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ORIGINAL PAPER

Population dynamics of tundra voles in relation to configuration of willow thickets in southern arctic tundra

John-André Henden · Rolf Anker Ims ·
Nigel Gilles Yoccoz · Raymond Sørensen ·
Siw Turid Killengreen

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Abstract The areal extent and configuration of thickets of willow shrubs are currently changing in the Arctic both as an effect of global warming and changed browsing pressure of reindeer. These changes have been predicted to impact the distribution and abundance of wildlife species relying on willow thickets as habitat. We assessed the relation between variables quantifying willow thicket configuration and population dynamics of tundra voles (*Microtus oeconomus*) in three riparian regions in Finnmark, northern Norway, which were subject to intense browsing by semi-domesticated reindeer. The tundra vole, which exhibits 5-year population cycles in Finnmark, is the dominant small rodent species in riparian landscape elements in southern arctic tundra. In the course of a 4-year trapping study, tundra vole populations went through the cyclic phases of increase, peak and crash, however, with distinct differences between the three regions in the population dynamics. Within regions, the occupancy pattern during the increase phase was positively related to willow thicket configuration (in particular edge density and willow height) only in the region attaining the highest abundance and occupancy. However, local abundance was not clearly related to habitat

features within any regions. The lack of consistency in the response of tundra vole populations to willow thicket configuration, as well as the positive relation between the degree of thicket shredding and tundra vole habitat occupancy in one of the regions, indicates that tundra voles will not be much affected by climate or browsing induced changes in the shrubbiness of the tundra in the future.

Keywords Over-browsing · Shrub expansion · Fragmentation · Abundance · Occupancy · Large-scale study

Introduction

Willow shrubs (*Salix* spp) forming thickets are conspicuous structural elements in southern arctic tundra, where they serve important ecological functions including habitat for wildlife (Bliss et al. 1973; Bliss 1997). There has been a recent surge of studies focusing on the dynamics of willow thickets in the Arctic. There are two main reasons for this. On one hand, an increased extent of willow thickets has been observed in parts of the arctic and this has been attributed to a warming climate (Sturm et al. 2001; Chapin et al. 2005; Tape et al. 2006). On the other hand, where herds of semi-domesticated reindeer (*Rangifer tarandus*) have increased substantially over the last decades, such as in Finnmark in northern Fennoscandia (Moen and Danell 2003; Tveraa et al. 2007) and in Yamal in western Siberia (Forbes et al. 2009), studies have shown that reindeer browsing may reduce the willow thickets (Olofsson 2001; Pajunen et al. 2008; Olofsson et al. 2009; Kitti et al. 2009). The effect of such changes in areal extent and height of willow thickets in tundra has begun to be explored in terms of their functions in local and global energy balance (Sturm

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J.-A. Henden (✉) · R. A. Ims · N. G. Yoccoz · R. Sørensen ·
S. T. Killengreen
Department of Arctic and Marine Biology,
University of Tromsø, 9037 Tromsø, Norway
e-mail: john-andre.henden@uit.no

Present Address:
R. Sørensen
Norwegian Wild Reindeer Centre North, 2661 Hjerkind, Norway

et al. 2005; Chapin et al. 2005). As yet, however, there have been no studies that have explicitly analyzed the effects of such changes on arctic wildlife populations using willow thickets as habitat, although such effects have been predicted (den Herder et al. 2004; Bråthen et al. 2007; Ims et al. 2007; den Herder et al. 2008; Forbes et al. 2009). Here, we provide such an analysis focusing on tundra voles (*Microtus oeconomus*).

