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SPREADING OF SHRUBS ON THE YAMAL PENINSULA AS A FACTOR IN BIOTOPIC DISTRIBUTION OF SMALL RODENTS

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Выпускная квалификационная работа

РАСПРОСТРАНЕНИЕ КУСТАРНИКОВ НА ПОЛУОСТРОВЕ ЯМАЛ КАК ФАКТОР БИОТОПИЧЕСКОГО РАСПРЕДЕЛЕНИЯ МЫШЕВИДНЫХ ГРЫЗУНОВ

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Spreading of shrubs on the Yamal Peninsula as a factor in biotopic distribution of small rodents

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Cold Region Environmental Landscapes Integrated Sciences (CORELIS) / 05.04.06 Ecology and Nature Management

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Abstract. The objective of this study is to investigate whether small rodents in the shrub tundra of southern Yamal exhibit density-dependent habitat use. All data were collected through trapping species at the Erkuta Tundra Monitoring Site (N 68.2, E 69.2◦) in three distinct habitats over a period of 16 years (2008-2023). The analyses primarily focused on the three most abundant species, namely, narrow-headed vole (60% of individuals caught) and Middendorf's voles (35%) and collared lemming (5%). Overall, there was a decrease in the presence of lemmings, which are specialized arctic species. In contrast, the presence of narrow-headed voles, which are mostly boreal or wide-spread species, increased and expanded northwards. A spill-over effect was observed on both small and large scales for the narrow-headed vole, as they began to inhabit open habitats adjacent to their preferred willow thickets more frequently at high abundance levels. The observed shifts may be attributed to the combined impact of several environmental change drivers, including winter and summer climate warming, spreading of shrubs as a result, as well as increased human activity, particularly related to intensive reindeer herding and industrial development.

Распространение кустарников на полуострове Ямал как фактор биотопического распределения мышевидных грызунов

Ефремова Александра Дмитриевна

ВМ.5710.2022 «Комплексное изучение окружающей среды полярных регионов (CORELIS)» / 05.04.06 Экология и природопользование

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Аннотация. Цель данного исследования состоит в изучении выбора местообитаний мелкими грызунами в кустарничковой тундре южного Ямала, а также определении зависимости изменчивости выбора предпочитаемой среды от плотности грызунов. В качестве исходных данных использовались данные отловов за 16 лет (с 2008 по 2023) на научно-исследовательском стационаре «Еркута» (N 68.2, E 69.2◦) в трех характерных местообитаниях. Анализ был сосредоточен на трех наиболее многочисленных видах: узкочерепная полевка (60% пойманных особей), полёвка Миддендорфа (35%) и копытный лемминг (5%). Было зафиксировано уменьшение численности леммингов, которые являются специализированными арктическими видами, в то время как численность полёвок, представляющих бореальные или широко распространенные виды, увеличивалась и распространялась на север. Наблюдался вторичный эффект распространения (spil-over effect) для узкочерепной полевки, которая все чаще использовала открытые местообитания, прилегающие к их предпочитаемым зарослям ив, при высокой численности. Наблюдаемые изменения могут быть вызваны совокупным воздействием нескольких факторов изменения окружающей среды: потепление климата как зимой, так и летом, распространением кустарников вследствие этого, а также увеличение антропогенного воздействия.

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Introduction

On the Yamal Peninsula, different tundra subzones alternate. Here several species of small rodents play a key role in the plant-herbivore-predator system. Nowadays, terrestrial Arctic ecosystems have undergone important changes (Ims et al., 2013; Ims and Fuglei, 2005). Climate change, namely warming, which during last 40 years occurs nearly four times faster at high latitudes than in the globe (Rantanen et al., 2022; Chylek et al., 2022), and is a major driver of biodiversity changes as well as other anthropogenic impacts such as industrial development and land use which play a significant role in interactions with climate (IPCC, 2023). Vegetation composition shifts, and in particular, shrub expansion across the Arctic tundra is the most important and widely described responses of high-latitude ecosystems to rapid climate warming.

Willow thickets (Salix spp) are prominent structural features in the southern Arctic tundra, where they serve important ecological functions by providing food, shelter, and/or breeding sites for wildlife. At the same time there is an increase in the area of willow thickets due to climate warming (Chapin et al., 2005; Tape et al., 2006). In general, communities of certain species prefer certain types of habitats. But with an increase in the area of willow thickets in the Arctic, southern species related to this microhabitat can penetrate into the tundra. So, the main habitat may not be able to accommodate all individuals as densities increase and some animals move to neighboring habitats, which in turn are native for local species. Therefore, one of the main predicted consequences of climate change, which has a serious impact on the structure and functioning of tundra food webs, is shifts in the ranges of species due to changes in their usual habitat as a result of shrubs spreading to the north, which leads directly to changes in biodiversity.

Long-term observations and possible explanations of such shifts caused by climate change are rare in the Arctic, while are critical for the entire food webs of terrestrial tundra ecosystems.

The purpose of the study - is to document, evaluate and predict changes in the small rodent’s community under spreading of willow thickets

Tasks:

- reveal the preference of different habitats by different species;

- assess the geographical patterns of long-term fluctuation density and identify trends in the abundance of small rodents;
- check the spill-over effect in the years of increase in the abundance of particular species;
- formulate a forecast of changes in the rodent community under the spreading of shrubs.

Hypotheses based on the assigned tasks:

- from literature analysis - the narrow-headed vole prefers thickets, the Middendorff's vole prefers wet tundra, and the collated lemming prefers dry tundra;
- all three study species would show spill-over effect with the growing density (i.e. “going out from their preferred habitat”).

Materials and method

1.2 General characteristics of the Yamal Peninsula and its vegetation cover

The Yamal Peninsula is situated in the northwest of Siberia. It is a region with multiple environmental influences, such as nomadic reindeer herding by the indigenous Nenets, petroleum development and variable climate shifts. To the west, the peninsula meets the Kara Sea, specifically - Baydaratskaya Bay. From the east and southeast, it is bordered by the Ob Bay. The northern section of the peninsula is adjacent to the Malygina Strait, which separates Bely Island from Yamal. The significant length of the Yamal Peninsula from north to south has resulted in a distinct zonation of both climate and vegetation cover.

The climate is determined by the presence of permafrost, the proximity of the cold Kara Sea, and the abundance of bays, rivers, swamps and lakes. The area is generally marked by lengthy winters that can last up to 8 months, brief summers, powerful winds, and scant snowfall. In winter, frosts down to minus 55 or even 60 degrees are not uncommon here. Ice drift on the rivers begins only in the second half of May, and water reservoirs are covered with ice already in October, sometimes freezing to the bottom. Relative humidity throughout the peninsula is high (70-90%) throughout the year. The average annual precipitation is 320-350 mm. Most precipitation falls in the period June – September (Yamal media. Online resource, URL: https://yamal-media.ru/).

The territory of the district is located mainly in three climatic zones: Arctic, subarctic and the northern zone of the West Siberian Lowland. The climate of the Arctic part which covers the islands, the northern part of the Yamal and Gydan peninsulas, is characterized by long, cold and harsh winters with severe storms, frosts and frequent snowstorms, low rainfall, very short summers, and heavy fogs. The subarctic zone occupies the southern part of the Yamal Peninsula. The climate here is sharply continental: precipitation is in the form of rain, summer is up to 68 days. The climate of the northern strip of the West Siberian Lowland (taiga) is sharply continental. The average temperature here is higher, summers are quite warm and pretty humid (up to 100 days). The small amount of precipitation in the northern part of the peninsula is mainly due to the low humidity of Arctic air masses. The annual amount of evaporation is small here (about 250 mm per year). The number of days with snow cover is about 240 days (Official website of the Government of the Yamalo-Nenets Autonomous Okrug. Online resource. URL: https://yanao.ru/).

Winter lasts 7-7.5 months, the average temperature in January is -23-25°C. Spring is usually short (35 days) and cold, with sudden changes in weather, with frequent returns of cold and frost. The growing season is about 70 days. Autumn is short, with maximum instability of the pressure gradient, sudden changes in temperature and frequent early frosts. The windiest weather is observed in autumn and winter. Southern and southeastern winds also predominate in winter and predominantly northern winds in summer.

The Yamal Peninsula is characterized as a relatively flat and low-lying accumulative plain, with absolute heights ranging from 0 to 70 meters, and the highest point reaching 90 meters (Morozova and Magomedova, 2004). The relief of the peninsula is formed by the West Siberian plate and is covered with a thick layer of sediments. It is primarily composed of marine, alluvial, and lacustrine sediments, which consist of sandy and clayey materials. The peninsula's geological composition primarily consists of Paleogene deposits. The structural features and lithology of Yamal are indicative of alternating periods of transgression and regression of the sea, as well as erosional incisions. (Markovsky, 1975).

The continuous distribution of permafrost and its presence at the surface facilitate the widespread development of cryogenic and karst landforms. This is associated with the formation of tuberculate, polygonal, and spotted tundra, as well as polygonal and hummocky swamps. The swamps in this region are typically confined to lowlands and basins.

