

Population dynamics of wood lemming (*Myopus schisticolor*) in different landscapes of the Northern Pre-Urals

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ABSTRACT. The paper presents the results of the monitoring (1988–2016) of wood lemming *Myopus schisticolor* (Lilljeborg, 1844) numbers from different landscape areas of the Pechora-Ilych Nature Reserve. It is shown that the population dynamics of this species differ considerably between marked landscapes. The lowland area is characterized by low number of animals with a rare irregular increase of abundance. The cyclic fluctuations were revealed in the foothills with a period of 3–4 years. In the years of depression the abundance indices dropped to zero and quite often it exceed over 100 individuals per 100 cone/nights in the years of number outbreaks. The migrations of animals are observed during the periods of high density. In the lowlands the wood lemming is marked only the next year after a sharp increase in its numbers in the foothills.

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KEY WORDS: wood lemming, *Myopus schisticolor*, autecology features, population dynamics, landscapes.

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Динамика популяций лесного лемминга (*Myopus schisticolor*) в разных типах ландшафтов Северного Предуралья

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РЕЗЮМЕ. В работе представлены результаты мониторинга (1988–2016 гг.) численности лесного лемминга *Myopus schisticolor* (Lilljeborg, 1844) в разных ландшафтных районах Печоро-Ильчского заповедника. Показано, что динамика популяций этого вида значительно различается между ними. Для равнинного района характерна низкая численность животных с редкими нерегулярными подъемами обилия. В предгорном районе выявлены циклические колебания с периодом в 3–4 года. В годы депрессий численности показатели обилия опускаются до нуля, а в годы вспышек численности нередко превышают 100 особей на 100 конусо-суток. В периоды высокой плотности наблюдаются миграции животных. В равнинном районе лесной лемминг отмечается лишь на следующий год после резкого подъема его численности в предгорьях.

КЛЮЧЕВЫЕ СЛОВА: лесной лемминг, *Myopus schisticolor*, аутоэкологические особенности, динамика численности, ландшафты.

Introduction

The wood lemming, *Myopus schisticolor* (Lilljeborg, 1844) (Fig. 1) is spreads from the western part of Norway and Sweden to Kamchatka and Sakhalin Island (Shenbrot & Krasnov, 2005). The distribution of this species is closely associated with the coniferous boreal forests. It occurs sporadically on the most of its area and it is a rare species (Henttonen & Hanski, 2000). At the same time, there are areas with a high animal density where wood lemming sometimes dominates in the population of small mammals (Volpert & Shadrina, 2002; Eskelinen *et al.*, 2004; Emelyanova & Leonova, 2016).

It is believed that the optimal conditions for this species are forming in the northern taiga (Emelyanova, 2015).

Population dynamics of wood lemming is in many aspects still an enigmatic phenomenon. Outbreaks were recorded in different parts of the area, which were repeated extremely irregularly (Nikanorov, 1986; Volpert & Shadrina, 1990; Mysterud, 2016). Infrequently they represented periodic (cyclic) fluctuations (Eske-linen *et al.*, 2004). In the cyclic populations of this species the years with high numbers alternated the years of deep depression. Moreover, some regions experienced temporary structural changes in the abundance of animals. As a result, the regular fluctuations changed to a period with consistently low density (Katayev & Katayeva, 2008).

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Fig. 1. Wood lemming, *Myopus schisticolor* (©Anatoly Bobretsov).

It is known that the specific character of the dynamics of small mammals abundance is formed as an integrated response of the population to the impact of the entire complex of environmental conditions (Shilov, 1991; Yoccoz & Ims, 2004; Ivanter, 2008; Zhigalski, 2016). The great importance has the landscape heterogeneity of the territory at the same time (Barrett & Peles, 1999; Duhamel *et al.*, 2000; Huitu *et al.*, 2003; Dalkvist *et al.*, 2011). Any differences in the dynamic character of small mammal populations can be related to landscape structure directly or indirectly (Loman, 2008). In this case, the landscape effect is expressed not only in reduction of the amplitude of abundance fluctuations, but also in the changing of dynamics type.

