaris* L., 1758) is common. For the last 26 years its mean annual population size has been 3650 individuals, with peaks of 6302, 6970 and 6354 individuals recorded in 1998, 2002 and 2015, respectively, and low points of 700, 1260 and 1655 individuals in 2005, 2006 and 2007, respectively.

The Bank Vole (*Myodes glareolus*) is still numerous. During the 1974–1987 period, this species constituted 67.5% of the total number of trapped rodents and 27.5% of the total number of trapped small mammals. The maximal population density was registered in the oak woodland (34 individuals per 100 traps in August 1981). In a nemoral-type spruce forest, the density was up to 21 individuals per 100 traps (August 1985) and in less favourable green moss spruce forest – up to 4 individuals per 100 traps (September 1975).

Carnivora

Newly emerged and nearly disappeared species

Over the past 80 years the species list of carnivores in the Valdai Lakeland has been supplemented by two introduced species: the Raccoon Dog *Nyctereutes procyonoides* (Gray, 1834) and the American Mink *Neovison vison* (Schreber, 1777) (Table 4). Raccoon Dogs were released east and west of the Valdai National Park in 1934 (near town Vyshny Volochok, Tver Region) and in 1935 (30 km southeast of town Staraya Russia, Novgorod Region). During the first years after the release, there were reports on the Raccoon Dog population explosion accompanied by a sharp decline of ground-nesting birds, primarily, of the grouse family – the capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*) and the hazel grouse (*Tetrastes bonasia*) (Morozov 1948). At present, it is a common species with its footprints and road-kills observed regularly.

The American Mink first appeared in the Novgorod Region in the 1970s. It spread into the Valdai District (central part of the Valdai National Park), apparently, from the neighbouring Borovichi District, where fur farms were located (Tumanov 2009). In 1987, individuals of both the native European Mink (*Mustela lutreola* L., 1761) and the alien American Mink were found in the Valdai District, with the latter population significantly growing and representing 80% of the total number of individuals of both species. In 2002, the American Mink was the only mink species found in the Valdai District. In the Demyansk and Okulovka Districts (the territories of which partly overlap with the south-western and northern parts of the Valdai National Park) in 2002, it only constituted 52 and 10% of the total number of individuals of both species, respectively, with the European Mink representing the remaining 48 and 90% of the total number of mink individuals (Tumanov 2009).

The native European Mink significantly declined after the appearance of the introduced American Mink, although competition between these species is not considered to be the main causal factor (Tumanov 2009). In 1987 the European Mink was still found in all districts of the Novgorod Region, but in 2002 it was found only in 11 out of 21 districts (Tumanov 2009) including Demyansk and Okulovka Districts (see above). According to I. L.

Table 4. Carnivora and Artiodactyla of Valdai Lakeland.

No	English and scientific Names	By Stroganov (1936b)	Late 20th – early 21st centuries	
			Abundance estimate	Comments
Carnivora				
47.	Raccoon Dog *Nyctereutes procyonoides* (Gray, 1834)	Absent	Common	Introduced in 1934
48.	Gray Wolf *Canis lupus* L., 1758	Common	Rare	
49.	Red Fox *Vulpes vulpes* (L., 1758)	Common	Common	
50.	Brown Bear *Ursus arctos* L., 1758	Common	Common	
51.	Pine Marten *Martes martes* (L., 1758)	Common	Common	
52.	Least Weasel *Mustela nivalis* L., 1766	Common	Rare	
53.	Stoat *Mustela erminea* L., 1758	Common	Rare	
54.	European Mink *Mustela lutreola* (L., 1761)	Everywhere	Very Rare	In the Red Data Books of Tver and Novgorod Regions
55.	Western Polecat *Mustela putorius* L., 1758	Common	Common	
56.	American Mink *Neovison vison* (Schr., 1777)	Absent	Common	Present since 1970, escapees from fur farms
57.	Wolverine *Gulo gulo* (L., 1758)	Rare	Single visits	Needs confirmation
58.	Eurasian Badger *Meles meles* (L., 1758)	Common	Common	
59.	Eurasian Otter *Lutra lutra* (L., 1758)	Rare	Rare	
60.	Eurasian Lynx *Lynx lynx* (L., 1758)	Common	Rare	
Artiodactyla				
61.	Wild Boar *Sus scrofa* L., 1758	Single visits	Common	
62.	European Roe Deer *Capreolus capreolus* (L., 1758)	Rare	Rare	In the Red Data Book of Novgorod Region
63.	Moose *Alces alces* (L., 1758)	Very Rare	Common	
64.	Red Deer *Cervus elaphus* L., 1758	Not mentioned	Single sightings, not naturalized	Escapees from game farms, into which they were imported
65.	Sika Deer *Cervus nippon* Temminck, 1838	Not mentioned	Not found	In the 20th cent. was imported into game farms for hunting