Small rodents are key herbivores in tundra ecosystems (Batzli et al. 1980). In landscape elements with willow thickets, such as moist and nutrient rich sediment plains along creeks and rivers, the tundra vole is often the dominant small rodent species both in arctic America (Batzli and Henttonen 1990; Tast 1966) and Europe (Tast 1966). These riparian habitats provide tundra voles with food plants such as herbs and graminoids, while the willow thickets most likely serve the function as cover and protection against avian (Tast 1968) and some mammalian predators. The importance of tall and dense vegetation cover for tundra voles has been well demonstrated through a series of small-scale model system experiments conducted on enclosed plots in temperate agricultural farmland (e.g. Ims et al. 1993; Andreassen et al. 1998). However, while tundra voles typically reside most of the time under the protective canopy of tall vegetation, they tend to forage along the edge toward open habitat providing more nutritious food plants (Hovland et al. 1999). The different functions of open habitats providing food and closed habitat providing cover can result in non-linear, context-dependent habitat selection functions (c.f. Mysterud and Ims 1998) and ultimately account for some counter-intuitive population responses in tundra voles to experimental habitat fragmentation. For instance, experimental shredding (Meffe and Carroll 1994) and fragmentation of habitat in previous model system studies have shown that higher tundra vole abundances may be attained in more shredded and fragmented habitats (e.g. Ims et al. 1993; Hovland et al. 1999; Johannesen et al. 2003). Moreover, these previous studies have also demonstrated how large-scale factors, in particular those determining regional predation pressure, can entirely overrule the impact of local habitat fragmentation (Ims and Andreassen 2000).

With the insight from these previous relatively small-scale and short-term experimental studies in mind, we analyze local and regional scale dynamics of natural tundra vole populations during the phases of increase, peak and crash of a typical population cycle. The study was conducted in three riparian regions in north Norwegian tundra landscapes, where willow thickets exhibited variable areal extents and fragmentation. This study setting allowed us to assess the effects of willow thicket configuration variables that are likely to be affected both by reindeer browsing and climate change.

Methods

Study area

The study was carried out during the years 2005–2008 in three riparian regions in northeastern Finnmark, northern Norway. Two of the regions were situated at the Varanger peninsula (70–71° N and 28–31° E), while the third was at Ifjordfjellet (71° N, 27° E) about 100 km west of Varanger peninsula (Fig. 1). The two study regions at Varanger peninsula were along the main river valleys of Vestre Jakobselv (VJ) and Komagdalen (KO), whereas in the region Ifjordfjellet (IF), several smaller rivers and creeks, mostly tributaries to the river Storelva, were included. The study regions are classified as erect low-shrub tundra belonging to the southern arctic zone in the north and east of Varanger peninsula (Walker et al. 2005) and sub-arctic mountain tundra in the south and west of Varanger peninsula and Ifjordfjellet (Moen 1999). The vegetation characteristics are grossly similar among the study regions (Killengreen et al. 2007). Heaths mainly composed of dwarf shrubs such as *Empetrum hermaphroditum*, *Betula nana* and *Vaccinium* spp., dominate the landscape (Oksanen and Virtanen 1995; Killengreen et al. 2007; Ims et al. 2007). In heath habitats, gray-sided voles (*Myodes rufucanus*) dominate numerically among the small rodent species (Oksanen and Oksanen 1981; Ekerholm et al. 2001), while Norwegian lemming (*Lemmus lemmus*) may be found in high numbers in the outbreak years which in Finnmark occur irregularly (Oksanen et al. 2008). Tundra voles prefer spatially much more restricted elements of the tundra landscape (Oksanen and Oksanen 1981), in particular moist depressions on sediment plains along creeks and rivers. In these riparian areas, the vegetation is substantially lusher than the surrounding landscape with meadows dominated by graminoids and herbs interspersed with patches of willow thickets (Ravolainen 2009). The edges between the meadows and the thickets are usually sharp (Figs. 1 and 2). While the two study regions at Varanger peninsula (i.e. KO and VJ) constitute summer pastures for more than 10,000 reindeer and are thus subject to intense grazing, the region IF is mainly a transition area for reindeer herds in spring and autumn and is thus subject to less grazing. Vole populations in Finnmark normally exhibit a synchronous 5-year cycle and the latest peak before the present study commenced was in 2002 (Yoccoz and Ims 2004; Killengreen et al. 2007; Oksanen et al. 2008).