On the territory of Yamal there are 3 types of soils: peat, gley, alphehumus. The first one is formed in lowlands and ravines from dying vegetation. The second one is made of loam and moss. This layer is formed in the tundra above the permafrost layer. The third is taiga-forest soils formed in the forest-tundra. The peculiarities of the soils are the poor mineralogical composition of the parent rocks and waterlogging.

The peninsula is located in the tundra zone and covers three bioclimatic subzones of the Arctic, defined on the circum-Arctic vegetation map (Walker et al., 2005). Starting from south to north, this is shrub tundra (subzone E), then typical (subzone D) and arctic (subzone C) tundra. These subzones differ in plant biomass, which increases from north to south, dominant plant species, and other vegetation characteristics, particularly the presence of upright shrubs and willows. The arctic tundra subzone occupies 19% of the peninsula's territory, typical and southern 26% and 55%, respectively (Magomedova et al., 2006). The most important components of tundra vegetation are mosses, lichens, shrubs and grasses (Figure 1).

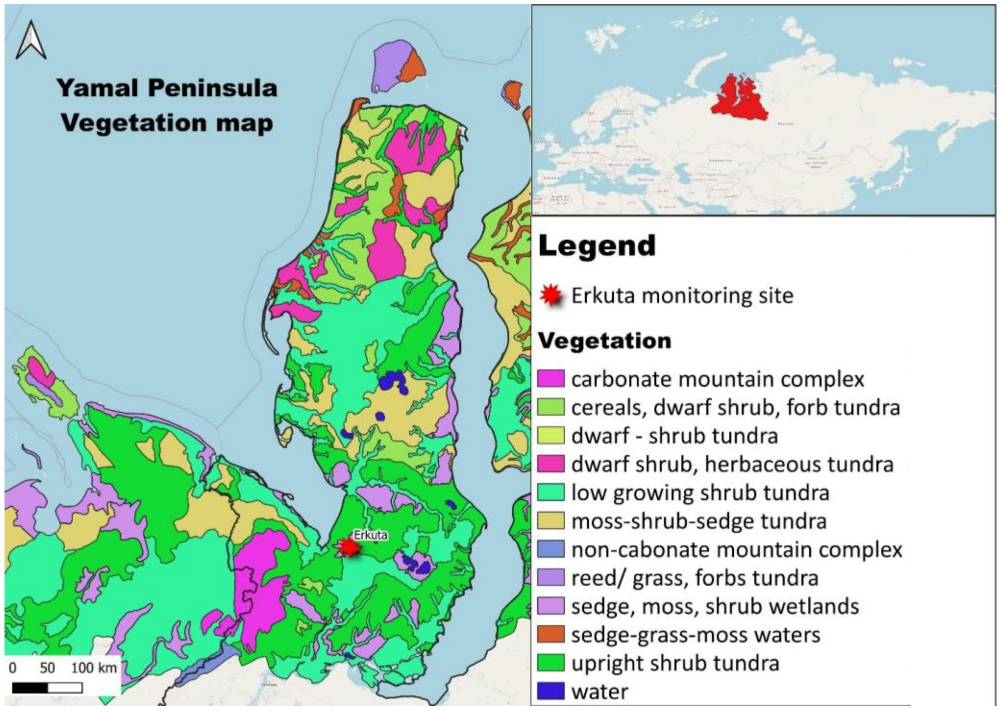

Figure 1. Map of the vegetation type distribution on Yamal peninsula with Yamal Peninsula in the center and a view (created by author, according to Walker et al., 2005).

Due to climatic conditions and a short growing season, the plants here are stunted, often have a creeping and cushion-like shape, and grow in patches, exacerbating the complexity of the vegetation cover (Magomedova et al., 2006). Arctic tundra exhibits limited plant primary productivity, a phenomenon that can be attributed to the region's cold temperatures, brief snow-free period, and soil that is deficient in nutrients (Callaghan et al., 2004; Ims et al., 2005).

In this region, shrubs, which are characterized as woody plants, display a variety of growth forms, ranging from upright dwarf shrubs with heights of 0.1 to 0.4 meters to prostrate dwarf shrubs that are less than 0.1 meters in height. (Myers-Smith et al., 2011). Erect dwarf shrubs are the most abundant group in the low Arctic. It includes two functional groups: deciduous shrubs and evergreen shrubs. Deciduous shrubs have a high leaf quality. They include Salix spp, Alnus spp Vaccinium uliginosum, and Betula nana. Evergreen shrubs (e.g. Empetrum nigrum, Ledum decumbens) are less palatable but are better at using organic nitrogen from the soil. Grasses and sedges are two fast-growing functional groups of plants appreciated by herbivores. They include Carex spp, Luzula spp and Eriphorum spp. Grasses are more palatable than sedges and have a short turnover. They include Poa spp and Festuca spp. All these characteristics or functional traits are important factors in plant-herbivore relationships since they can predict how plants will react to a disturbance in the system, such as herbivory.

The difference between the two subzones D and E of the low Arctic is reflected in the different participation of shrubs in the vegetation cover, as well as in the combination of plant communities on the tops and slopes of watersheds. In general, willow thickets typically grow along rivers or on slopes and are often the tallest plants in a tundra landscape that is otherwise characterized by short plants. The predominant structural component in this region is the shrub thicket, which demonstrates higher productivity levels in comparison to the surrounding open tundra vegetation. Thus, in a typical tundra, the vegetation is represented mainly by non-tussock sedge, dwarf-shrub, moss tundra and erect dwarf-shrub tundra. Sedges, mosses and shrubs (Dryas, Cassiope tetragona, Arctous rubra, Vaccinium spp.) are predominate here. Shrubs form low-growing thickets on the slopes - willow thickets up to 40 cm high. Meadow-like communities in subzone D are represented mainly by cotton grass and sedges, but are characterized by low productivity.

In the shrub tundra (subzone E), willow thickets are a more noticeable structural element. They grow in the most productive parts of the landscape and provide food and shelter for numerous animals. In the southern subarctic tundra, shrub tundra occupies watersheds, including their tops, in combination with grass-moss and shrub-moss tundra. Here shrubs overlook the watersheds. They grow in the most fertile places and can be considered productivity hotspots in conditions of fairly low productive vegetation. Here thickets of willow can be one to two meters high, and in some places can be higher and are interspersed with alder (Alnus spp.). The vegetation also is dominated by wild rosemary (Ledum decumbens), sedges, grasses, forbs, and sometimes thick moss carpets (Sphagnum spp., Sanionia uncinata). So, in the southern tundra, the species diversity of meadows increases, the height of plants also increases - tall grass cereal cenoses are common here.

On the other hand, the main feature of the Arctic tundra is the virtual absence of shrubs, some of which can be found only in the south of the subzone in some communities near watersheds. The vegetation of subzone C consists mostly of graminoid, prostrate dwarf-shrub, forb tundra and prostrate/ hemiprostrate dwarf-shrub tundra. The vegetation here is mainly represented by grasses, sedges (Carex spp., Eriophorum spp.), mosses (e.g., Polytrichum sp., Sphagnum sp.) and forbs. Erect willows of at most 15 cm height are also found (Sokolova et al., 2024). Grass-moss tundra and grass-moss swamps play a significant role in the structure of vegetation cover. Meadow-like communities form in river valleys.

1.2. Community of small rodents on the Yamal Peninsula

In the category of small herbivores, voles and lemmings have distinct dietary preferences. Voles, specifically the Microtus species, consume a variety of grasses, sedges, and forbs, while lemmings primarily feed on sedges and mosses. Dicrostonyx lemmings, for instance, have a diet that consists mainly of grasses and shrubs. Small rodents have burrows and feeding areas, which are usually connected by well-trodden paths along which there are numerous feeding areas (Figure 2).

Figure 2. Example of holes and trodden paths of small rodents (photo is taken by the author on the study units of Erkuta tundra monitoring site)

The community of small rodents in the shrub tundra zone of the Yamal Peninsula is quite rich in species and includes several species of voles, the most numerous of which are Middendorf's voles (Microtus middendorffii) and Narrow-headed voles (Microtus gregalis), also the red-backed vole (Cl. Rutilus), as well as lemmings – collared lemmings (Dicrostonyx torquatus) and Siberian lemmings (Lemmus sibiricus). Arctic lemmings and voles are unique in that they remain active throughout the year, even during the winter months when they are beneath the snow. Additionally, they possess remarkably high metabolic rates.

The Microtus species are morphologically similar but exhibit distinct distribution patterns. Thus, M. Gregalis (narrow-headed vole) has a disjunctive distribution and is found in both the Arctic and Subarctic regions of Russia, as well as in steppe regions. In Yamal, it primarily inhabits river valleys, water meadows, and willow thickets. Its diet consists of various sedges, grasses, forbs, and shrubs. These voles typically live in colonies comprising individual burrows connected by paths and underground passages. The narrow-headed vole in the tundra retains some ecological characteristics indicative of its steppe origin, such as building deep burrows, which limits the range of suitable biotopes and consequently, its distribution in the tundra (Sokolova et al., 2024). Overall, the availability of natural shelters for M. Gregalis in the steppe and tundra zones is limited, and their placement largely depends on the presence of durable turf formed over many years.