Tumanov (2009), the European Mink population size in 1987 and 2002 was 200 and 192 individuals, respectively, in the Demyansk District, 243 and 32 individuals in the Okulovka District and 40 and 0 individuals in the Valdai District.

The Wolverine *Gulo gulo* (L., 1758) used to visit the Novgorod Region in the past. Its sightings were reported in the area of Borovichi town in the late ninetieth century and east of Lake Seliger in the late 1930s (Stroganov 1936b). There is only scarce verbal information on Wolverine visits in the second half of the twentieth century. Two animals were reported in the Valdai District (near the village Bainyovo) by the hunter V. Tichanov in 1965–1966. Two young animals were reported in the Kholm District southwest of the Valdai National Park (Doynikova, personal communication). The current presence of Wolverine requires confirmation.

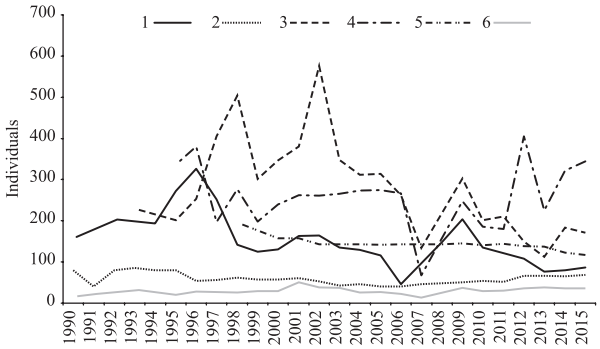

Figure 3. Long-term population dynamics of some Carnivora species in Valdai National Park (results of the data processing of Winter Transect Surveys and Brown Bear accounting). 1 – Red Fox (*Vulpes vulpes*); 2 – Brown Bear (*Ursus arctos*); 3 – Pine Marten (*Martes martes*); 4 – Western Polecat (*Mustela putorius*); 5 – Eurasian Badger (*Meles meles*); 6 – Eurasian Lynx (*Lynx lynx*).

Number of some species

The Brown Bear is still common (Table 4), although its numbers are relatively low compared to other carnivores (40–80 individuals from 1990 to 2015) (Figure 3). Traces of Brown Bear activity are registered in all 13 Forestry Departments of the Valdai National Park. The southern and central parts of the Park (Demyansk and Valdai Districts) are characterised by the optimal combination of food and shelter resources that provide for successful reproduction of this species (Doynikova and Zavorovskaya 2001). There have been slight fluctuations in the Brown Bear population size over the last 26 years: from around 80 individuals in the first half of the 1990s to 40–41 individuals in 1991, 2005 and 2006, with a recent increase to 69 individuals in 2015 (Figure 3). The Brown Bear is legally hunted, however, the number of killed animals is low (only 0–1 per year), which is explained by difficulties of bear hunting and the general desire of hunters to get a large animal, with no interest in smaller individuals that prevail in the population.

In addition to the Brown Bear, common carnivores of the Valdai Lakeland, both in the past and at present, include the Red Fox *Vulpes vulpes* (L., 1758), Eurasian Badger *Meles meles* (L., 1758), Pine Marten *Martes martes* (L., 1758) and the Western Polecat (*Mustela putorius* L., 1758), with the latter two being most numerous (Figure 3). The Pine Marten population varied from 113 to 504, and that of the Western Polecat – from 68 to 405

individuals. The Pine Marten prevailed in 1997–2011, the Western Polecat has been prevalent since 2011. The Red Fox population size fluctuated from 116 to 326 in 1990–2005. It fell to 45 individuals in 2006, rose to 204 individuals in 2009, and for the last 3 years it has been varying within the range of 76–87 individuals. The Eurasian Badger population was relatively stable, although a slight tendency for the abundance to decline can be seen.