Study design

This study was designed to assess the effect of configuration of willow thickets in riparian landscape elements. For this purpose, we strategically selected study units to span the existing variation in the areal extent and degree of

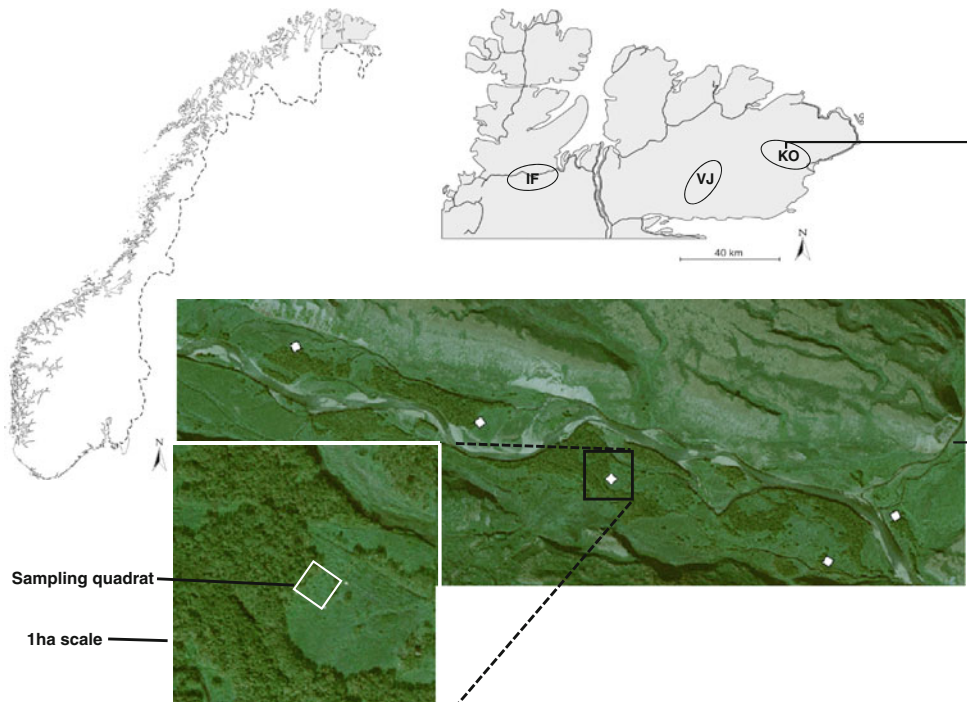


Fig. 1 Map giving the location of the three study regions (*IF* Ifjordfjellet, *VJ* Vestre Jakobselv and *KO* Komagdalen) in eastern Finnmark, northeastern Norway and an aerial photograph showing the distribution of willow thickets and the location of 5 sampling quadrats (white

squares) in study region *KO*. The enlarged square of the photograph highlights the measurement scale (1 ha scale) of 100×100 meter for the area-based willow thicket variables

fragmentation of willow thickets within each of the study regions. All study units were situated on mineral soils where the willow thickets are imbedded in lush meadow vegetation. The study units were 15×15 meter square plots hereafter referred to as sampling quadrats. To further standardize the selection of sampling quadrats, it was required that they should not have more than 30% mires or be flooded. Each sampling quadrat was placed so that one side of the quadrat was lining the edge of the thicket, while the quadrat extended into the surrounding meadow (Fig. 1). The distance between two adjacent sampling quadrats was at least 164 meters, and the average distance to the nearest quadrat was 652 meters (SD = 524 meters). We placed 12 sampling quadrats in each of the regions *KO* and *IF*, while there were 13 sampling quadrats in region *VJ* (i.e. in total $N = 37$ sampling quadrats).

Small rodent population census

Small rodent populations were censused in all sampling quadrats according to the small quadrat method of Myllymäki et al. (1971). According to this method, 3 snap traps baited with raisins and rolled oat were selectively set (e.g. on vole runways or in front of tunnels) within a radius of 2 meters from each corner of the sampling quadrat (i.e. 12 traps per quadrat). There were two trapping periods per year (2005–2008), one in summer (mid July) and one in

autumn (early September). Each trapping period extended two trap nights and traps were checked daily, i.e. two checks, one every 24 h. The short-term trapping effort, the small spatial extent of each of the small quadrats as well as their scattered distribution within each of the regions makes it reasonable to assume that the removal trapping had negligible effect on the tundra vole population dynamics (Myllymäki et al. 1971).

