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Original Investigation

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

Natalya A. Sokolova^{a,b,*}, Aleksandr A. Sokolov^{a,b}, Rolf A. Ims^c, Gunhild Skogstad^c, Nicolas Lecomte^{c,d}, Vasilii A. Sokolov^e, Nigel G. Yoccoz^c, Dorothee Ehrlich^c^a Ecological Research Station, Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Labytnangi, Russia^b Science Center for Arctic Studies, State Organization of Yamal-Nenets Autonomous District, Salekhard, Russia^c Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway^d Department of Environment, Government of Nunavut, PO Box 209, Igloolik, Canada^e Institute of Plant and Animal Ecology of Ural Branch of Russian Academy of Sciences, Ekaterinburg, Russia

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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*

* Corresponding author at: Ecological Research Station, Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Labytnangi, Russia. Tel.: +7 3499251889; fax: +7 3499251887.

E-mail addresses: nasokolova@yandex.ru, sokhol@yandex.ru (N.A. Sokolova).

(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.

Voies 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 to 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

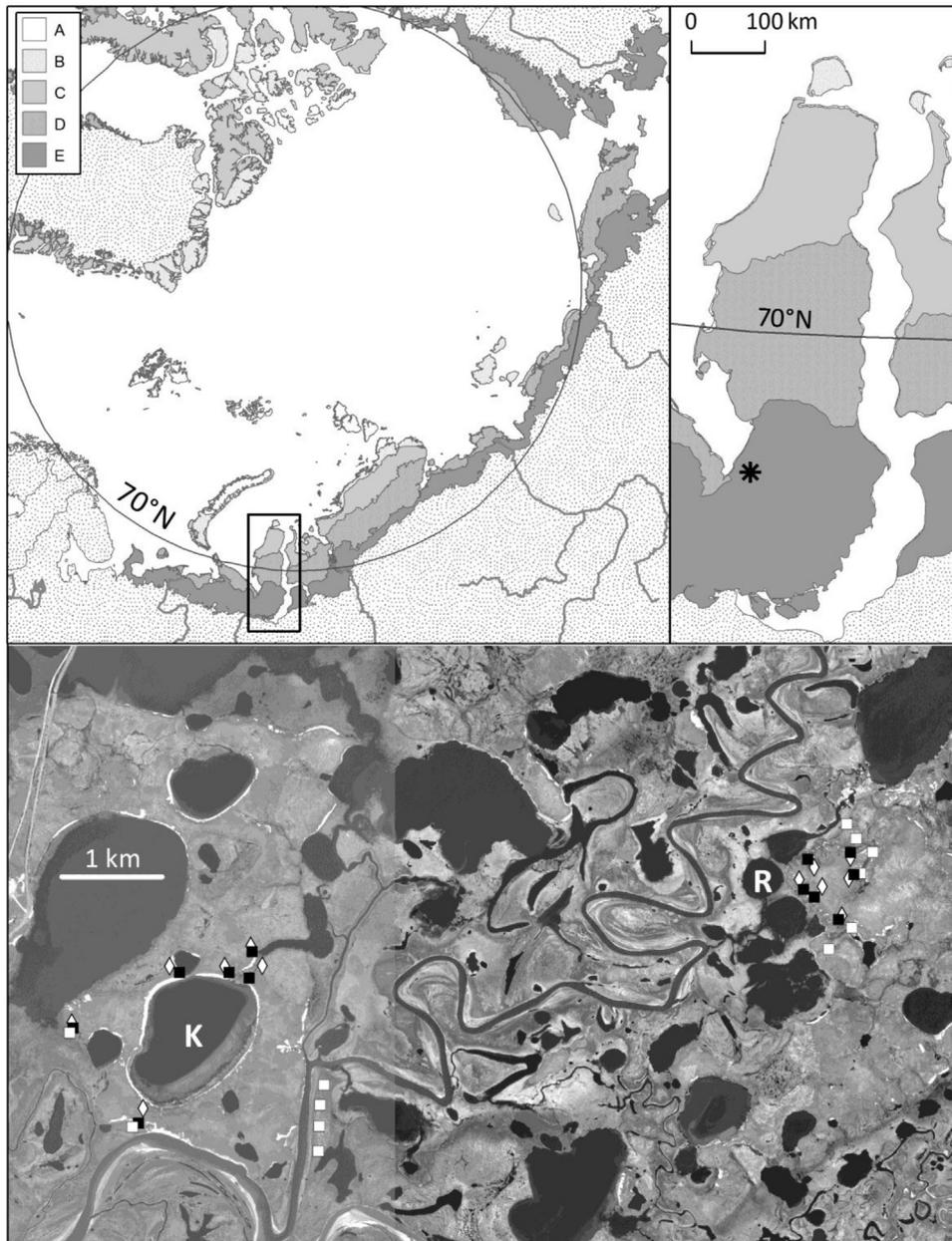


Fig. 1. Top: maps showing the location of the study area in southern Yamal. The shading represents the five bioclimatic subzones of the Arctic (A–E) as used by the Circumpolar Arctic Vegetation Map (Walker et al. 2005). Bottom: map of the study area with the trapping plots. The plots were placed in 2 distinct groups (units K and R). Black squares represent plots in Thicket habitat, diamonds are plots in Dry habitat and white squares area plots in Wet habitat.

a large number of traps, so trapping was extended for an additional day. Because of short trapping sessions, the small spatial extent of each of the small quadrats relative to the total area occupied by each habitat type, and their scattered distribution in the area, it is reasonable to assume that the removal trapping had a negligible effect on the population dynamic of the local small rodent populations (Myllymäki et al., 1971; Hanski et al., 1994). For the same reasons it is unlikely that it affected their habitat use.

Because in most cases it is very difficult to distinguish *M. gregalis* and *M. middendorffii* based on external morphological characteristics (Flint et al., 1970), heads of all *Microtus* were conserved in ethanol. In the laboratory, they were boiled, cleaned and examined to confirm species determination based on the first molar of the lower jaw (Borodin, 2009).

Statistical analysis