In contrast, M. middendorffii has a limited distribution range that is confined to the Russian Arctic and subarctic regions, including forest-tundra and shrub tundra. This species is commonly found in lower-lying humid tundra areas, particularly in swampy habitats where mosses, dwarf birch, and sedges are prevalent. The diet of the Middendorf's vole primarily consists of the roots and shoots of cereals, with a preference for sedges and woodlands (Sokolova et al.,2024).

The red-backed vole is a boreal species, although it is also found in the lower Arctic - usually in floodplains near thickets of willows and alders. Their diet consists of herbs, berries, mosses, lichens and mushrooms (Sokolova et al., 2024).

Unlike voles, lemmings are characterized by an arctic distribution (Figure 3).

Figure 3. The distribution area of collared lemmings, Middendorf's voles and Narrow-headed voles (A.N. Severtsov Institute of Ecology and Evolution. Data base. Online resource, URL: http://www.sevin.ru/vertebrates/index.html?Mammals/162.html)

Lemmus sibiricus exhibits a preference for humid tundra areas, typically found in low relief forms and almost exclusively in moss-dwarf birch tundra. They feed on sedges and mosses, with occasional consumption of dwarf birch shoots and willows. Collared lemmings inhabit preferentially moss-dwarf birch tundra (Dunaeva, 1948). They feed on various types of deciduous and evergreen shrubs, but their diet also includes sedges, grasses, and forbs. Lemmings construct nests and dig an intricate network of holes in the sub-root layer of snow to access food resources. Besides, lemmings have undergone co-evolution with the tundra biome since the beginning of the Pleistocene epoch, resulting in their ability to withstand the harsh conditions of the Arctic environment. Through convergent adaptations, they have become well-suited to life beneath the snow. These adaptations include the growth of large claws for efficient digging, as well as the development of sturdy teeth, powerful jaws, and large guts. These features enable them to subsist on low-nutrient plant matter (Ehrich at al., 2020).

Lemmings and voles are renowned for their population cycles that occur every 3-5 years, characterized by significant periodic outbreaks that result in boom-and-bust dynamics. These cycles have substantial implications for the entire vertebrate tundra food web. However, the duration of these cycles can vary, with some populations displaying shorter cycles, such as the 3-year cycle of Siberian lemmings on the Taimyr Peninsula (Summers and Underhill, 1987), or longer cycles, such as the more than 4-year cycle of

Norway lemmings in northern Norway (Angerbjörn et al., 2001). Numerous theories have been put forth to account for these cycles, with the most widely accepted one suggesting that food availability and predation are critical factors (Fauteux et al., 2015). Nevertheless, climate shifts, particularly changes in snow conditions, may also influence the cyclic dynamics of small mammals, as they spend the majority of the year living, feeding, and reproducing beneath the snow (Ims et al., 2008; Fauteux et al., 2015).

1.3 Study area

The study is conducted at the Erkuta Tundra Monitoring Site located in the south of the Yamal Peninsula, Russia (68.22° E; 69.15° N). Erkuta belongs to the Low Arctic zone (bioclimatic zone E) (Figure 4).

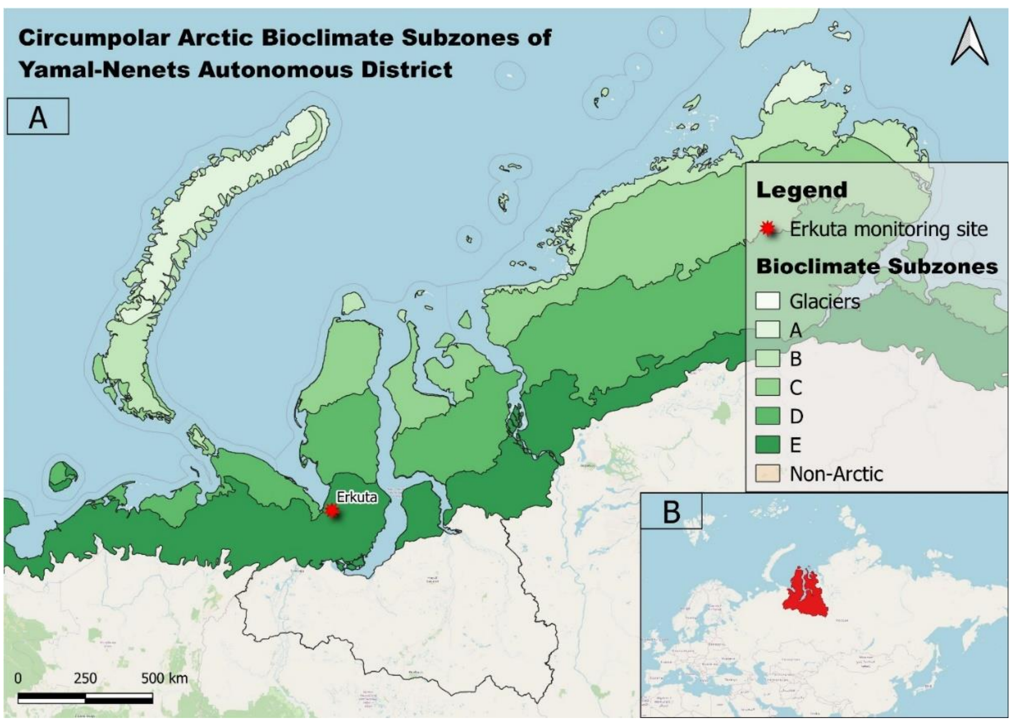

Figure 4. Map (A) of the Yamalo-Nenetskiy Autonomous District in Northwest Siberia (Russia) with Yamal Peninsula in the center and a view (B) of the studied area. The five bioclimatic subzones of the Arctic (A high arctic tundra, B northern arctic tundra, C southern arctic tundra, D northern hypo arctic tundra, E southern hypo arctic tundra) are shown in various shades of green (created by author according to Walker et al., 2005)

The area is also characterized by a gently sloping tundra landscape with low hills typically around 30 meters in height, and several steep slopes and sandy cliffs along the banks of rivers and lakes (Fufachev et al., 2019). The study area is also located near the confluence of the Payutayakha and Erkutayakha rivers.

The dominant vegetation types here are erect dwarf shrub and low shrub tundra, according to Circumpolar Arctic Vegetation Map (CAVM) (Walker et al., 2005). The landscape is primarily composed of continuous shrubland, with shrubs ranging from 50 cm to 2 meters in height. These shrubs can be deciduous or evergreen, usually surrounded by graminoids, forbs, true mosses and lichens. Low shrub tundra is more prevalent in this area than the drier, lichen-rich upright shrub tundra. Dense stands of willow (Salix spp.) and alder (Alnus fruticosa) are found along rivers and lakes, and numerous bodies of water also create extensive wetlands. On dry ridges, vegetation cover can be sparse (5–50%), but usually continuous (80–100%) (Walker ey al., 2005). The study area is also located in the permafrost zone, resulting in the presence of tuberculate, polygonal, and spotted tundra, as well as polygonal and hummocky swamps.

1.4 Method of snap trapping and abundance of small rodents

Small rodent dynamics were monitored from 2008 to 2023 by snap trapping, which was carried out according to the small quadrat method (Myllymäki et al., 1971). All trapping of small rodents was undertaken under the scientific plan of IPAE, and approved by its Bioethics Commission (IPAE, Bioethics Commission (protocol #014 dated 12/05/2023). Online resource, URL: https://ipae.uran.ru/information/bioethics_comission). Snap trapping method is widely used for study the habitat and dynamics of boreal populations and Arctic rodent communities. To compare data obtained on lines with different numbers of traps, the abundance index is used, which is calculated as the number of animals caught per 100 trap-nights (Sheftel, 2018).

As described in Myllymäki et al. (1971), the small quadrat method is designed to encompass the home range of the resident rodents within a defined habitat. Thus, it is can be used to estimate relative rodent densities and has been used extensively for both short- and long-term rodent population monitoring.

Small rodents were trapped in three habitat types (willow thicket edge, mesic dwarf shrub tundra, and wet-lands), defined as the key landscape elements for the study area:

- Wet (W) – moist areas in flat, low-lying tundra or in small valleys, dominated by thick layers of Shagnum moss together with Carex spp и Eriphorum spp tussocks;

• Dry (D) – dwarf-shrub tundra on hillsides or in the upland tundra (but not in the driest places, like on the tops of ridges), with predominance by lichens and evergreen woody shrubs, sometimes together with B. nana and Eriophorum spp;

• Thicket (T) - willow thicket edge at least 0,5 m high (Salix glauca-Carex aquatilis type or Salix lanata-Myosotis nemorosa).

The selection of all sites was based on a visual evaluation of the habitat, in accordance with the specified criteria. These sites were situated in areas that are not prone to flooding during the spring season. Such types are already used for rodents' monitoring on the station for many years.

The overall study area is divided into units called K, L and R, which are separated by approximately 5 km from each other (Figure 5).