Quantifying willow thicket configuration

The areal extent and degree of fragmentation of willow thicket size were derived from aerial photographs taken in the summer of 2006. The photos were ortho-rectified in raster tiff-format and had a ground resolution of 0.20 meter. For converting the photographs from .tiff to .img-format, we used ARC GIS-software, version 9.1 (Environmental Systems Research Institute 2002). All willow thickets within the different regions were digitized in GRASS, version 6.1 (Grass Development Team 2006). The appropriate raw data files were imported in FRAG-STAT, version 3.3 (McGarigal and Marks 1995). FRAG-STAT was used to obtain area-based variables quantifying the areal extent and degree of fragmentation of the willow thickets within a 100×100 meter square (i.e. 1 ha) centered on each of the sampling quadrats. The areal extent of willow thickets was quantified as the



Fig. 2 Upper panel shows one example of the area-based configuration of willow thickets around one sampling quadrat in study site KO. Lower panel shows one example of the vertical configuration of willow thickets in one sampling quadrat in study site KO

percent cover of thickets. To describe the degree of fragmentation of willow thickets, we used two variables that are straightforward to interpret in terms of biological significance for small mammals. These were *patch density* (number of patches per ha) and *edge density* (meters of edge per ha). Increasing values for both of these variables indicate increased shredding or fragmentation of thickets. For all analyses, we defined a willow patch as consisting

of an aggregation of pixels that were spatially connected using the eight neighbors rule (McGarigal and Marks 1995).

As reindeer browsing has been shown to also affect the vertical structure of willow thickets (den Herder et al. 2004; Kitti et al. 2009; Pajunen et al. 2008) and climate warming affects the vertical growth of willow shoots (Forbes et al. 2010), we measured the *height* and *density* of the thickets in the field. These two variables were measured at four points along the side of the sampling quadrat lining the thicket. Willow density was assessed by point frequency, placing a telescopic stick vertically 1 meter inside the thicket and counting the number of hits with secondary stems and branches. Willow height was measured as the highest willow branch inside a circle with 20 cm radius surrounding the telescopic stick. The sampling quadrat score for the willow height and density variables was taken as the mean of the four measurements.

The measurement scale (1 ha) for the three area-based thicket variables was chosen as it gave non-overlapping measurements and corresponded to the trapping grid size used in many studies of *Microtus* species (Stenseth and Lidicker 1992). However, to evaluate whether the choice of measurement scale mattered, we also quantified the same variables within a 200 × 200 meter square. Measurements were strongly correlated (Pearson correlation >0.8) between the two scales indicating that our choice of measurement scale did not influence the results. Further, exploratory analyses of the willow thicket fragmentation variables showed, however, that patch density and edge density were strongly correlated (Pearson correlation = 0.72). Thus, we chose to only include one of them in the statistical modeling of tundra vole population dynamics. We included edge density because of the preference by tundra voles for edge habitat demonstrated in previous studies (Hovland et al. 1999). None of the other thicket variables was strongly correlated. Moreover, although the mean of the thicket variables differed somewhat between the three study regions, their ranges were highly overlapping (Table 1), meaning that regional effects could be statistically separated from the effect of willow thicket variables.

Table 1 Mean and range of the selected willow thicket configuration variables at the 100 × 100 m (1 ha) scale

Variables	Measure	All regions		Ifjord		Komagdalen		V. Jakobselv	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Willow cover	%	27.06	[5.41,58.89]	31.15	[6.01,58.89]	24.09	[7.33,57.40]	26.01	[5.41,46.19]
Edge density	m	661.68	[250.90,1,839.29]	824.70	[401.61,1,839.29]	520.75	[250.90,965.07]	641.29	[263.33,1,290.78]
Willow height	cm	160.68	[77.50,270.00]	117.30	[77.50,220.00]	210.63	[145.00,270.00]	154.62	[110.00,220.00]
Willow density	no. of hits	2.50	[0.25,5.50]	2.71	[2.00,3.25]	2.58	[0.75,5.50]	2.04	[0.25,4.25]