In this study we describe the regularities of the wood lemming population dynamics in the Northern Pre-Urals. As well we discuss the peculiarities of long-term changes in abundance of *M. schisticolor* in different landscape areas of the Pechora-Ilych Nature Reserve and analyze the reasons of these differences and the role of landscape conditions in it.

Material and methods

The investigations took place in the lowland and foothill landscape areas of the Pechora-Ilych Nature Reserve located in the South-East of the Komi Republic (Russia) from 1988 to 2016. The sites of researches were located at a distance of 86 km from each other.

The natural conditions of the areas vary considerably.

It is known that the wood lemming can not be registered by the trap-lines catching method. Therefore, we used, for example, a scoring system consisting of several indirect characteristics to evaluate the abundance of this species in Scandinavia (Eskelinen *et al.*, 2004). The registrations of the wood lemming in the Pechora-Ilych Nature Reserve were carried out by catching ditches and covered different habitats. The ditches 50 m long with five cones were opened in the second half of the summer for 12–15 nights. The number of animals caught per 100 cone/nights (individuals per 100 cone/nights), was taken as an index to measure the relative abundance of lemmings. In the lowland region, there were seven ditches in five habitats, in the foothill region 6 ditches in 4 habitats. During the whole period of researches there were work out 9580 cone/nights in the lowlands, and 6085 cone/nights in the foothills. It was caught 196 wood lemmings in the first area, and 1405 animals in the second one.

Depending on the nature of variability in the animal numbers the wood lemming populations from different landscape areas were classified to one of three types of population dynamics (Korpimäki *et al.*, 2004): cyclic, unstable, and stable. Cyclic type is characterized by regular (periodic) changes in the number individuals, and large amplitude of abundant oscillations. An unstable type includes populations with a low number and rare increases of abundance on background. Stable type



Fig. 2. Photography of a typical lowland forest with *Pinus sylvestris* and *Cladonia lichens* in dominants.

of dynamics refers to populations with low numbers and minor amplitude of fluctuations.

The method of spectral densities analysis was used to a precise mathematical definition of the cyclicity (e.g. see Boonstra & Krebs, 2012). Previously the procedure of normalization of the initial data was done as a taking its logarithm since the distribution of the annual number indexes was strongly deviated from normal distribution (the compliance was determined with the Kolmogorov–Smirnov test). At the same time appropriated to zero indicators the minimum value 0.1. Visualization of periodic components and their significance was carried out on periodograms. The software package Statistica 6.0 for Windows was used for statistics calculations.

Description of the landscapes

Our investigations, as mentioned above, were conducted in lowlands, so-called “plane region”, and foothill regions. Both regions (areas) are characterized by different landscapes.

The flat in plane lowland area is located in the eastern part of the Russian Plain. It is characterized by a uniform relief and heights from 50 to 150 m a.s.l. Forests predominates on the most part of the investigated area (about 86% of the total area), with dominated the Scots pine, *Pinus sylvestris*. In the ground cover of almost a half of them (43%) dominates the several

species of lichens, namely *Cladonia rangiferina*, *C. abuscula* and *C. stellaris*. The most common species among the dwarf shrubs is *Vaccinium vitis-idaea*. In the lowered areas the *Cladonia* lichens are replaced by green mosses *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum scoparium*. The dwarf shrub *Vaccinium vitis-idaea* is replaced by *V. myrtillus*. Marshes are the second essential element of this landscape. A characteristic feature of the plain zone is the alternation of pine forests and marshes. The share of Siberian spruce *Picea obovata* forests accounts for only about 11% of the forest covered area. These forests are located mainly in river valleys and are highly fragmented of mesorelief (Fig. 2).

