Original Investigation

Small rodents in the shrub tundra of Yamal (Russia): Density dependence in habitat use?

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ABSTRACT

Northern small rodents are well known for their population cycles which represent a key process for the functioning of arctic and boreal ecosystems. Habitat use often changes in the course of the cycle. Higher densities can either lead to spill-over into secondary habitats or to increased habitat specificity because of interspecific competition. Here we investigate whether voles in the shrub tundra of southern Yamal exhibit density dependent habitat use. Voles were trapped at the Erkuta Tundra Monitoring Site (N 68.2°, E 69.2°) in three characteristic habitats over five years covering all phases of the population cycle. Our analyses focused on the two most numerous species *Microtus gregalis* (52% of individuals caught) and *M. middendorffii* (36%). A small-scale spill-over effect was observed for *M. gregalis*, which increasingly used the open habitat adjacent to their preferred willow thickets at high abundance. At a larger scale no such effect was observed for the two *Microtus* species – a result which is explained by the overall moderate densities of voles and the large spatial extent of the primary habitat of *M. middendorffii*: moist moss dwarf shrub tundra.

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Introduction

Small rodents are key species in many ecosystems, and in particular in the arctic tundra (Batzli et al., 1980; Krebs et al., 2011). Their regular density fluctuations – cycles – are a conspicuous phenomenon that has attracted the attention of scientists for nearly a century (Elton, 1924; Stenseth, 1999). In most communities the individual species exhibit clear preferences for specific habitat types, although some overlap occurs (Dunaeva, 1948; Batzli and Henttonen, 1990). The habitats occupied by each species can change with abundance during the small rodent cycles (Morris et al., 2000). If intraspecific competition is the main determinant of spacing, the animals will exhibit density-dependent habitat use (Rosenzweig, 1981, 1991). The core habitat may not be able to host all individuals when density increases and some animals will

spill-over into more marginal habitats. In this case, segregation of species in different habitats will appear most clearly at low densities, when voles are localized in isolated small demes (Benenson, 1982; Petrov, 1994). At high densities there may be more overlap between species (Hansson, 1983; Löfgren, 1995; Sundell et al., 2012). However, interspecific competition may also be important. Larger voles are in general competitively superior to smaller species. The larger *M. oeconomus* excludes for example *M. agrestis* from common habitats at high densities (Henttonen et al., 1977). If interspecific competition is the dominant factor affecting habitat selection, and the competing species prefer different habitats, habitat specificity may increase with density, at least for competitively inferior species (Löfgren, 1995; Johannesen and Mauritzen, 1999). The latter may then be excluded from the primary habitat of the competitively superior species. This may also be the case when densities of both species fluctuate in synchrony as they normally do in rodent communities with multi-annual population cycles (Hanski and Henttonen, 1996).

The small rodent community in the shrub tundra zone of the Yamal Peninsula is rather species rich comprising several species of voles, the most numerous of which are *Microtus middendorffii*

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(Middendorff's vole) and *M. gregalis* (narrow-headed vole), as well as collared lemmings (*Dicrostonyx torquatus*) and Siberian lemmings (*Lemmus sibiricus*). The two *Microtus* species are morphologically very similar, but differ in their distributional range. Whereas the distribution of *M. middendorffii* is limited to the Russian Arctic and subarctic east of the Ural Mountains (Tsytsulina et al., 2008), *M. gregalis* has a disjunct distribution. It occurs both in the Arctic and subarctic of Russia, and in steppe areas in the south of Russia (Batsaikhan et al., 2008). While little has been written about the ecology of these species in international scientific publications, many aspects are well covered in the Russian literature. Thus, a three year cycle is typical for *Microtus* voles in southern Yamal (Balakhonov and Shtro, 1995; Danilov, 2000). Dunaeva (1948) wrote that *M. gregalis* occurs in river valleys where it inhabits flooded meadows, willow thickets and steep river banks with lush vegetation. *M. middendorffii* mainly uses lower laying humid tundra areas with bogs characterized by mosses, dwarf birch and sedges (Dunaeva, 1948) and is more of a habitat generalist (Schwartz and Pyastolova, 1971; Sokolov and Sokolova, 2006). Other studies showed more overlap in the habitat use of the two species. Elshin (1983) trapped the highest numbers of both species in willow thickets close to rivers, whereas the second best habitat for *M. gregalis* was sedge-herb tundra and for *M. middendorffii* it was bogs. Sokolova (2004) trapped most *M. gregalis* in willow thickets and most *M. middendorffii* on river banks and in bogs, revealing partly similar habitat preferences. Changes in habitat use with population density have not been addressed previously for either of these closely related but ecologically different species, and it is not known whether they compete for space or resources.

Here we investigate whether habitat use of two closely related vole species, *M. middendorffii* and *M. gregalis*, is related to the population cycles of these species. In particular we test two alternate predictions: (1) the voles are restricted to their primary habitat at low densities, expanding to other habitats in peak years, as observed for two sympatric voles species in Finnish forests (bank vole *Myodes glareolus* and field vole *Microtus agrestis*; Sundell et al., 2012), indicating that intraspecific competition is most important; or (2) habitat specificity increases at high densities, which would indicate that strong interspecific competition is operating between the two species. Analyses are carried out at the scale of the study area for both species (landscape scale), and at the scale of plots for *M. gregalis*.