To represent fluctuations in abundance, the mean and standard error of the number of animals captured on each plot per 24 trap nights was calculated for each trapping session and species. The primary habitat of each species was defined as the habitat where most individuals of the respective species were caught. At the scale of the study area, our predictions about the relationship between habitat use and abundance were tested with generalized linear mixed effect models (GLMM) using the proportion of animals trapped in the primary habitat as response variable. As the number of trapped animals was rather low, the analysis was carried out at the level of units and the two *Microtus* species were analyzed together. The response variable was thus the proportion trapped in primary habitat per species, unit, season (i.e., first versus second trapping

session) and year (species–unit–season–year combinations where no animals were trapped were excluded resulting in 26 data points). Unit was included in all models as random intercept term. The main explanatory variables of interest regarding our predictions concerning density dependent habitat use were the natural logarithm (log) of the number of animals of the focal species captured in that season and unit – considered a proxy for the density of the species (cf. Hanski et al., 1994) and thus potentially affecting the level of intraspecific competition – and the log of the total number of small rodents trapped – a proxy for the overall density potentially affecting interspecific competition. We also included the log of the total number of small rodents trapped each year in the whole study area to reflect the stage of the small rodent cycle in that year, as well as season and species. As there was only one trapping session in 2007 in the middle of the summer, we used twice the number of small rodents trapped in that session as indicative of the total number in 2007. The GLMMs were fitted with a logit link and a binomial distribution (cf. Mysterud and Ims, 1998) using the function `lmer` of the package `lme4` (Bates et al., 2008) in R ver. 2.15.2 (R Core Team, 2012). Because of the small number of data points we could not include all explanatory variables in one model. Candidate models comprising one explanatory variable were compared to the simplest model, which was a constant response. Log-likelihood ratio tests were used to compare candidate models with different fixed effects, and a model was considered superior to the next simpler model when $P < 0.05$. Subsequently additive effects of season and species were added to the model retained in the first round of selection, and a log-likelihood ratio test was used to assess whether this improved the model. The selected model was checked for trends in the raw residuals, presence of outliers, and approximate normality of the random effects. An approximate estimate of the dispersion parameter was obtained from the sum of squared Pearson's residuals divided by the residual degrees of freedom.