The foothill region is located within the Ural mountainous country (Northern Urals). It is represented by a hilly elevation intersected by several low ridges (300–400 m a.s.l.) in the meridional direction. Most of the territory (about 76%) is occupied by polydominant dark coniferous taiga. Forest massifs consist of *Picea obovata* with significant share of Siberian fir *Abies sibirica*, Siberian stone pine *Pinus sibirica*, white birch *Betula pubescens*. Scots pine is a rare species here. These overripe forests are characterized by the development of powerful moss cover (Fig. 3). In the relief depressions of the ridges there are forests with domination of *Picea obovata*. Green mosses of *Polytrichum commune*, *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum scoparium* and dwarf shrub *Vaccinium*



Fig. 3. Photography of a typical foothills forest with *Picea obovata* and green mosses *Polytrichum commune*, *Hylocomium splendens*, *Pleurozium schreberi*, as optimal habitats of wood lemming.

myrtillus are dominates in their ground cover. The slopes of the ridges are covered with forests of *Picea obovata* and *Abies sibirica*. Large ferns *Dryopteris dilatata* are dominated in the lower tier of these forests. Species *Vaccinium myrtillus*, *Oxalis acetosella* and green mosses *Pleurozium schreberi*, *Dicranum scoparium* are abundant here. Forests of *Picea obovata*, *Abies sibirica*, *Pinus sibirica* grow in the river floodplains. The lower tier of these forests is formed by *Aconitum septentrionale*, *Geranium sylvaticum*, *Crepis sibirica*, *Paeonia anomala*, *Dryopteris dilatata*. There are very few mosses here.

Results

The average number of wood lemming in the lowlands of the reserve was 3.2 (0–38.6) individuals per 100 cone/nights. On the general background of low abundance (0.4 individuals per 100 cone/nights) two sharp increases in the animal abundance were noted here over 29 years of observations (Fig. 4A). The first rise occurred in 1989 (38.6 individuals), the second took place in 2005 (33.0 individuals). In both cases, the increase in number of lemmings was recorded on the eve of the outbreak: 9.5 individuals per cone/nights in 1988, and 2.7 individuals in 2004. The wood lemming was absent in the catches during the period from 1990 to 1997. Significant periodic components in the time

series of numbers could not be identified. The dynamics of population of this species in the lowland part of the reserve belongs to the unstable type.

The significant fluctuations in the number of wood lemmings were revealed in the foothills (Fig. 4B). Here the years of deep depression, when animals were absent in catches or caught in a single number, alternated with years of sharp rise of abundance. The most significant increases were recorded in 1988–89, 1998–99, 2004–2005 and 2013. Abundance indices of exceeded 50 individuals in these years with an average multi-year value of 25.7 individuals per 100 cone/nights. The maximum number was recorded in 1988 (133.0 individuals per 100 cone/nights). It reached 182 individuals per 100 cone/nights in optimum habitats (*Picea obovata* with *Polytrichum*) in this year. As a rule, a high number of animals was observed for two years, after which there was a sharp decline which lasted two years. A similar situation is described for the wood lemming of Eastern Fennoscandia (Skaren, 1963; Katayev & Katayeva, 1999).

The maximum frequency of the spectrum variations in number of wood lemming is 3.5 years in the foothill region (Fig. 5). This indicates the existence of periodic (cyclic) fluctuations in the populations of this species with a 3–4 years length. In the cyclic population of this species from Eastern Finland have been identified a 3-year cycles (Eskelinen *et al.*, 2004). At the same time,