Statistical analyses

We focused on two aspects of tundra vole population dynamics that could be affected by willow thicket variables. First, we highlighted the colonization of habitat during the increase phase of the cycle by analyzing the patterns of occupancy in the 2 years (2005 and 2006) tundra vole populations were increasing in all study regions. Second, local abundance variation among the sampling quadrats was analyzed including the entire sampling period. In the first case (i.e. occupancy during colonization), generalized linear mixed-effects models (GLMMs) were applied to a binary response variable (presence or absence of tundra voles in the sampling quadrats per 2 trap nights) with a logit link function and a binomial distribution. In the second case, abundance variation was analyzed with linear mixed-effects models (LMMs) applied to log transformed number of tundra voles ($\log[N + 1]$) captured per quadrat. Fixed effect in both classes of models was the four willow configuration variables, year (2005–2006 in the occupancy models and 2005–2008 in the abundance models), season (summer and autumn) and region (VJ, KO and IF). Sampling quadrat identity was specified as random effects (Pinheiro and Bates 2000). Willow configuration variables were standardized (i.e. scaled with Mean = 0 and SD = 1) to ease comparison of their effects. Both GLMMs and LMMs were fitted using the lme4 package (Bates et al. 2008) in the software R (R Development Core Team 2009).

Model selection started from a model containing all two-way interactions between the continuous willow variables and categorical variables year, region and season as well as the two-way interactions region*year and region*season to account for different dynamics between the regions (Table S1 & S2, Appendix). From this model, we formed four candidate models (c.f. Burnham and Anderson 2002) by removing sets of two-way interactions, sequentially (see Table S1 & S2, Appendix). Log-likelihood ratio tests (LRT) were used to compare candidate models and to subsequently identify the final best model (Table S1 & S2 Appendix). Following Pinheiro and Bates (2000), maximum likelihood (ML)-fitted LMM's was used when models were compared to each other; whereas restricted maximum likelihood (REML)-fitted LMM's was used for parameter estimation. GLMM's was fitted using the Laplace approximation (Bates et al. 2008). Models were checked for constant variance of the residuals and presence of outliers and approximate normality of the predicted random effects.

Results

Regional population dynamics

During the 4 years of the study, a total of 624 small rodents were caught; of which, 431 (69%) were tundra voles, 101

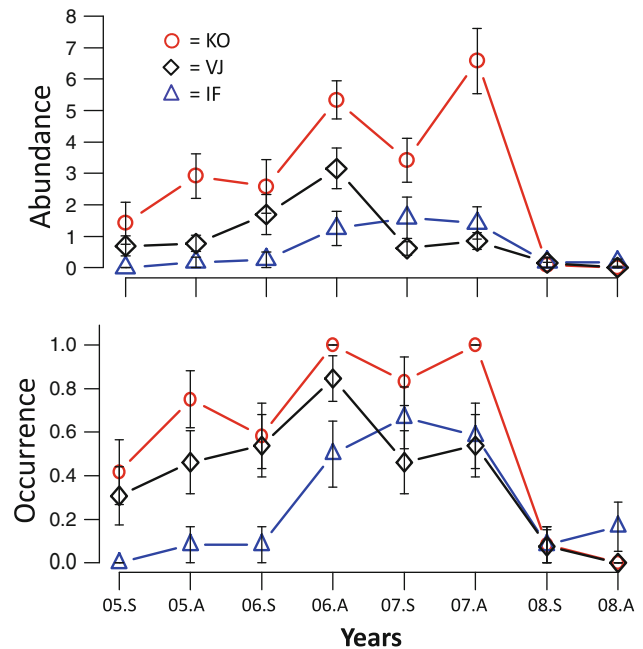
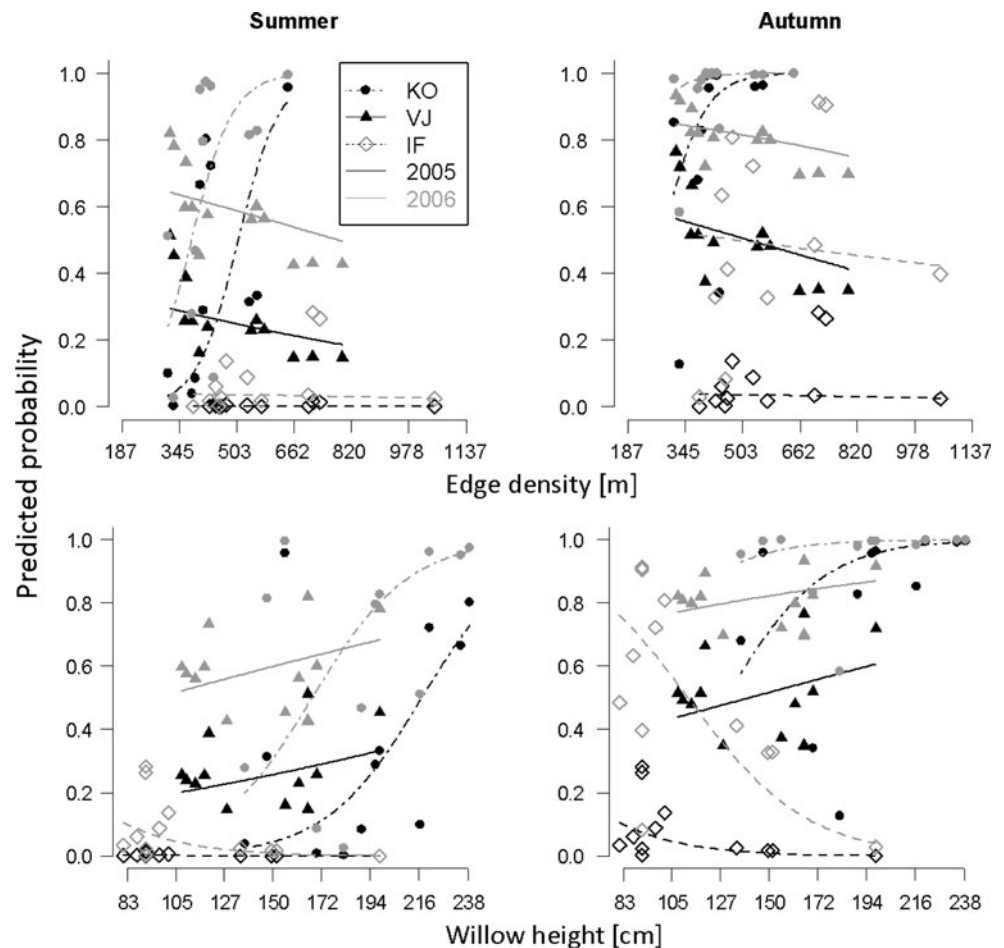