The Eurasian Otter *Lutra lutra* (L., 1758) remains rare, with only 30–40 individuals within the Valdai National Park and generally low numbers throughout its distribution range. Several other carnivore species that were mentioned as common by Stroganov (1936b) have become rare now – the Eurasian Lynx *Lynx lynx* (L., 1758), Grey Wolf (*Canis lupus* L., 1758), Least Weasel (*Mustela nivalis* L., 1766) and the Stoat (*Mustela erminea* L., 1758) (Table 4). The number of the Eurasian Lynx decreased from 51 to 14 individuals in the 2001–2007 period, and stabilised at 36–38 animals in the last 4 years (Figure 3).

Despite the new tendency for the appearance of feral dogs and cats, the total number of carnivorous mammals in the Valdai Lakeland is generally decreasing.

Artiodactyla

Newly emerged species

The list of three species of native even-toed ungulates has not changed for the past 80 years (Table 4). Local game farms also import the Sika Deer (*Cervus nippon* Temminck, 1838) and the Red Deer (*Cervus elaphus* L., 1758). Individuals of the latter species occasionally escape into the wild and can be seen in the Valdai National Park. One escapee was killed by poachers in the northeast of the Park (Okulovka District of the Novgorod Region, near its border with the Tver Region) (Privalov 2011). However, there is no evidence of this species naturalisation. In our opinion, this deer species is only going through the first phase of the invasive process and should not be included into the list of modern Valdai fauna.

The Reindeer *Rangifer tarandus* (L., 1758) had disappeared from Valdai by the early twentieth century according to Stroganov (1936b). Nevertheless, relict 'island' populations of the Reindeer were found in 1938 north of Tver city, beyond the Valdai Lakeland area (Orshinsky Mokh bog) (Geptner, Nasimovich, and Bannikov 1961). There have been no indications of the Reindeer occurrence in the study region in more recent years. Regardless of the opinion that during the retreat of the Reindeer to the north in the twentieth century, a few small groups of these animals could have remained in some remote isolated places (Kuznetsov and Tishkov 2012; Tishkov 2013), we did not include this species into the list of the twentieth century fauna of the Valdai Lakeland.

The Wild Boar used to be a rare visitor previously, but now it is common and legally hunted. The long-term population density of the Wild Boar within the Valdai District (30–40 individuals per 100 km^2) is among the highest in the Novgorod Region due to the optimal combination of forest and field areas therein and the regular use of biotechnological and conservation measures (Doynikova and Chistyakova 2000). The Wild Boar population significantly fluctuates depending on wintering conditions, particularly, on snow depth. In the Valdai National Park population peaks (427–458 individuals) were recorded in 1991, 2007 and 2008 and low points (46–80 individuals) in 1995–1997. In recent years, the Wild Boar population has also decreased (with current numbers no higher than 200), following the unfavourable (very snowy) winter of 2010–2011 and the epizootic of African swine fever in the neighbouring districts of the Tver Region.

Number of some species

The population of the Moose *Alces alces* (L., 1758) has significantly grown like in many other regions of the European part of Russia (Kuznetsov 1983; Kuznetsov and Tishkov 2012). In the last 26 years, its highest numbers within the Valdai National Park were recorded in 1992 and 1993 (576 and 625 individuals, respectively). There was a decrease (192 individuals) at the turn of the century, which was followed by the increase to 386 individuals in 2015.

The European Roe Deer *Capreolus capreolus* (L., 1758) remains rare. Its numbers in the Valdai National Park are fluctuating. It is listed in the Red Data Book of the Novgorod Region as a near-threatened (NT) species (Doynikova et al. 2015). The boundaries of its distribution range continuously vary depending on snow depth variations across the years. In the Novgorod Region, which is officially considered to be part of the European Roe Deer distribution range, this species regularly disappears and reappears. The main limiting factors controlling the European Roe Deer population within this locality include snow depth, poaching levels and predation by wolves (Doynikova et al. 2015). The European Roe Deer was very rare in the 1960s – early 1970s (Kuznetsov and Tishkov 2012), but its numbers have started to grow since the late 1990s due to the control of the Grey Wolf population, hunting ban, regular implementation of biotechnology and also reduced snow depth during winter seasons of the first decade of the twenty-first century. A total of 10 individuals of the European Roe Deer have been reported in the Valdai region. In the course of the winter surveys of 2006–2010 in the Valdai National Park this species was recorded only in 2008. The latest sighting of the European Roe Deer in the Valdai region dates back to autumn 2015 (Kuznetsov, personal communication). Obviously, the recent trend for the European Roe Deer population recovery would cease without the constant support provided by people: supplementary feeding,

hunting ban, control of the Grey Wolf population, etc. (Maksymiuk and Doynikova 2007).