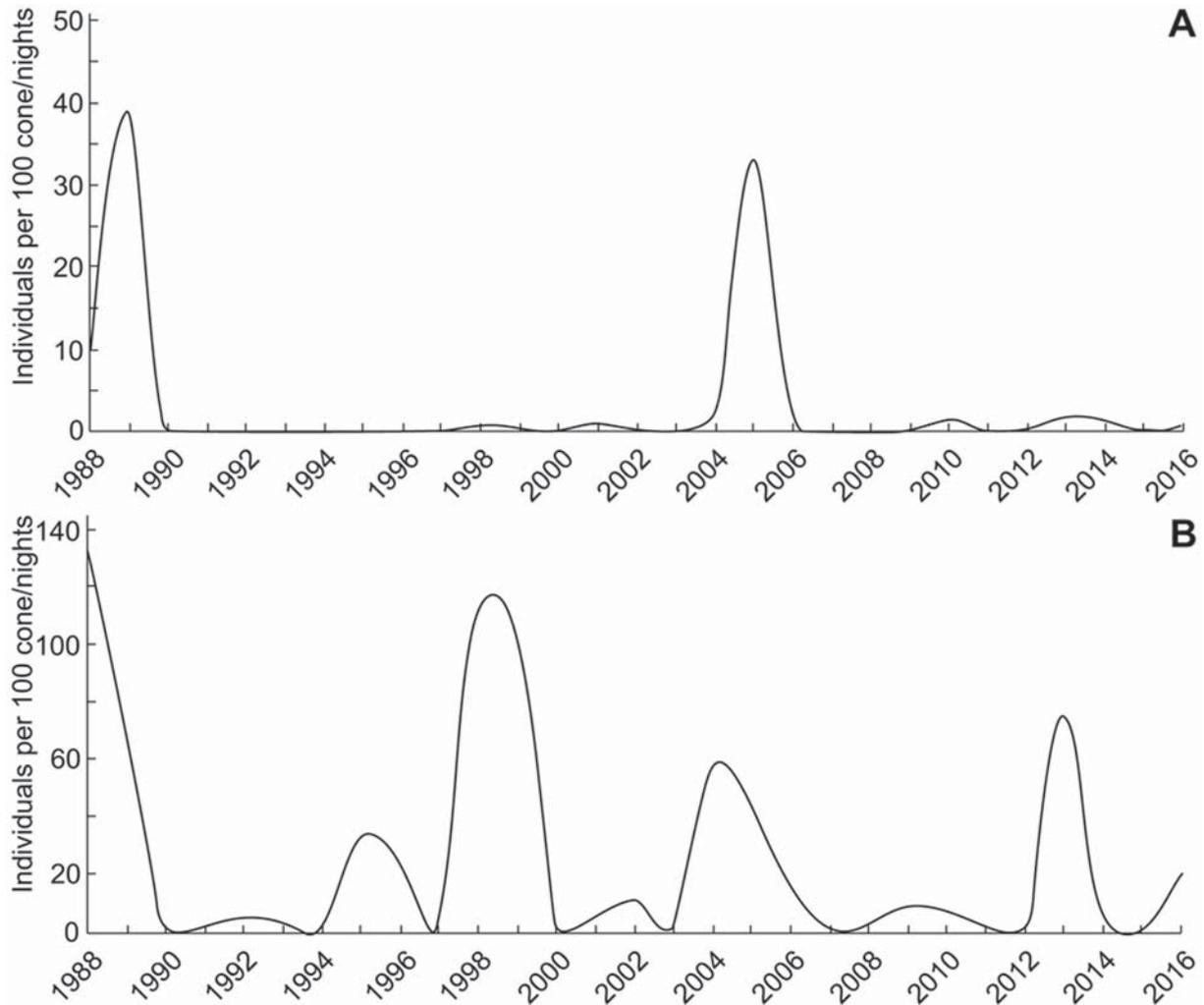


Fig. 4. The dynamics of wood lemming number in the lowlands (A), and foothills (B) of Pechora-Ilych Nature Reserve.

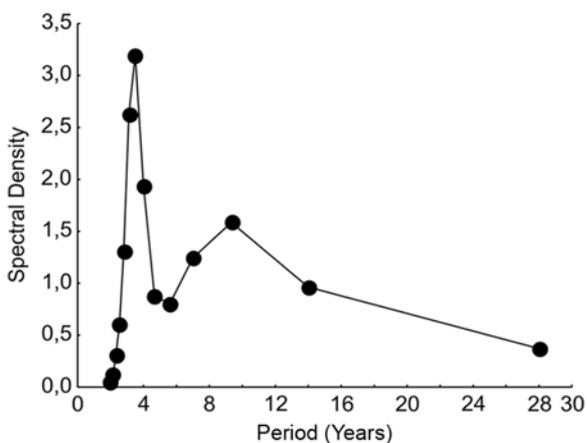


Fig. 5. Spectral densities of the wood lemmings from foothill area.

according to data of other authors the periods between cycles in the western part of the area can be at least 5 years (Emelyanova & Leonova, 2016).