Fig. 3 Seasonal and multi-annual dynamics in local abundance (number of tundra voles caught per sampling quadrat, *upper panel*) and occupancy (proportion of sampling quadrats with at least one tundra vole caught per 2 trap nights, *lower panel*) of tundra voles in the three study regions. All estimates are seasonal (S Summer, A Autumn) mean values with standard error limits. Note that the equivalent “number per 100 trap nights” metric of the highest (07.A = 6.58) and lowest (08.S = 0.08) abundance in KO (*upper panel*) is 27.43 and 0.35, respectively

(16%) were Norwegian lemmings and 92 (15%) were gray-sided voles. Of the tundra voles, 103 (24%) was caught in VJ, 268 (62%) in KO and 60 (14%) at IF. The tundra vole populations in all three study regions were in the increase phase of the population cycle from the onset of the study in summer 2005 until autumn 2006, and all populations had crashed to similar low levels of abundance and occupancy by summer 2008 (Fig. 3). However, besides these two common features of the regional population dynamics, the three regions differed substantially in their mean levels of abundance and occupancy as well as their timing of population peaks and onset of the crash. KO had clearly the highest abundance and occupancy of the three regions. In this region, almost 100% occupancy was attained in autumn 2006, whereas the abundance continued to increase and peaked in autumn 2007 (Fig. 3). In VJ, occupancy peaked at approximately 80% in autumn 2006, when the crash phase commenced (i.e. 1 year before KO). In IF, the region with lowest abundance and occupancy of tundra voles in the increase phase of the cycle, the peak was attained in summer 2007 with approximately 60% occupancy. Compared to the other two regions, KO appeared to exhibit the most consistent seasonal dynamics in the increase and peak of the cycle with distinct increases between summer and autumn and decreases between autumns and summers (Fig. 3).