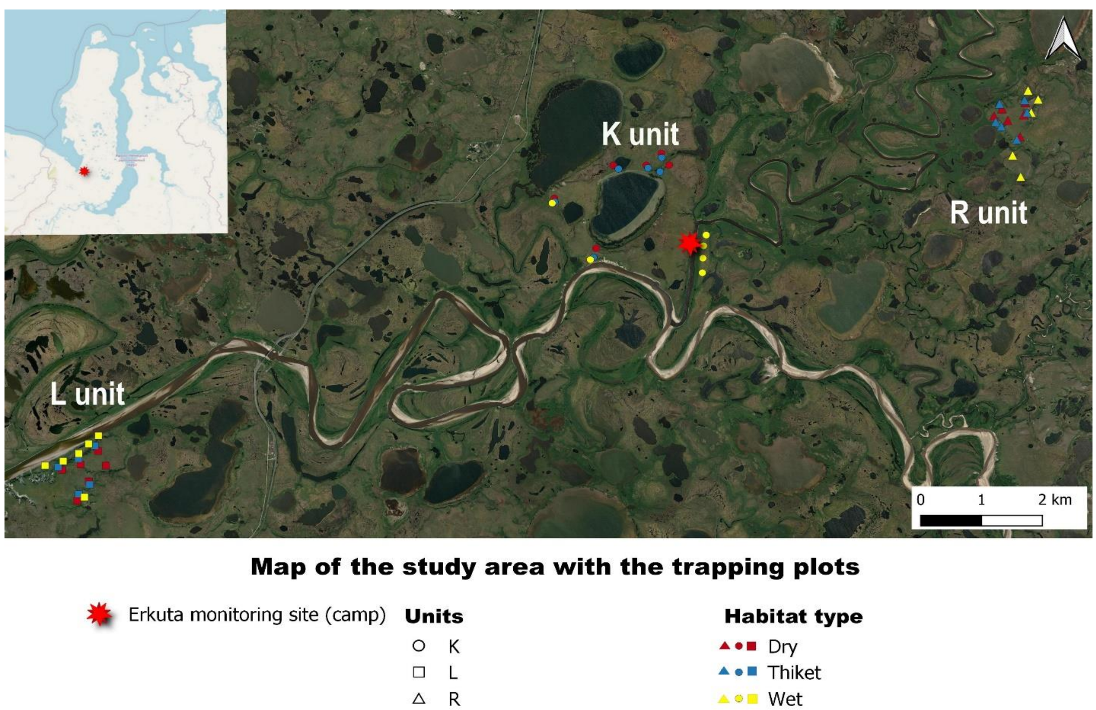

Figure 5. Map giving the location of the three study units (K, L, R) with 18 trapping plots (quadrats) in each. The symbol form represents the unit, its color – the habitat type. The location of a station is shown with a red star dot (Erkuta, Yamal, N 68,2°, E 69,2°) (created by an author).

The 2 sessions were complete during the 2023 year, namely in second part of June and the beginning of August. Each trapping session extended over two days and traps were checked once per day, resulting in two checks per session (2 × 12 = 24 trap nights per quadrat plot per session).However, from 2008 to 2011, permanent small quadrats were placed only in two spatial units, namely K and R units, for two nights per season resulting in 2 × 3 × 6 = 36 quadrats in total (in details: 2 units × 3 habitats × 6 quadrats × 12 traps × 2 nights × 2 sessions = 1,728 trap nights per year). In 2012, a third unit L consisting of quadrats in the same habitat types was established resulting in a total of 2,592 trap nights per year. So, with occurrence of third L unit, it started to be 54 quadrats in total for each trapping session in each year. In 2016, only one session was carried out for logistic reasons.

In each of the study sites, traps were positioned within small 15 × 15 m quadrats, with the four corners of the quadrat serving as the sampling locations for the traps. At each of these corners, three traps were arranged within a 2-meter radius, resulting in a total of 12 traps per sampling square. In cases where thickets were present, two of the corners were situated within the thickets, typically 1 meter inside, while the remaining two corners were located outside the thickets. (Figure 6).

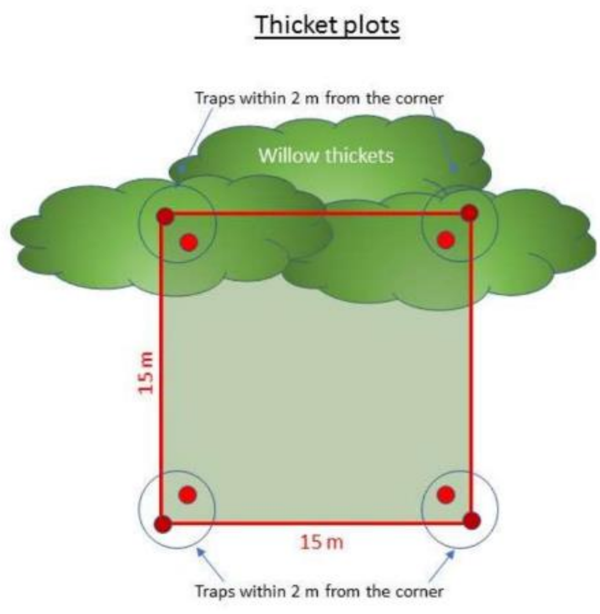

Figure 6. Snap-trapping method in various habitats. (with contributions from O.Pokrovskaya). (IPAE, Bioethics Commission (protocol #014 dated 12/05/2023). Online resource, URL: https://ipae.uran.ru/information/bioethics_comission)

The vegetation adjacent to the thickets consisted of productive meadows dominated by forbs and grasses or of dwarf shrub tundra. Traps were placed along natural paths for rodents or in front of their burrows and fed with raisins and oats.

Three focus groups of rodents were selected for the study: the narrow-headed vole, the Middendorff's vole, and the collared lemming. Then, based on the results of trapping from 2008 to 2023, data was summarized as total number of individuals of lemmings and voles respectively, trapped per 100 trap nights and averaged over units and habitats.

Abundance indexes were calculated for each rodent in each habitat type for each unit. The abundance of rodents is calculated using the following formula:

$$V=(N * 100)/ n*d \text{ (individuals/100 trap-nights)}$$

Where, V - abundance; N - number of individuals caught in the trap; n - number of traps in the line; d - number of days.

Thus, it was examined whether the study species were trapped in their typical habitats—the narrow-headed vole in a thicket habitat, the Middendorff's vole in a wet habitat, and the collared lemming in a dry habitat—or in other nontypical habitats, and whether this dominance changed with increasing numbers of voles, season, and year, thereby testing predictions about the relationship between habitat use and abundance.

All statistical analyses were carried out in R version 3.3.0 +. At the scale of the study area, predictions about the relationship between habitat use and abundance were tested with Fitting Generalized Linear Models. It is used to fit generalized linear models, specified by giving a symbolic description of the linear predictor and a description of the error distribution.

1.5 Climate data

The Yamal region is very sensitive to climate warming over the past 30 years. Forbes has reported an increase in average air temperature of 1-2°C (Forbes and Stammler, 2009).

Many studies have noted that the Arctic region has experienced a stronger warming trend in recent decades than much of the rest of the globe. It can be seen how climate change has affected the Yamal Peninsula region over the past 40 years (Figure 7).

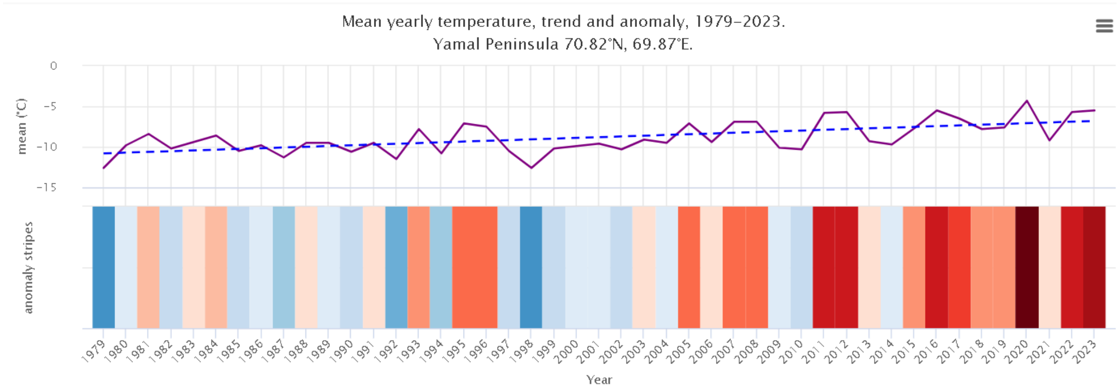

Figure 7. Yearly Temperature Change on Yamal Peninsula (dashed blue line is the linear climate change trend, each colored stripe represents the average temperature for a year - blue for colder and red for warmer years.) (Climate Change Yamal Peninsula. Meteoblue. Online resource, URL: https://www.meteoblue.com/en/climate-change/yamal-peninsula_russia_11497697?month=7)

The graphs presented in this study were generated using data from ERA5, the fifth-generation atmospheric reanalysis of the global climate produced by the European Centre for Medium-Range Weather Forecasts (ECMWF). ERA5 provides a comprehensive dataset spanning the years 1979 to 2021, with a spatial resolution of 30 km. This dataset is made available by the Copernicus Climate Change Service (C3S) at ECMWF. According to this graph, it can be said that the mean temperature for the region was -5.5 C. The hottest year over the last decade was 2020 with the mean temperature of -4.3. It could be seen the since nearly 2010 the trend and the temperatures has changed significantly and now only warmer years can be seen.