Discussion

In total, 65 species of mammals were recorded within the Valdai Lakeland in the twentieth century. Stroganov (1936a, 1936b) reported 55 species including the Tundra Shrew, which was probably incorrectly identified, and the Brown Rat, which, as we now know, had not spread into the Valdai Lakeland at that time. Therefore, the local mammal fauna of the 1930s should have been correctly estimated at 53 species. However, over the next 80 years, researchers have also recorded previously unidentified species, such as the Natterer's Bat, Wood Lemming and the European Pine Vole. Moreover, the Whiskered Myotis and Brandt's Myotis, which were considered as subspecies by Stroganov (1936a), are now considered as two independent species. In addition, the systematics of the voles *Microtus arvalis* s. l. has changed. By now, there is firm evidence of the presence of *M. levis* in the Valdai Lakeland. The presence of other sibling species (*M. arvalis* s. str.) is likely, but requires confirmation. The Eurasian Beaver has been reintroduced. The Muskrat, Raccoon Dog and the American Mink have been introduced. The Red Deer and Sika Deer have been imported (into game farms), but not naturalised. The Brown Rat has colonised the region and is now common. The Wild Boar, which used to be a rare visitor in the 1930s, has also become common. Species that have disappeared include the Russian Desman and the Forest Dormouse, which were rare only in the past, and the Black-bellied Hamster, which started to spread into the region following agricultural intensification, but did not persist here due to the recent arable land area decrease. The current presence of the Wolverine and the Black Rat in the Valdai Lakeland requires confirmation. Data on bats are insufficient, particularly, there is a lack of evidence of the current presence of the Whiskered Myotis, Common Pipistrelle and the Parti-coloured Bat.

The Valdai Lakeland mammal fauna (excluding Chiroptera) includes three large zoogeographical groups of species, which are: (1) widespread within the Palearctic region, (2) spread mostly in the European (western) part of the Palearctic region and (3) spread mostly in the north-eastern part of the Palearctic region. Over the last 80 years, the number of species in these groups has changed from 17, 11 and 4 species (Stroganov 1936b), to 16, 21 and 5 species, respectively. The increase in the number of the Western Palearctic species is explained, in our opinion, by improved knowledge of the distribution ranges of mammals.

For example, Stroganov (1936b) included 11 species of mammals into the second group. Two species of this group (the Russian Desman and the Forest Dormouse) later disappeared from the investigated territory. Other 9 species (the Western European Hedgehog, European Hare, Garden Dormouse, Bank Vole, Herb Field Mouse, Yellow-necked Field Mouse, European Pine Marten, European Mink and theWestern Polecat) are in the modern list of the Western Palaearctic group now. We also included the Eurasian Least Shrew, Eurasian Common Shrew and the Field Vole into the second group. These species were widely spread according to Stroganov, but their areas mostly cover Europe. We also enlarged the second group by including 6 species (the European Mole, Northern Birch Mouse, European Water Vole, Common Vole, Eurasian Badger, European Roe Deer) that Stroganov had discovered in the Valdai fauna but had excluded from the zoogeographical analysis and 3 species (the Eurasian Beaver, European Pine Vole, East European Vole) that were found in the Valdai region after Stroganov's publications.

Besides species of the above three groups, the modern fauna comprises 7 alien species. The House Mouse and the Black Rat are ancient invaders; 5 other species – the Brown Rat, Muskrat, Raccoon Dog, American Mink, and the Wild Boar[1] – are modern invaders. All these species have colonised areas far outside their native distribution ranges. Human-induced formation of their modern distribution range does not allow us to attribute these species to any of the three aforementioned zoogeographical groups. Apart from the 7 alien species specified above, there is another species that appeared in Valdai in the second half of the twentieth century – the Eurasian Beaver, which was reintroduced in Valdai after a period of absence longer than 100 years. For the first 20–40 years after the reintroduction, the Eurasian Beaver has been comparable to modern invaders in its unanticipated impact on ecosystems and its population growth pattern (Petrosyan et al. 2013, 2016), yet we can attribute it to the second zoogeographical group (Western Palearctic species) judging from the boundaries of its former and restored distribution ranges.