Fig. 4 Predicted probability of occurrence (occupancy) of tundra voles as a function of edge density (*upper panels*) and thicket height (*lower panels*) per season (summer and autumn), year (2005 and 2006) and region (KO, VJ and IF). Note that the figure legend is identical for all four panels



Effects of willow thicket configuration

Besides the terms that accounted for the region-specific dynamics (see above and Fig. 3), the best occupancy model for the increase phase of the cycle (years 2005 and 2006) included the two-way interaction between the four willow thicket variables and region (Tables S1 and S3, Appendix). The most influential of these two-way interactions was due to the effect of edge density and height of thickets on tundra vole occupancy in region KO (Fig. 4). Specifically, the probability of tundra vole occupancy increased steeply with density of thicket edges (estimate: 2.771, 95% CI: [0.407, 6.002]) and height of thickets (estimate: 2.008, 95% CI: [0.539, 3.996]) in region KO.

The best model for tundra vole abundance displayed a more complex structure than the occupancy models, with two-way interactions between the willow thicket variables and both region and year (Table S2 and S4, Appendix). However, none of the region- or year-specific slope estimates for thicket variables was statistically significant (Table S4, Appendix).

Discussion

In the present study, we employed a large-scale study design, which allowed us to demonstrate that tundra vole populations to some extent may become affected by changes in the configuration of willow thickets. However, the relations we found between thicket variables and tundra vole dynamics were not consistent. The configuration of willow thicket was only influential in terms of probability of patch occupancy and only in one of the three study regions in the increase phase of the multi-annual population cycle. Consequently, just as in previous studies conducted in a completely different setting (Ims and Andreassen 2000), region-specific factors appeared to be most influential to overall population dynamics, including to what extent local habitat features played any role. However, whether the regional influence was due to the action of predators (such as in the study of Ims and Andreassen (2000)) or whether some other mechanism responsible for the generation of cyclic dynamics was involved, cannot be determined based on the present analysis.

Interestingly, the relation between willow thicket configuration and tundra vole dynamics was only prevalent in the region KO, where tundra voles attained their highest occupancy and abundance. In this region, tundra vole occupancy increased with edge density and height of thickets. This was not an artifact of the higher number of voles caught in KO, as the catch of tundra voles in VJ in 2006 exceeded the catch in KO in 2005. The positive effect of edge density was expected based on a previous study demonstrating that tundra voles prefer to forage in edge habitats (Hovland et al. 1999). Edge habitats may provide both food and cover, which are generally considered to be the most important components of habitat quality in *Microtus* voles (Tast 1966; Rose and Birney 1985). Why such food resource related to habitat features did not affect habitat occupancy of root voles in the two other regions is not clear. However, it is likely that some factors other than the habitat features examined in this study acted to limit the spatial distribution of tundra voles in the regions VJ and IF. Indeed, in these two study regions, the habitat occupancy never attained the levels they did in KO. Moreover, the consistent increase in occupancy and abundance over the plant growth season (i.e. between summer and autumn) witnessed both in the increase and peak phase of the cycle in region KO was not evident in VJ and IF. A general lesson from our demonstration of highly contrasting responses of tundra voles to willow thicket configuration between similar study regions is that results from spatially restricted studies of habitat effects on small mammals may have limited applicability. In fact, most habitat selection studies in small mammals are conducted on spatial scales that are much smaller than the individual regions included in our study.

It has been proposed that reindeer overbrowsing in Finnmark could have detrimental effect on the population levels on other tundra herbivores (Tømmeraas 1993; Kjellen and Roos 2000; Angerbjörn et al. 2001; Ratcliffe 2005). This could be mediated by a reduced extent or increased fragmentation/shredding of willow thickets or reduced height and density of thickets due to intense reindeer browsing in riparian habitats (Ims et al. 2007). Ravolainen (2009) found indications that reindeer imposed a habitat shredding effect on the willow thickets, while several authors have shown that reindeer reduce the height of thickets (Olofsson 2001; Pajunen et al. 2008; Olofsson et al. 2009; Kittl et al. 2009). On the other hand, climate warming is expected to increase the height (Forbes et al. 2010) as well as the extent (e.g. Sturm et al. 2001; Tape et al. 2006) of thickets. The lack of effects of willow configuration variables on tundra vole dynamics in two out of three riparian regions subject to the present study, and the specific effects of willow thicket shredding and height in one region, indicates that we do not have evidence for strong and consistent impacts of future

climate or browsing induced changes of tundra shrubbiness on tundra voles.

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