Moreover, published research shows that “longer, warmer summers are promoting the growth and northward expansion of willow thickets” (Mekonnen et al., 2021; MyersSmith et al., 2011, Heijmans, M. M., 2022).

1.6 Shrubs expansion

Shrub expansion occurs across large parts of the tundra biome, and its potential ecological consequences are widely debated. Many research supports the increase and spread of both deciduous shrub species such as birch (Betula spp.), willow (Salix spp.), and alder (Alnus spp.), as well as prostrate evergreen shrubs in response to warming in the Arctic region (Wilson and Nilsson, 2009; Vowles et al., 2017; Myers-Smith et al., 2020).

The present-day distribution of shrubs in the Arctic is consistent with past episodes of vegetation change. Paleoecological findings suggest that shrub species are highly adept at colonizing and/or expanding their range within tundra ecosystems during periods of optimal growing conditions. Pollen data reveal that alder, birch, and willow species were more prevalent in mid- and upper Arctic circumpolar ecosystems during post-Last Glacial Maximum periods, which were characterized by warmer and wetter conditions than those of the present day (Myers-Smith et al., 2011).

Thereby, shrubification (expanding of shrubs northward) can be divided into three categories, involving either changes in vegetative growth or recruitment (clonal or vegetative) (Myers-Smith et al., 2011) (Figure 8).

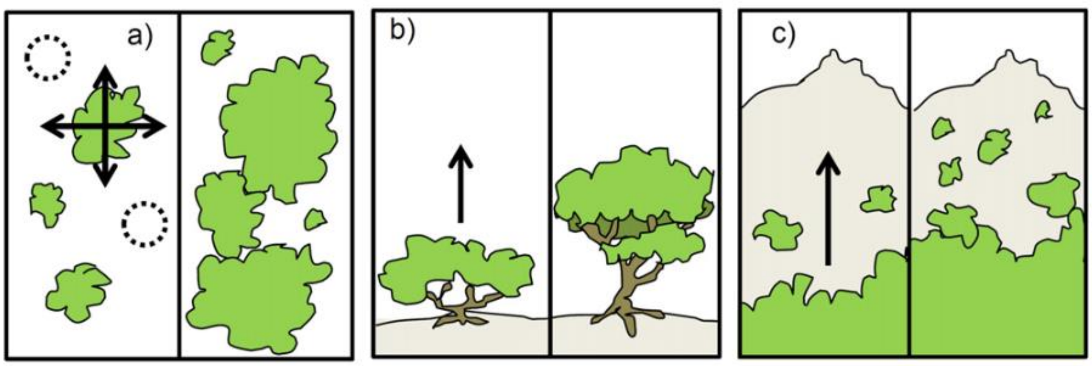

Figure 8. The three general categories of shrub increase including (a) infilling of existing patches, (b) increase in growth and (c) an advancing shrubline (Myers-Smith et al., 2011)

The three categories of shrub expansion are: (a) infill, which involves lateral growth of existing shrubs and recruitment between established sites, resulting in increased shrub cover; (b) enhanced growth potential, which includes changes in growth habit, such as increased canopy height of shrub cover; and (c) range expansion, which refers to the colonization of areas beyond the previous range limit, also known as advanced shrubline.

Results

In total, over 16-year study period, 1169 individuals of three selected small rodents' species were trapped, including: 705 (60%) - narrow-skulled vole, 407 (35%) - Middendorff's vole, 57 (5%) - collared lemming. Thus, the focus groups were the Middendorff's vole and the narrow-headed vole - they were the most common. Overall, vole abundance was lower in 2016-2019, increased in 2020, peaked in 2021, and declined slightly by 2023. The graph illustrates the absolute number of species trapped in the three habitats by year (Figure 9).

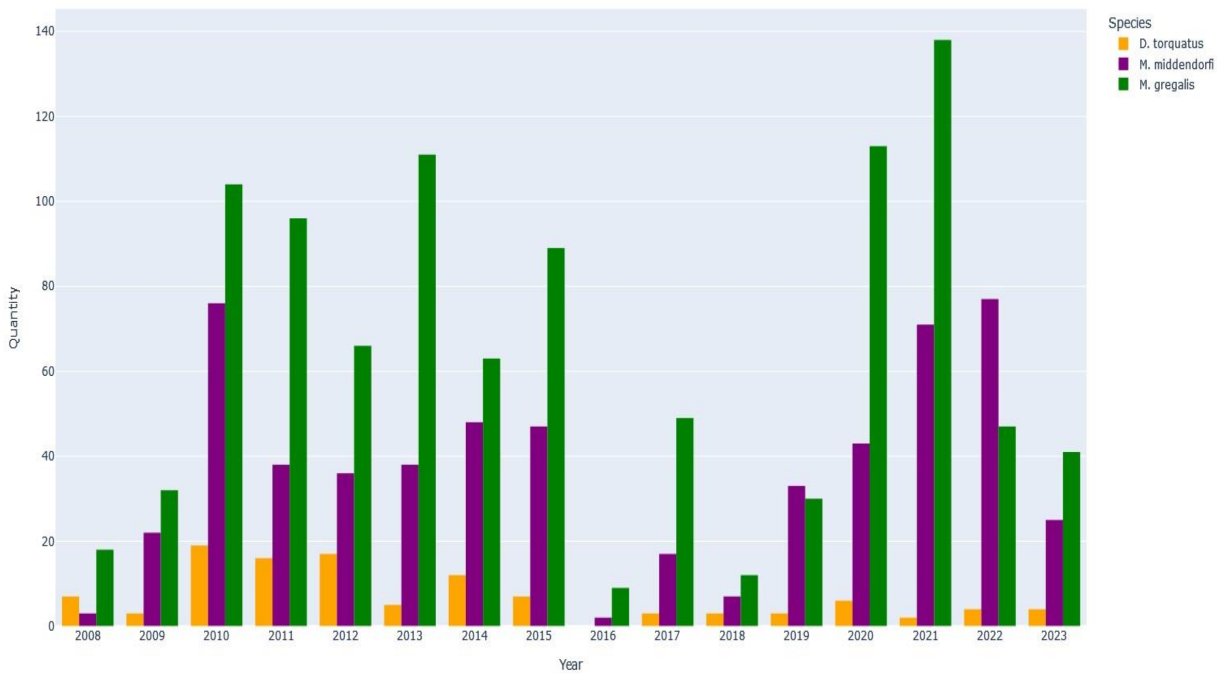

Figure 9. The absolute number of each species trapped in summer in the years 2008–2023 at the Erkuta tundra monitoring site (Yamal, Russia).

Data of the number of small rodents trapped per 100 traps/nights (abundance index) in each habitat type were also plotted (Figure 10-12).

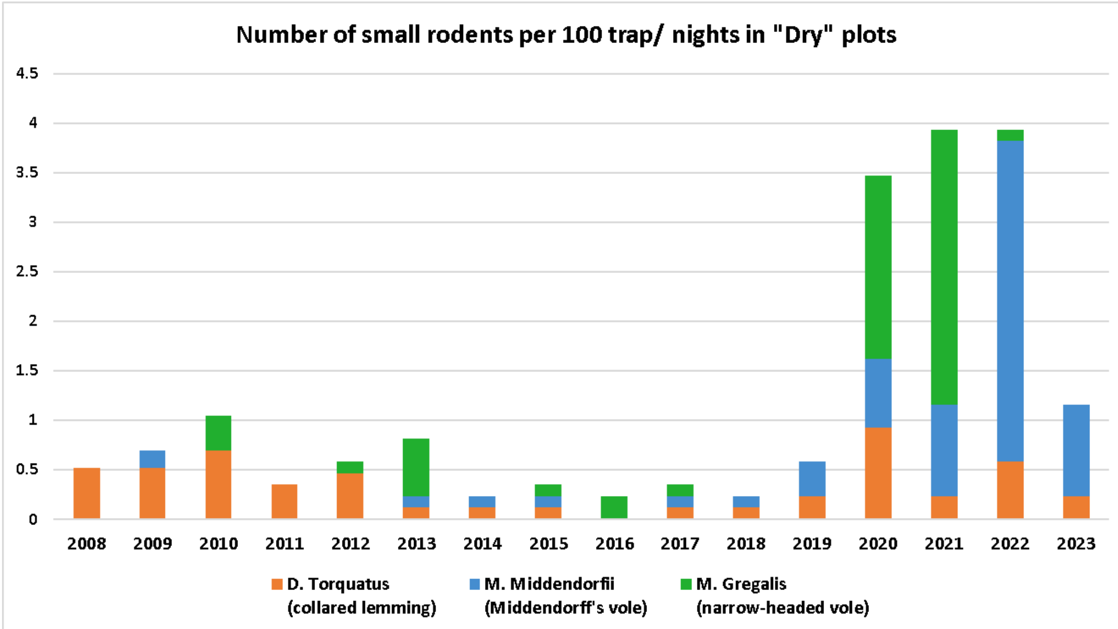

Figure 10. Number of small rodents per 100 trap/ nights in "Dry" plots (habitat type).