Thus, the above-presented latest data serve as a basis for reconsidering the composition of the zoogeographical groups and also for considering alien species as forming a new, fourth group. The general attributes of the Valdai fauna composition still remain the same: (1) the presence of different groups of fauna species, (2) low number of the Eastern Palearctic species and (3) a significant contribution of the Western Palearctic species. The presence of species with different histories of the distribution range formation is generally due to the preservation of refuges for various groups of animals within the boundaries of the last Valdai glaciation. The zoogeographical analysis of the Valdai Lakeland fauna shows that the Western Palearctic species had many more ways to get into the study area and also more opportunities for survival within local wildlife refuges than the Eastern Palearctic species. It should be mentioned that all the three species that disappeared from

Valdai (the Russian Desman, Forest Dormouse and the Black-bellied Hamster) belonged to the group of Western Palearctic species, i.e. this group of species was the most vulnerable to the combined impact of modern factors, including the human impact.

The anthropogenic impact has also led to the prevalence of alien species over the number of Eastern Palearctic species in the present-day Valdai Lakeland fauna. This is a general trend in the development of the modern mammal fauna in Russia, as the existence of alien species has been reported throughout practically its entire territory (Khlyap, Warshavsky, and Bobrov 2011).

The ecological analysis of fauna composition shows species distribution in relation to natural zones, taking into account their habitat preferences. Five large zonal-ecological groups have been distinguished on the basis of the existing data on the Valdai Lakeland:

Group 1

Forest species. The group is subdivided into 4 subgroups: 1.1. Widespread forest spp. – including 8 species: the Mountain Hare, Siberian Flying Squirrel, Eurasian Red Squirrel, Brown Bear, European Pine Marten, Eurasian Badger, Eurasian Lynx, Moose. 1.2. Northern and middle taiga (boreal) spp. – 7 species: the Laxmann's Shrew, Even-toothed Shrew, Eurasian Pygmy Shrew, Wood Lemming, Northern Red-backed Vole, Field Vole, Wolverine. A special position in this subgroup belongs to the Even-toothed Shrew, which prefers richer wet grasslands in Valdai (Shvarts, Demin, and Zamolodchikov 1992). 1.3. Southern taiga spp. – 5 species: the European Mole, Eurasian Common Shrew, Eurasian Least Shrew, Northern Birch Mouse, Bank Vole. 1.4. Broad-leaved forest (nemoral) spp. – 5 currently present species: the Garden Dormouse, European Pine Vole, Herb Field Mouse, Yellow-necked Field Mouse, European Roe Deer; and the recently disappeared species: the Forest Dormouse.

Group 2

Meadow-field species, including forest-steppe species – 7 currently present species: the Western European Hedgehog, European Hare, Common Vole, East European Vole, Eurasian Harvest Mouse, Striped Field Mouse, Western Polecat; and also the Black-bellied Hamster that started to spread into Valdai in the early twentieth century through fields of cereal crops, but has currently disappeared.

Group 3

Species living in several landscape zones – 6 species: the Raccoon Dog, Grey Wolf, Red Fox, Least Weasel, Stoat, Wild Boar.

Group 4

Semi-aquatic and aquatic species – 8 currently present species: Eurasian Water Shrew, Eurasian Beaver, Muskrat, European Water Vole, Root Vole, European Mink, American Mink, Eurasian Otter; and the disappeared Russian Desman.

Group 5

Synanthropic (commensal) species (see terminology explained in Khlyap, Glass, and Kosoy 2012) – 3 species: the House Mouse, Brown Rat and the Black Rat.