The Thicket plots were composed of two habitat components, the willow thicket itself and the open habitat adjacent to it (productive meadow or dwarf shrub tundra). For *M. gregalis*, which was abundant on these plots, we examined whether animals were trapped predominantly in thickets or in adjacent open habitat, and whether this predominance changed with the number of voles trapped (as proxy for density as above), season and year, thus testing our predictions about the relationship between habitat use and abundance also at the small scale of plots. GLMMs were fitted to a dataset consisting of all Thicket plots with one entry per trapping session where *M. gregalis* had been caught ($n = 39$). We used the proportion of animals trapped on the thicket side per plot, year and season as response variable, a logit link and a binomial distribution. Trapping plot was included as random effect in all models to account for possible differences in habitat among plots. Fixed effects were log number of trapped *M. gregalis* in the respective plot and trapping session, the log of the total number of *M. gregalis* captured in the respective year, and season. Candidate models comprising one explanatory variable were compared to the simplest model which was a constant response (4 models in total). Log-likelihood ratio tests were used to compare the candidate models and model fit was assessed as above.

Results

Population dynamics

In total 215 small rodents belonging to five species were trapped during the five years of the study. Among these, 189 (88%) belonged to the two focal *Microtus* species. *M. gregalis* was the most abundant species, followed by *M. middendorffii*. In addition, we caught a few *D. torquatus*, *Myodes rutilus* (northern red-backed vole) and *L.*

Table 1

Total number of animals of each species trapped in each habitat type in the years 2007–2011 at the Erkuta tundra monitoring site (Yamal, Russia).

Species	Dry	Wet	Thicket
<i>Microtus gregalis</i>	2	7	102
<i>Microtus middendorffii</i>	2	69	7
<i>Dicrostonyx torquatus</i>	13	1	7
<i>Lemmus sibiricus</i>	0	1	0
<i>Myodes rutilus</i>	0	2	1

sibiricus (Table 1). The small rodent dynamics were therefore dominated by the population fluctuations of the two *Microtus* species. In total, vole numbers were low in 2007 and 2008, increased in 2009, reached a peak in 2010 and decreased somewhat in 2011 (Fig. 2). The amplitude of the observed fluctuations was moderate with about 10 times increase in overall abundance between the low and peak year. The peak year 2010 was characterized by the highest spring abundance observed during the study period, as well as by a high number of *M. gregalis* trapped in August when 23 times more animals of this species were caught than in August 2008 and the trapping index reached 4.5 individuals per 24 trap nights in Thicket habitat (i.e. 14.5 individuals/100 trap nights). The numbers of *M. middendorffii* varied less but they were clearly lower in 2008 than in the other years. Nevertheless, the density fluctuations of the two vole species were in general in synchrony (Spearman's correlation coefficient between the average number of animals trapped per plot and trapping session = 0.81; Appendix Fig. A2). Vole numbers increased over the summer each year and were always higher in August than in June.

Density dependent habitat use: scale of the study area

Most *M. gregalis* were captured on Thicket plots (all corners of the plot together) and most *M. middendorffii* on Wet plots (Table 1). The two species were trapped on the same plot in the same trapping session only twice. This happened on two different Wet plots in June 2010 and August 2011. Analyzing the proportion of *Microtus* voles per unit and trapping session captured in their primary habitat (Thicket for *M. gregalis* and Wet for *M. middendorffii*) showed that habitat specificity varied with the total number of small rodents captured in each year (Fig. 3). Based on likelihood ratio tests the GLMM with the log of the total number of small rodents trapped in each year in the whole study area as predictor variable was the most appropriate model among the ones considered (Appendix Table A2). An additive effect of species or season did not improve this model significantly. This means that habitat specificity of the

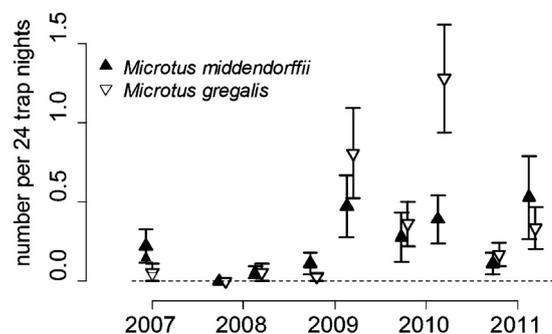


Fig. 2. Mean number of *Microtus middendorffii* and *M. gregalis* trapped per session and trapping plot (24 trap nights) at the Erkuta Tundra Monitoring Site, Russia. Error bars represent standard errors of the mean. For each year except 2007, numbers for June and August are shown. For 2007, the smaller symbols represent the trapping index when taking into account that the session lasted 3 days (see main text). For comparison 1 animal per 24 trap nights corresponds to 4.2 animals per 100 trap nights.