Despite the differences in the population dynamics of animals in different landscape areas the synchronous changes are noted between them ($r = 0.68$, $t = 4.81$, $p < 0.001$). Outbreaks of the wood lemming number in the lowlands occurred against a background of high density of animals in the foothills. However, this species appeared in a relatively large number in the lowlands only in the second year after a sharp increase of population in the foothill taiga, as was first mentioned by Teplova (1952). At the same time the density of animals in the foothills decreased. So, in 1988 the abundance of lemming reached 133 individuals per 100 cone/nights in the foothills, and 9.5 individuals in the lowlands. The next year it decreased in the foothills up to 65.1 individuals, and increased to 38.6 individuals per 100 cone/nights in the lowlands. A similar situation developed in 2004–2005, when the wood lemming showed very low abundance or full absence in the catches from lowland

area. A similar redistribution of numbers of this species in adjacent years through different landscapes was described for the Indigirka river basin (Volpert & Shadrina, 2002). In high-density years the animals may migrate from congested areas to the adjacent districts with low numbers (Kalela, 1963; Uino, 1963; Eskelinen *et al.*, 2004).

Discussion

The population dynamics of wood lemming in two adjacent landscape areas of the Northern Pre-Urals varies considerably. It was cyclic in the foothills, and irregular in the lowland part. A stable type of population dynamics of this species is characteristic for many taiga regions of the European North where the maximum annual abundance indices did not exceed eight individuals per 100 cone/nights.

Estimates of the role of various factors affecting the variability of wood lemming numbers are quite contradictory. Eskelinen (2004) believes that predator-specialists are the main reason of cyclical fluctuations of this species in Finland. In his opinion, the synchronism in the dynamics of wood lemming with other vole species evidences in favor of this hypothesis. Feed resources do not play a great role. Some effect they can have only in peak years of abundance. Other authors (Sadykov *et al.*, 1986; Bondrup-Nielsen & Ims, 1988) believe that the number of this species is strictly limited by forage base, while the abundance of other rodent species is limited by other factors.

The ecological requirements of the wood lemming are quite specific. It is a specialized bryophage (moss-eater) in contrast to other boreal rodent species. His diet consists of mosses on 75–90% according to various estimates (Tishkov, 1986; Bondrup-Nielsen, 1993; Eskelinen, 2002). According to these studies, the most preferred mosses species are representatives of genera *Dicranum*, *Polytrichum*, *Ptilium crista-castrensis* and *Pleurozium schreberi*. Green moss *Hylocomium splendens* was well eaten by animals in some areas, but not in others. Sphagnum mosses are almost not used. The diet of the wood lemming in a small amount was consisted of shoots and leaves of blueberries (*Vaccinium uliginosum*) and cranberries (*V. oxycoccos*), leaves of wavy hair grass (*Avenella flexuosa*) and wood rush fibrous (*Luzula pilosa*) (Kalela *et al.*, 1963). In the second half of the summer the proportion of herbaceous plants can reach 11% in the diet of animals (Revin, 1989). Another important feature of the ecology of this species is the large need of water in comparison with voles (Ilmen & Lahti, 1968).

These features play an important role in habitat selection of wood lemming. Optimal conditions for it are formed in moderately and excessively wet dark-coniferous forests with abundant moss cover. A close connection with similar types of habitats was marked for different parts of the area (Revin, 1989; Ims *et al.*, 1993; Abramov *et al.*, 2013). The ratio of optimal and

pessimal habitats (landscape structure) in different landscape areas of the Pechora-Ilych Nature Reserve has significantly influenced the formation of animal numbers.

The lowland area of the wood lemming habitat is a highly fragmented landscape where optimal habitats are rare and isolated from each other. Its total area is amounted 3% of the entire forested area. It is known that fragmentation of landscape influences the dynamics of animal populations (Wiegand *et al.*, 2005), including decrease of the small mammals abundance (Hornfeldt, 2004) and the reducing an amplitude of fluctuations (Hansson, 2002). This is the most likely reason for the low density of lemmings in this part of the reserve. Irregular and rare outbreaks of abundance of this species here are explained by the effect of “periodic travelling waves” described for some vole species of the Northern Europe (Sherratt & Smith, 2008). In this case, the high number of animals leaved territories with high density, and goes to the territories with low density relatively quick. Two conditions are necessary to appear an effect of “travelling waves”: first is the spatial landscape heterogeneity, and, second, considerable migration activity of animals (Johnson *et al.*, 2006; Berthier *et al.*, 2014).