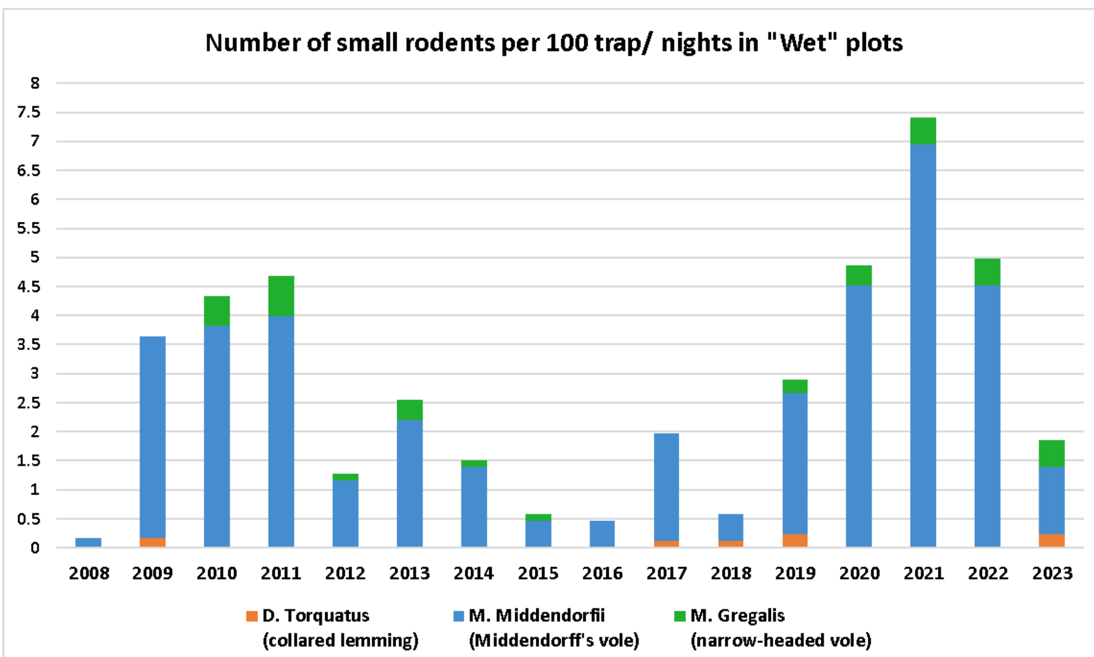

Figure 11. Number of small rodents per 100 trap/ nights in "Wet" plots (habitat type).

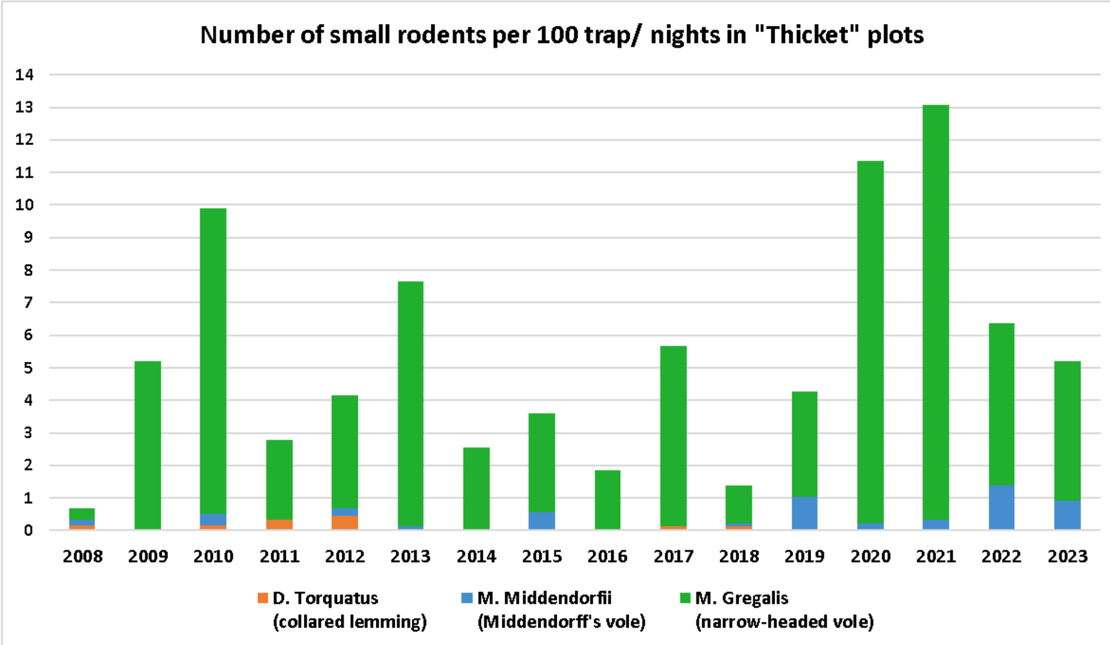

Figure 12. Number of small rodents per 100 trap/ nights in “Thicket” plots (habitat type).

Thus, the graphs show that the preferred habitat for the collared lemming is Dry plots. It was occasionally trapped in alternative habitats. Middendorf's vole also remained in its usual habitat for a long time, but in recent years it has begun to move a little more into the dry and thicket tundra. The graphs also confirm the narrow-headed vole’s adherence to thicket habitats throughout all years of traps. However, it can be seen that its penetration into alternative neighboring habitats is much higher compared to the two previous species. Almost every year, part of its quantity per 100 traps/day was accounted for in dry and wet biotopes.

Linear models were also constructed: the ratio of the abundance index of the narrow-headed vole, Middendorff's vole and collared lemming to adjacent biotopes. Thus, the collared lemming (p value<0.001; KS test = 0.09; Dispersion test = 0.9; Outlier test = 0.16) and Middendorff’s vole (p value<0.001; KS test = 0.09; Dispersion test = 0.9; Outlier test = 0.16) do not show a tendency to spread to other biotopes.

So, according to the results of traps in three fundamentally different biotopes (wet tundra, dry tundra, willow thickets), the narrow-skulled vole is mainly caught in thickets, but quite often this species is present in the other two biotopes.

To assess the extent to which the narrow-skulled vole is able to move beyond its typical habitat, two analyzes were carried out: the tendency to disperse at scales up to 15 m from willow thickets (Figure 13) and the tendency to disperse to alternative habitats (Figure 14).

The plots for trapping in willow thickets are oriented in a way that one side of a 15m*15m square is located directly on the border of the thickets, extending 1-2 meters into the thickets, the opposite side is in an open area (productive meadow or shrub tundra). To assess the tendency to dispersal at a level of up to 15 m from the willow thickets, a generalized linear model with a binomial distribution was built. A binomial variable was used as the dependent variable, which reflects the occurrence of the narrow-headed vole on the open side in the capture plot. The abundance index of the narrow-headed vole for the year from all biotopes was used as an independent variable. The independent variable of narrow-headed vole abundance was transformed on a logarithmic scale to better distribute the model residuals.

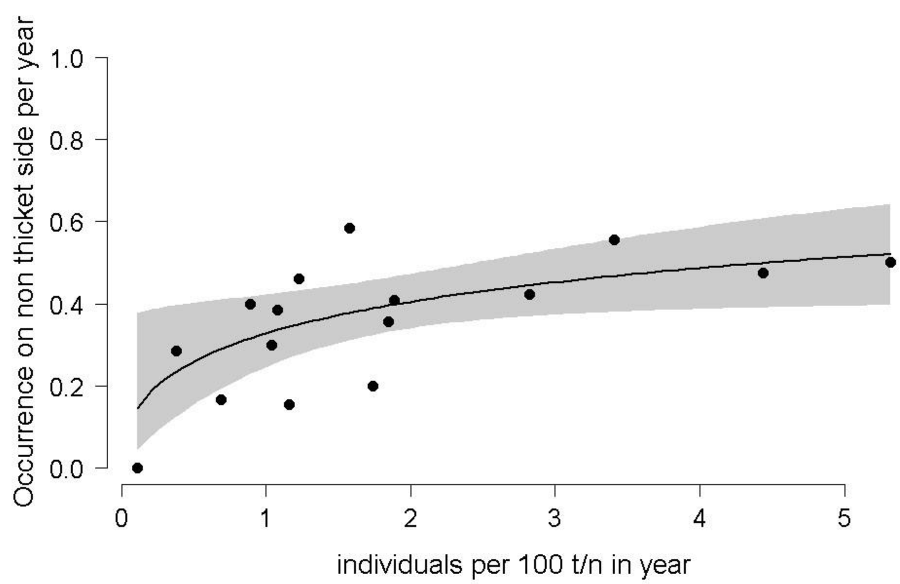

Figure 13. Tendency of dispersal of the narrow-headed vole to alternative biotopes at scales up to 15 m from the border of willow thickets (independent variable - index of narrow-headed vole abundance for the year from all biotopes, dependent variable - occurrence of narrow-skulled vole on open side in the catch square, the dots reflect annual abundance indexes)

- Estimate = 0.4794, Std. Error = 0.2190. P value = 0.028
- Number of Fisher Scoring iterations: 4
- Ks test = 0,361, Dispersion test = 0,9, Outliner test= 1

To assess the tendency for the narrow-headed vole to disperse to alternative biotopes, the abundance indexes of the narrow-headed vole in each biotope were calculated in June and August for each year. Next, a linear model was built, where the index of abundance in alternative biotopes was used as the dependent variable, and the abundance index of the narrow-headed vole in willow thickets was used as the independent variable (from 0 to a maximum value of 33). Both variables were transformed by square root transformation to better distribution of the model residuals.