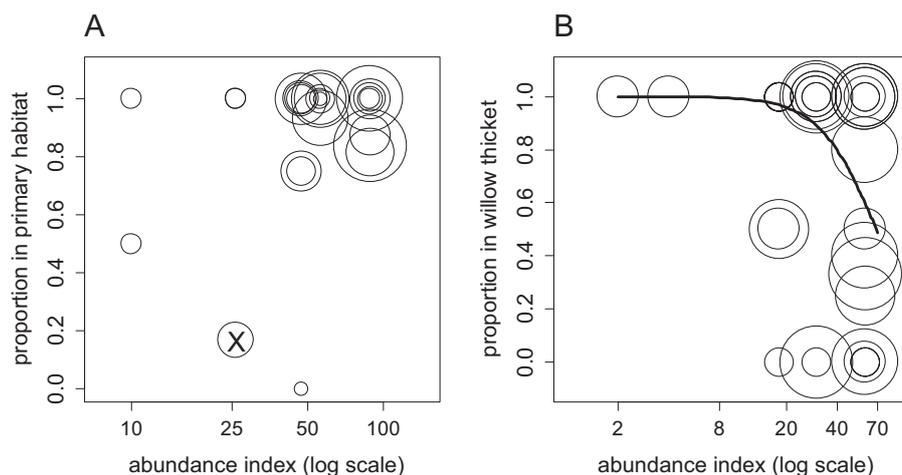


Fig. 3. (A) Proportion of *Microtus gregalis* and *M. middendorffii* trapped in their primary habitats (Thicket and Wet respectively) relative to the log of the total number of small rodents trapped per year at the Erkuta Tundra Monitoring Site, Russia (abundance index). Each circle represents a proportion per unit, year and season, and the area of the circle is proportional to the number of voles involved in the calculation of this proportion (smallest circle: 1 ind.; largest circle: 25 inds.). The cross indicates the influential value (*M. middendorffii* in unit R in 2007; see main text). (B) Proportion of *Microtus gregalis* trapped in Thicket plots that were trapped in the willow thicket and not in the adjacent open habitat relative to the log of the total number of *M. gregalis* caught that year (abundance index). Each circle represents a proportion per plot, season and year as above (smallest circle: 1 ind.; largest circle: 6 inds.). The thick line indicates the relationship estimated by the GLMM.

two *Microtus* species (for their respective primary habitat) was approximately the same. The results of the model indicated that the proportion of animals captured in their primary habitat increased with the total abundance of small rodents (logit estimate = 1.21, SE = 0.46; Appendix Table A2). Diagnostic plots showed that the distribution of the raw residuals and of the random effects were satisfactory, however two outliers were identified. After excluding the value for *M. middendorffii* in unit R in 2007 (Fig. 3A), the model did not reveal any significant effect of the log of the total number of small rodents trapped in each year on habitat specificity any more (logit estimate = 0.32, SE = 0.63; Appendix Table A3). Removing the other outlier had only a minor effect on the results. Approximate dispersion parameters were 1.89 and 1.61 with and without the influential outlier indicating moderate overdispersion. As overdispersion leads to the estimation of too narrow confidence intervals, this will however not affect our conclusion that there was no significant effect of the total number of small rodents trapped in each year on habitat specificity.

Density dependent habitat use: scale of plots

Considering *M. gregalis* on Thicket plots in particular, more animals were on average caught in the thicket itself than in the adjacent open habitat. The most appropriate GLMM based on likelihood ratio tests included the log of the total number of *M. gregalis* captured that year (Appendix Table A4), and revealed a negative relationship between overall abundance and habitat specificity (Fig. 3B). The probability for a vole to be trapped on the thicket side decreased with an increase in the log of the total number of *M. gregalis* captured that year (logit estimate = -2.55, SE = 0.91; Appendix Table A5). Assessing the distribution of random effects revealed two outliers, but as the results remained nearly the same when removing them, we present estimates based on the total dataset. The approximate dispersion parameter was 0.82, indicating no overdispersion.