Results of the above ecological analysis confirm that the core of the Valdai mammal fauna consists of forest species. Altogether forest species represent about half of the total number of mammal species of Valdai, i.e. 25 of the 49 species analysed (except Chiroptera and disappeared species). The first and second positions in the order of prevalence are occupied by subgroups of the widespread non-specific forest type (8 species) and boreal type (7 species) species. Numbers of southern taiga and nemoral species are equal (5 species each), with the southern taiga species subgroup, particularly, that of the Eurasian Common Shrew and Bank Vole, having the highest number of individuals. Three other southern taiga species: the European Mole, Eurasian Least Shrew and the Northern Birch Mouse are common. Among boreal species, the Laxmann's Shrew is dominant by the number of individuals; this species also ranks second in abundance of *Sorex* shrews. The abundance of nemoral species is limited: the Forest Dormouse has disappeared and the Garden Dormouse is very rare and sporadic. The same probably also applies to the European Pine Vole, although data on its distribution within the Valdai region are insufficient. Contributions of the Herb Field Mouse, Yellow-necked Field Mouse and the European Roe Deer to the nemoral species subgroup are slightly higher, but still of low significance. Therefore, it can be suggested that modern fauna development in Valdai shows a tendency towards increased significance of southern taiga mammals.

The large total area of water bodies within the Valdai Lakeland predetermines the important contribution of semi-aquatic mammals, which further increased due to the reintroduction of the Eurasian Beaver, and the introduction of the Muskrat and the American Mink that now have outnumbered indigenous species of this group.

The recent decrease in the area of arable lands and meadows due to their natural reforestation has led to the on-going decrease in the significance of meadow-field species. As a result of the overall decrease of the large mammal population size, the role of species from non-specific habitats has decreased with the exception of the Wild Boar, which has recently increased in numbers, especially where it has been supplementary fed for hunting purposes.

As regards synanthropic species, the House Mouse has disappeared from small villages due to the general tendency towards villages' abandonment and reduction of cattle numbers around villages (Istomin 2008). There are no recent data on Black Rat populations. Also, there

is a new tendency for feral dogs and cats to appear in the fauna.

Conclusions

The modern mammal fauna of the Valdai Lakeland is estimated at 60 species, but the current presence of at least 6 of them needs confirmation. Changes in the species list of this location over the last 80 years include the loss of 3 species, the addition of 5 species (resulting from the differentiation of sibling species and the identification of previously unidentified species) and the appearance of 6 modern invaders, among which 3 were introduced (the Muskrat, Raccoon Dog and the American Mink), 1 reintroduced (the Eurasian Beaver) and 2 entered from adjacent regions (the Brown Rat and the Wild Boar). The intraspecific structure of several Rodentia and Eulipotyphla species was verified on the basis of modern genetic analyses.

The current stage of fauna development in the Valdai Lakeland is characterised by the appearance of a new group of alien species, which outnumber the group of Eastern Palearctic species.

The current increase in the forest cover through natural reforestation processes explains the prevalence of forest fauna, which has remained the core of the Valdai mammal fauna since the beginning of the twentieth century. Altogether such forest species represent about half of the total number of mammal species in Valdai. The forest species group (not including Chiroptera) comprises the following subgroups: boreal (7 species), southern taiga (5), nemoral (5) and widespread non-specific forest type species (8). Among them, the southern taiga species subgroup is distinguished for the highest number of individuals, while the abundance of nemoral species is limited. Therefore, it can be suggested that significance of southern taiga mammals in the modern Valdai fauna is increasing.

The large total area of water bodies within the Valdai Lakeland predetermines the high importance of semi-aquatic mammals, which has further increased after the appearance of introduced and reintroduced species that have now outnumbered indigenous inhabitants of these biotopes. These species have not only increased the faunal diversity, constituting about 13% of the total, but have also changed features and functioning of semi-aquatic ecosystems in the region.

Changes in land management over the last decades have resulted in a decreasing significance of meadow-field species and synanthropic species. Among species living in several landscape zones, the Wild Boar has recently become more numerous, especially where it has been supplementary fed for hunting. The appearance of feral dogs and cats is a new tendency of change in the fauna.

The data of modern genetics (i.e. diversity of races and chromosomal polymorphism *of the Eurasian Common Shrew and* chromosomal polymorphism *of the* Root Vole) confirm the important role of the last glaciation in local fauna formation. Significant changes in landscapes, which occurred in prehistoric times in response to glacial and post-glacial processes and in historic times due to the significant human impact, have caused mixing and interlacing of faunal elements that have persisted to the present day.

Note

1. The Wild board was absent from the Valdai Lakeland for at least a few centuries, so for this reason we consider it to be a modern invader.

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