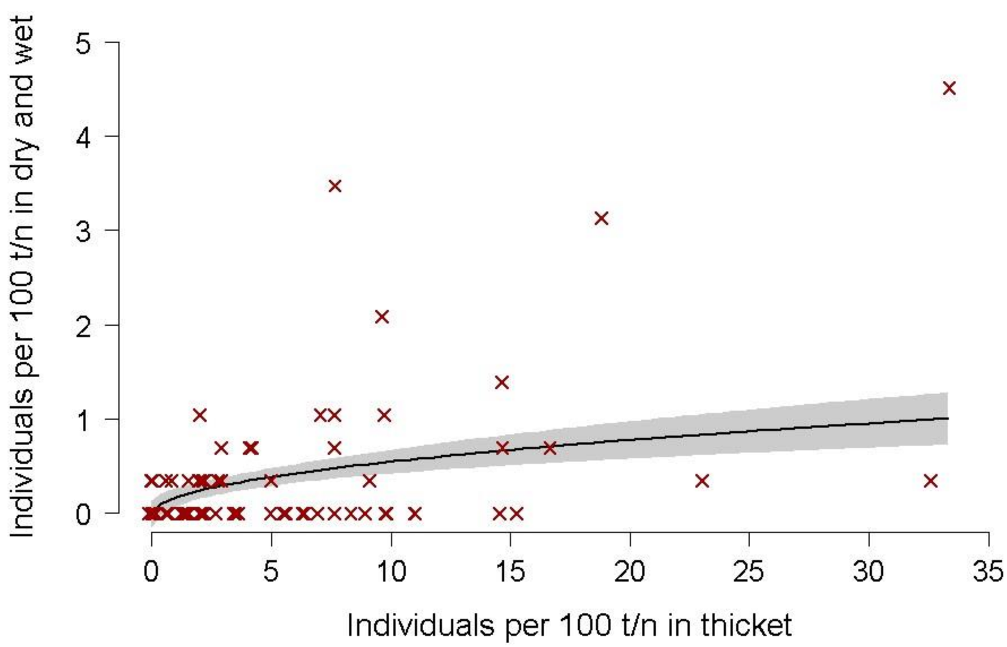

Figure 14. Tendency of dispersal of the narrow-headed vole into alternative biotopes (“Wet” and “Dry” plots) (independent variable - index of abundance of narrow-headed vole in willow thickets, dependent variable - index of abundance in alternative biotopes, crosses reflect 1 catch in 1 season July/August on thicket sites in 1 unit)

- Estimate =0.174453, Std. Error = 0.032713, P value <0,001
- KS test = 0,09, Dispersion test = 0,95, Outlier test = 0,16

Standard Error is 0.17 ±0.03. Thus, with an increase in the abundance index of the narrow-headed vole by 1, the M.gregalis index on non-Thicket plots increases by 0.17 individuals per 100 trap/nights. The maximum value for the narrow-headed vole in alternative biotopes is 1 individual per 100 trap/nights.

Thus, both models indicate that the probability of trapping a narrow-headed vole in other biotopes, including on the non-Thicket side, increases with a rise in the total number of rodents caught per year. The results support the prediction that high density leads to expansion into less preferred habitat for the narrow-headed vole, including at the local scale of sites.

Based on data from the CRU TS 4.01 spatial climatic dataset (Harris et al., 2014), and local HOBO meteostation the graph of mean annual summer temperature on Erkuta tundra monitoring site from 2008-2023 was obtained (Figure 15).

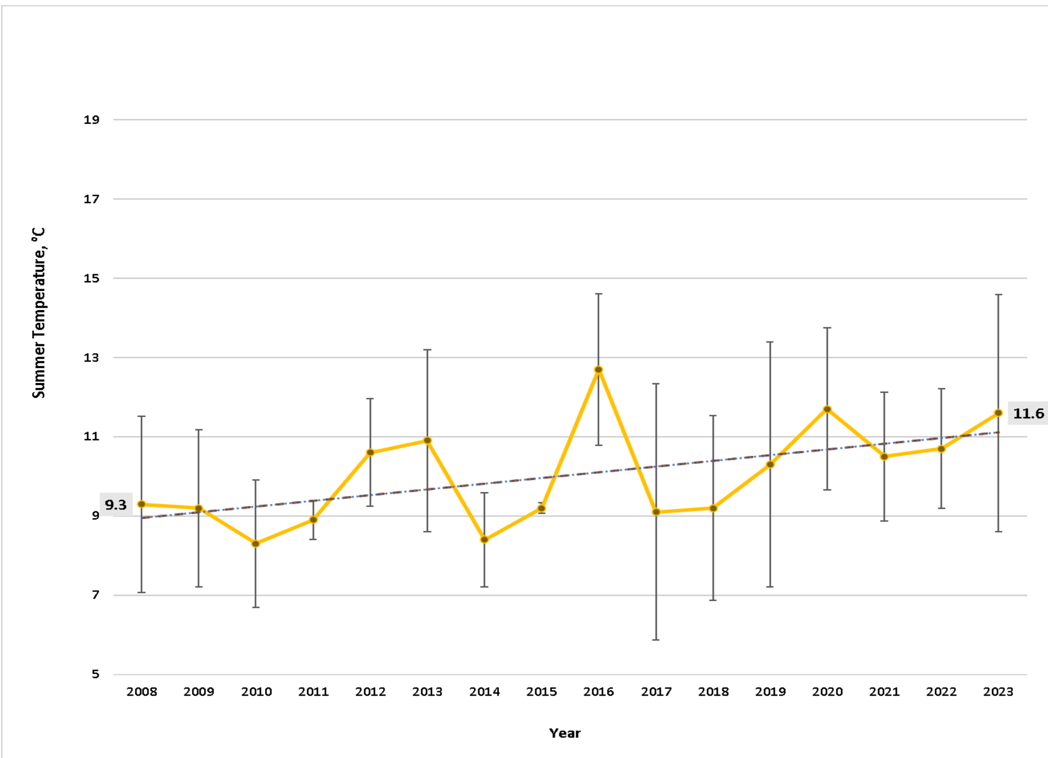

Figure 15. Mean annual summer temperature on Erkuta tundra monitoring site from 2008-2023 (the dash line is the linear climate change trend) Based on data from the CRU TS 4.01 spatial climatic dataset (Harris et al., 2014) and local HOBO meteostation (created by author).

It is noticeable that mean July temperature during the study period was 12,7°C and mean August temperature was 10,8°C. Here we also see an increase of mean summer temperature from 9,3 up to 11,6 degrees. In general, there are wave-like peaks of temperature rise in summer approximately every 3 years. The trend line is marked as positive.

Discussion

The study revealed a decline in the population of lemmings and an expansion of certain vole species. The habitat preferences of these species are largely in line with others previous research (Dunaeva, 1948), as swampy plains with mosses and dwarf birch are prevalent in the study area. At the same time, the narrow-headed vole was observed to inhabit willow thickets in river valleys, feed in neighboring productive meadows, and construct extensive burrow systems in the well-drained soil of river banks.

In the Erkuta territory, the narrow-headed vole was also observed on steep slopes with well-drained soils and diverse herbaceous vegetation, but without willow thickets, which aligns with other studies conducted at the Erkuta monitoring station over many years (Sokolova et al., 2014; Sokolova et al., 2024). It is possible that this species selects landscape features that are frequently associated with willow thickets, but not necessarily exploiting the thickets themselves. Furthermore, these studies also indicate an increase in the occurrence of narrow-headed voles in Yamal across all three tundra subzones (subzones C, D, and E). Consequently, this species is currently the most prevalent throughout the peninsula, with its distribution recorded up to the northern region of the Yamal Peninsula (Sokolova et al., 2024).

Prior research conducted on Erkuta has also documented the northward expansion of Middendorff's vole (Sokolova et al., 2024). Although the vole was infrequently observed in subzone D, recent findings indicate its presence in the high latitudes of the Arctic, with the first trapping in subzone C recorded in 2015 and again in 2022. Furthermore, a water vole, predominantly a boreal and temperate species, was trapped for the first time in the territory of the Erkuta station in 2020 in subzone E (Sokolova et al., 2024). It is also noted that in the southern tundra, Middendorf's voles were the most prevalent species until 2007, after which narrow-headed voles became dominant (Fufachev et al., 2019).