Discussion

The small rodent community in the shrub tundra area of southern Yamal was dominated by two *Microtus* species, *M. gregalis*, which was the most abundant species on our trapping plots, and *M.*

middendorffii. *M. gregalis* was trapped mostly on plots situated at the edge of willow thickets whereas *M. middendorffii* was trapped mostly in wet tundra characterized by a thick layer of *Sphagnum* moss. This habitat use is largely in accordance with the available literature (Dunaeva, 1948). The primary habitat of *M. middendorffii*, boggy plains with moss-dwarf birch tundra dominated by *Sphagnum*, is widespread in our study area and corresponds to our Wet plots. *M. gregalis* uses the willow thickets growing in river valleys, feeds on the productive meadows which are often adjacent to the thickets and digs large burrow systems in the well-drained ground of the river banks. Dunaeva (1948) suggested that suitable substrate for these burrows may be the main habitat requirement for *M. gregalis*, as well as food from lush growth of meadow plants. In our study area, we also recorded *M. gregalis* on steep slopes with well drained soils and varied herbaceous vegetation, but without willow thickets. It is thus possible that this species selects for landscape attributes that are often associated with willow thickets, without necessarily exploiting the thickets themselves.

Investigating how habitat specificity at the landscape scale changed during our study period revealed no evidence for increased use of secondary habitats with increasing small rodent densities as expected from more intensified intraspecific competition. At the landscape scale, prediction 1 was thus not supported. The absence of the predicted spill-over effect, as observed notably by Sundell et al. (2012), may be due to lower overall abundance of voles in our study area and period. Indeed Sundell et al. (2012) reported based on the same sampling method a trapping index of 17.8 individuals per 100 trap nights on average over their study in the boreal zone of southern Finland, whereas at Erkuta the maximum trapping index observed for *M. gregalis* in Thicket plots was 14.5 animals per 100 trap nights in August 2010 (Fig. 2), and the average index for small rodents (all species pooled) over the study period was 7.4 animals per 100 trap nights. At lower densities, intraspecific competition may not have been strong enough to make animals move to secondary habitats. The primary habitat of *M. middendorffii*, humid bogs dominated by *Sphagnum* and dwarf shrubs, is widespread in the study area. Assuming that with increasing abundance small rodent populations expand from small isolated demes to occupy more of the available habitat, it is thus unlikely that all available spaces will be filled by voles. The number of trapped voles in our study was in the range of values observed in other areas of the

southern tundra for *M. oeconomus* (Henden et al., 2011b; Pokrovsky et al., 2014), suggesting that density dependent spill-over of the studied vole species into secondary habitats is likely to be rare in the shrub tundra. It may be that small rodent communities in southern arctic ecosystems most often are limited or regulated at densities below thresholds where competitive interactions become important.

Including all data points, our analysis could have suggested a positive effect of abundance on habitat specificity, which would be in accordance with prediction 2, but this result was dependent on one influential value and was thus not robust. Considering the overall densities in our study area, it seems however very unlikely that interspecific competition plays a role here. Biologically, such a relationship could be interpreted in the light of negatively density-dependent dispersal which has been documented for periodically fluctuating vole populations of different species based on experimental (Ims and Andreassen, 2005; Smith and Batzli, 2006) and genetic data (Ehrich et al., 2009).

On a smaller spatial scale within trapping quadrats a spill-over of individuals to secondary habitat could be documented for *M. gregalis* in accordance with prediction 1. Most voles were caught in the traps placed within the willow thicket, but the proportion of individuals that were trapped in the open habitat adjacent to the thicket (within 15 m) increased in years when more *M. gregalis* were trapped in total. Interestingly the proportion of voles trapped in the thicket was not correlated with the number captured in the respective plots and trapping sessions, but with the overall abundance in the different years. This is likely to be due to large imprecision of the abundance estimates at plot level, where only a few voles were caught. The fact that voles mostly use the thickets themselves can be related to favorable ground for digging and nutritious plants in the undergrowth of the thickets. In addition the shrub cover may provide some protection from avian predators. Increased use of the adjacent habitat at high densities may indicate that resources become limited in the thickets, forcing the voles to move to open habitat to feed. The traps in open habitat were however located less than 15 m from the edge of the thicket, suggesting that animals trapped there were making foraging excursions into the open habitat (see Hovland et al., 1999), but that this open habitat was probably not included in the core area of their home ranges. Data on movements of individuals would however be necessary to confirm this explanation.

Altogether our results support the prediction that high densities lead to spill-over into less preferred habitat for *M. gregalis* at the local scale of plots, which may be attributed to intraspecific competition. At the landscape scale, this prediction could be rejected. On the contrary there may have been a tendency for increased habitat specificity at lower densities, which could be related to negatively density-dependent dispersal.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2014.04.004>.

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