Material and methods

Study area and trapping design

The study was carried out at the Erkuta Tundra Monitoring Site, near the confluence of the Payutayakha and Erkutayakha rivers in the southern part of the Yamal Peninsula (68.2° N, 69.2° E; Fig. 1). The study area is characterized by flat tundra interspersed with hills (up to 40 m high) with some steep slopes, and sandy cliffs along rivers banks and lakes (Sokolov et al., 2012; Ehrich et al., 2012). The landscape is subdivided by a dense network of rivers and lakes, and many low-lying areas are flooded in spring. It lies at the border between erect dwarf shrub tundra and low shrub tundra (Walker et al., 2005). Low shrub tundra is more common in the area than the drier, lichen-rich erect dwarf shrub tundra (Magomedova et al., 2006). Dense thickets composed of willows and occasionally alder (*Alnus fruticosa*) occur along streams and lakes.

Voles were trapped in three habitats defined as landscape elements which are typical for the study area. Dry plots (Dry) were situated on hillsides or in upland tundra, however not in the driest places such as on the top of ridges. The vegetation on Dry plots consisted of dwarf-shrub tundra typical for bioclimatic zone E

(Walker et al., 2005). Wet plots (Wet) were situated in moist areas in flat, low-lying tundra or in small valleys, often in bogs. They were dominated by thick layers of *Sphagnum* moss. Thicket plots (Thicket) were placed along the edge of willow thickets which were at least 0.5 m high and were growing on the slopes of small valleys or hills. Thickets belonged to the *Salix glauca-Carex aquatilis* type or to the *Salix lanata-Myosotis nemorosa* type as defined by Pajunen et al. (2010). Willow thickets are a conspicuous structural element in the shrub tundra. They grow in the most productive parts of the landscape and provide both food and shelter for numerous animals (Henden et al., 2011a,b; Ehrich et al., 2012). The vegetation adjacent to the thickets consisted of productive meadows dominated by forbs and grasses or of dwarf shrub tundra. Being placed at the edge of thickets, these plots represent a very favorable habitat combining cover and food. All plots were chosen by assessing the habitat by eye according the criteria listed above, and located in areas which are not flooded in spring.

The difference in vegetation among the three focal habitats was quantified by point intercept data, a proxy for biomass (Bråthen and Hagberg, 2004), obtained for 13 plant functional types (Chapin et al., 1996). A triangular sampling frame of 40 cm × 40 cm × 40 cm with tree pins (diameter 0.4 mm) was placed every 3 m, and 1.5 m from the outer edge of the plots used as trapping units for small rodents (quadrats of 15 m × 15 m; see below), giving 25 triangles for each quadrat. For each triangle, we counted the number of times plants of the different functional groups touched one of the pins. A correspondence analysis on the sums of plant intercepts for each quadrat showed that rushes, lichen and evergreen woody shrubs were important on Dry plots, Vascular cryptogams, herbaceous dycotyledons, grasses as well as *Salix* sp. were characteristic of Thicket plots, and sedges were associated with Wet plots, although some overlap in vegetation composition occurred among habitat types (Appendix Fig. A1). At the landscape scale, tundra of the Dry type was the most widespread habitat, followed by Wet. Willow thickets that are not flooded in spring covered a much smaller area (Ehrich et al., 2012).

Trapping was carried out following the small quadrat method of Myllymäki et al. (1971), which is a method that has been used extensively to study habitats use and population dynamics in boreal and arctic rodent communities (Steen et al., 1996; Ekerholm et al., 2001; Brommer et al., 2010; Ims et al., 2011; Sundell et al., 2012). Three snap traps baited with raisins and rolled oats were placed at each corner of a 15 m × 15 m quadrat (i.e. 12 traps per quadrat). In Thicket habitat, two corners of the quadrat were located approximately 1 m inside the willow thicket, whereas the two other corners were situated in the adjacent habitat (dwarf shrub tundra or meadow). Traps were set selectively within a radius of 2 m from the corner point, e.g. on vole runways or in front of holes if available. Trapping plots (quadrats) were placed according to a nested design consisting of 2 units (unit K and unit R; Fig. 1), which each included six trapping quadrats in each of the three focal habitats (i.e. 2 units × 3 habitats × 6 quadrats = 36 quadrats in total). The average distance between plots of the 2 units was 6.46 km (min = 5.12 km, max = 8.14 km). The distance between plots in the same habitat within units was between 0.13 km and 2.79 km and the minimum distance between plots in different habitats was 0.05 km. As far as possible plots in different habitats were spatially grouped as triplets within units (Fig. 1), but the landscape configuration prevented complete implementation of the planned nested design (Ehrich et al., 2012). The triplet level will therefore not be used in the analysis. Trapping was carried out in mid-July 2007, and in late June and early August in subsequent years (2008–2011; see appendix table A1 for exact dates). Each trapping session extended over two days and traps were checked once per day, resulting in two checks per session (i.e. 24 trap nights per plot per session). In 2007, an exceptionally strong storm and high rainfall closed