In contrast to voles, early studies, including those at the Erkuta Monitoring Site, note that the occurrence of Siberian lemmings has decreased in all four bioclimatic subzones (Sokolova et al., 2024). Such tendency is also observed in other parts of Arctic like Alaska (Plein et l., 2022). And when a species declines to a level where it is only found in very low numbers, it loses its ecological functions. In this study, Siberian lemmings were encountered in a small number in 2009, 2010, 2012 and 2014, after which they were not observed to be captured and were therefore not included in the statistical analysis.

The occurrence of collared lemmings was more stable. A significant decrease was observed only in the forest-tundra according to long-term stationary studies (Sokolova et al., 2024). Other sources report that until 1990, small rodents of Southern Yamal were characterized by 3–5-year high-amplitude cycles. Moreover, both species of lemmings reached high numbers in the south of Yamal until the 1990s, including in areas located more than 100 km south of the study area (Balakhonov et al., 1997; Danilov, 2000).

Many studies confirm that climatic shifts influence significantly on the rodents' distributions – on the predominance of some species over the others, on their habitual changes from typical biotops into the adjacent ones.

The decline in lemming populations is linked to changes in winter climate. It was noted that specifically shorter seasons with unstable weather in autumn and winter are more often can be met in the Arctic (Malkova et al., 2022). Warm rains and elevated temperatures result in soil icing, while warm weather and strong winds in autumn or snow rains at the end of winter lead to the formation of hard basal snow at the base of the snow cover. This hard basal snow restricts access to food and impedes reproduction, ultimately leading to low spring and summer populations. Studies conducted in Fennoscandia, where precipitation is significantly higher, and the climate is much warmer than in the high Arctic, provide support for this hypothesis (Domine et al., 2018).

Furthermore, a negative correlation has been documented between the hardness of the lower layer of snow and the growth of lemming populations in both the high latitudes of the Arctic (Domine et al., 2018) and the mountain tundra of Fennoscandinavia (Kausrud et al., 2008). In other regions of the Arctic, changes in winter climate, particularly in the physical properties of snow and shorter winter seasons, have been found to have adverse effects on lemmings that typically breed under snow (Poirier et al., 2019). These conditions are particularly detrimental to lemmings, which rely on winter breeding under snow to achieve high population densities, compared to voles (Domine et al., 2018). In contrast, soft snow enables access to food and promotes reproduction under the snow, resulting in a large population at snowmelt and creating favorable conditions for a population irruption (Fauteux et al., 2015).

These climatic changes are particularly harmful to Siberian lemmings, which can be attributed to the fact that collared lemmings develop large claws on their front legs in early winter, enabling them to dig through hard snow more effectively. While Siberian lemmings prefer fertile open swamps as their winter habitat, collared lemmings favor snow thickets on steep slopes with dwarf birch trees in low Arctic conditions (Dunaeva, 1948) - a habitat where the snow is likely to remain loose. This explains the low abundance of lemmings in the southern part of the peninsula and the decline in their population, as evidenced by long-term trapping data.

Therefore, current and previous research on Erkuta indicates that Siberian lemmings are no longer the primary prey for specialized predators in southern Yamal (Fufachev et al., 2019), and it is likely that they no longer serve a significant role as herbivores (Baubin, 2016).

Moreover, numerous studies indicate that longer, warmer summers are facilitating the growth and northward expansion of willow thickets in certain regions of the Arctic (Mekonnen et al., 2021; Myers-Smith et al., 2011). Shrub expansion, also known as shrubification (where tall shrubs, primarily willow thickets, are advancing northward), has positive feedback loops on climate warming. These feedback loops include a decrease in the albedo of the vegetation surface, changes in nutrient circulation (Sokolov et al., 2012; Koltz et al., 2022), and acceleration of carbon cycling, which ultimately leads to further warming.

Additional research has also demonstrated that extended growing seasons and increased average summer temperatures are causing alterations in plant communities, specifically an increase in the growth of erect shrubs and a decrease in less competitive groups such as lichens and mosses (Berner et al., 2020; Mekonnen et al., 2021). These changes, in turn, facilitate the expansion of bird and mammal species that are closely associated with willow forests as their primary habitat (Sokolov et al., 2012). Other observational evidence also suggests that rapid climate warming over the past few decades has led to such shifts in phenology (Myneni et al. 1997, McManusy et al. 2012, Prevei et al. 2019, Bjorkman et all 2020).

For instance, a recent study has identified a positive correlation between the summer heat index and plant biomass on a large-scale transect over Yamal (Ermokhina et al., 2023). Consequently, ongoing warming could potentially have a beneficial impact on both plant species diversity and biomass northward of the peninsula. This could result in grass- and forb-dominated vegetation replacing the low-productivity moss-dominated habitats that are common in subzones D and C and typical for Siberian lemmings. Simultaneously, such changes could expand potential habitats for voles. Furthermore, a recent study has shown a northward shift of 50–100 km in the boundary between the upper and lower Arctic in Yamal (Ermokhina et al., 2023).

Other studies have also linked the effects of warming climate on the cycles of small rodents, which typically change every 3-5 years. Thus, it is noted that warming leads to periods with damped amplitudes and the absence of typical years of peak abundance (Cornulier et al., 2013; Ims et al., 2008). At the Erkuta site, such changes also occur - at the beginning of the study, two peaks were observed in lemmings with an interval of 5 years, but subsequently their density remained low (Fufachev et al., 2019). The loss of regular lemming peaks could have catastrophic consequences for specialist predators. For example, such consequences are already happing to snowy owls (Bubo scandiaca) in eastern Greenland (Schmidt et al., 2012) or arctic foxes (Vulpes lagopus) in northern Scandinavia (Ims et al., 2017). These changes are especially unfavorable on Yamal too, since rodents are the key to the reproductive success of all predators. Thus, on Yamal the abundance of mythages (Arctic foxes, Buzzards, Skuas, gulls, snowy owls) and the success of their reproduction directly depend on the population density of lemmings and also have a cyclical nature.

Moreover, this climate influence is further dramatized by the fact that since the peak number of lemmings occurs in April, by the time the predators begin breeding, food for reproduction is already available. When voles breed in the summer, their numbers reach their peak in August - at this time predators no longer breed. As their numbers decline, predators will be forced to switch to other food, for example, geese or bird eggs. And that would lead to the reorganization of the whole food web.

It is important to acknowledge the impact of reindeer herding and industrial development on the peninsula, which are also contributing factors to the changes in

Yamal's vegetation. These activities can result in damage or even complete loss of lichen cover, suppression of shrub growth, and the emergence of secondary plant communities dominated by grasses (Forbes and Stammler, 2009; Spiegel et al., 2023). Such plant conditions are advantageous for voles.

In addition, the indigenous Nenets residing in Yamal have also reported a general trend of expansion and increased growth of willow thickets on the peninsula (Forbes and Stammler, 2009).

Conclusion

The aim of this work was to document, evaluate and predict changes in the small rodent’s community under spreading of willow thickets. As the results it was recorded that the rodent community in the shrub tundra of Southern Yamal was dominated by two species: the Middendorff's vole and the narrow-headed vole, which were the most numerous species in the trapping areas. The narrow-headed vole was trapped mainly in areas located at the edge of willow thickets, when, as for the Middendorff's vole, the mostly wet tundra with a thick layer of sphagnum moss was the most preferred habitat. The predominance of collared lemmings has been documented in dry tundra. Hence, it supports the 1st hypothesis of this study.

Narrow-headed voles have shown a statistically significant tendency of moving out of their preferred habitat (thickets) not only to neighboring meadows, but even into the alternative types of biotopes (wet and dry areas of tundra). Contrary, two native arctic species (colored lemming and Middendorff' vole) doesn’t show such significant trend despite of their high abundance in some years. That conclusion is partly contrary to 2nd hypothesis of the study.

The obtained long-term climatic data also support positive trend and increase of mean summer temperatures on the study area and in the region (from 9,3 up to 11,6 degrees). At the same time many studies confirm the positive relation between climate change (namely warming) and the expansion of shrubs. Many studies confirm the increase and spread of both deciduous shrub species such as birch (Betula spp.), willow (Salix spp.), and alder (Alnus spp.), as well as prostrate evergreen shrubs in response to warming on Yamal and in other parts of Arctic. And since narrow-headed and Middendorff's voles feed on grasses and forbs, their increasing distribution is most likely caused by the growth of shrubs, forbs and grasses due to longer and warmer summers.

To reach our task about formulating a forecast of changes in the rodent community under the condition of spreading shrubs, our findings allow us to predict explosion further to the north of more southern species (narrow-headed vole) into the tundra, where it possibly can negatively affect native arctic species in their preferred habitats. It will ultimately affect the entire food webs of terrestrial arctic ecosystems, namely abundance and breeding performance of symbolic arctic species, such as snowy owls and arctic foxes.

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