Migrations of wood lemming are well known and had been described for different parts of the spatial area (Kalela, 1963; Volpert & Shadrina, 1990; Eskelinen, 2004). In the years of high numbers the animals in mass are found in all habitats including pessimal biotopes, such as meadows. So, during the outbreak of 1998 in the haircap-moss spruce forest were caught 113.4 individuals per 100 cone/nights, in the spruce herbal habitats — 112.4 individuals and 135.0 individuals were caught in the meadows. In the second half of the summer the lemmings often swim across rivers, some of them drown or become a prey of predatory fish. In the middle August 1989 in the upper stream of the Pechora River while 2 km route were found 18 dead animals. In the second half of August of the same year there were 50 dead individuals on the banks of the Ilych River. According to Teplova (1952) the share of wood lemming founded in stomachs of umber *Thymallus thymallus* and pike *Esox lucius* reached 81% among other species of small mammals during one of such periods.

The optimal habitats of the wood lemming in the foothill region occupies is a huge space (over 70%). Besides, this area receives on 170 mm more of precipitation in compare with the lowlands. Dark coniferous forests are characterized by a powerful development of the moss layer, the height of which reaches 30–40 cm. Such a “hypertrophy” of the moss cover in forests is a consequence of high humidity of the western slopes of the Northern Urals and primeval (virginity) of the taiga forests (Korchagin, 1940). Apparently, huge stores of food resources and the moisture of the territory are the main causes of high density of lemmings in this area. The decrease in abundance of this species from the Southern Yakutian foothills to the lowlands is also

explained by the reduction of the atmospheric precipitations volume, and respectively in reduction of the general watering of the territory (Revin, 1989).

The reasons of cyclic fluctuations of wood lemming in the foothills of the Northern Urals can not be explained within the frames of the hypothesis of depletion of forage resources and by the role of predators. Undoubtedly, this species plays an important role in population dynamics of mosses (Rydgren *et al.*, 2007). In some areas of Sweden there were suffered 73% *Ptilium crista-castrensis* and 57% of *Dicranum scoparium* during the years of high lemming numbers (Ericson, 1977). The share of eaten green mosses at the study sites in Finland ranged from 2 to 30% (an average 13%), prevailed in summer (Eskelinen, 2004). The stores of food resource in the foothill taiga of the Urals are great and therefore it could not be a limiting factor of voles density change. Indirect confirmation of this is synchronism in the change in number of wood lemming with other cyclic species that consume completely different fodder (Bobretsov, 2016). So, the value of the Spearman' correlation index between the indices of abundance of *M. schisticolor* and *Microtus agrestis* (Linnaeus, 1761) was 0.69 ($t = 4.92, p < 0.001$), *Alexandromys oeconomicus* (Pallas, 1776) was 0.67 ($t = 4.54, p = 0.000$), *Craseomys rufocanus* (Sundevall, 1846) was 0.65 ($t = 4.32, p < 0.001$). Outbreaks of number and depressions of these species coincided in time. However, not predators are the reason of numbers synchronization in this case, although they are often called as one of the main mechanisms (Korpimäki *et al.*, 2005). The snow cover developing, the duration of its bedding, the density of predator specialists are important attributes of the forming of vole cycles in Scandinavia (Hansson & Henttonen, 1985). These characteristics vary considerably in different landscapes. So, the height of snow cover is on 25 cm larger, and the density of predator-specialists is in three times higher in the foothills rather in the lowland habitats. In these conditions there should be observed a synchronous changes in the numbers of different small mammal species between different landscapes. Nevertheless, agreed-upon fluctuations of voles and shrews abundance are noted between them in fact.

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