



MASTER'S THESIS IN ECOLOGY/ZOOLOGY

Responses of small rodents to fragmentation of
willow thickets: A large scale study in the southern
arctic tundra

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ABSTRACT

While willow thickets expand in large parts of the arctic because of global warming, they appear to be shrinking in the northern part of Fennoscandia, due to overbrowsing by semi-domesticated reindeer. This has offered the opportunity to study the effect of variation in area and degree of fragmentation of willow thickets on small rodent abundance and dynamics, through a large scale observational study in parts of Finnmark, northern Norway. Indices of abundance and population growth were obtained from snap trapping conducted in two consecutive years in 37 sampling quadrates distributed over three study sites. Landscape variables, describing willow thicket area and degree of fragmentation on riparian sediment plains, were derived from aerial photos. The root vole (*Microtus oeconomus*) was the dominant small rodent species on the riparian sediment plains where graminoid rich meadows were interspersed with willow thickets. On a local scale (0.0255 ha), root voles selected the edge of willow thickets over open meadows. However, this local scale habitat selection did not predict the more large scale patterns of abundance and population dynamics. At a small spatial scale (1ha) I found inconsistent effects with a shifting sign of the effects of willow thicket area and willow shrub density on root vole populations abundance and growth rate among the different study sites. I suggest that there might be other factors determining site specific dynamics, not analysed in this study, explaining this inconsistency.

Key words: habitat fragmentation; root voles; abundance; population growth rate; willow thicket; Arctic; large scale study; habitat selection; context dependency.

1. INTRODUCTION

The Arctic is currently subject to changes threatening the integrity of tundra ecosystems (CAFF 2003). Global warming, pollution and exploitation of resources are all anthropogenic factors discussed in this context. Global warming and pollution in the Arctic are both well known issues with a circumpolar importance (Aarrestad & Aamlid 1999, Callaghan et al. 2004). However, exploitation of resources can be locally important. The Saami people in northern Norway have exploited the arctic tundra through semi-domesticated reindeer (*Rangifer tarandus*) husbandry for centuries (Suominen & Olofsson 2000). During the last decades, this husbandry has undergone large changes and the present practice is controversial, as the grazing intensity has been claimed to be non-sustainable (Moen & Danell 2003). In Finnmark reindeer have peaked to density levels claimed to render “an ecological disaster” (Moen & Danell 2003). Such claims have been backed up by documentation of severe reductions of the amount of lichen forage on winter pastures (Johansen & Karlsen 2005) and strongly negative spatial density-dependent growth of calves within reindeer husbandry (Tveraa et al. 2007). Reindeer densities in Finnmark are regionally at least 10-50 times higher than most places outside Fennoscandia (e.g. N-America; Batzli et al. 1980 and Russia/Siberia; Chernov & Matveyeva 1997).

Mammal herbivores are well known to have the capacity to cause shifts between alternative states of vegetation and thereby ecosystem structure and functioning (Hobbs 1996, Augustine & McNaughton 1998). To what extent this applies to reindeer overabundance in Finnmark is uncertain, but reindeer grazing and browsing have a strong effect on the abundance and performance of main components of vegetation such as shrubs and tree saplings (Hofgaard 1997). Long-term experiments on the Fennoscandian tundra have suggested that exclusion of grazers leads to increased abundance of woody plants (Moen & Oksanen 1998), whereas intense summer grazing by reindeer virtually eliminates them (Olofsson et al. 2001). While willow thickets expand in large parts of the arctic because of global warming (Chapin et al. 2005) there is some evidence that they are shrinking in the northern part of Fennoscandia, due to overbrowsing by semi-domesticated reindeer (Bråthen et al. 2007).

In the southern arctic tundra willow (*Salix spp.*) thickets are common on riparian sediment plains, providing food and shelter for animals that range in size from large ungulates to rodents and insects (Keigley et al. 2002). Willow thickets in the Arctic may therefore serve as potential hot spots (see e.g. Bråthen et al. 2007) for biodiversity. Biodiversity hotspots

represent areas of high conservation priority, because a potentially large proportion of a regional flora or fauna can be preserved within their bounds (Gaston & David 1994). Fragmentation and destruction of natural habitats is considered to be one of the main threats to the viability of wildlife populations (Kareiva & Wennergren 1995). Thus, landscapes need to be managed in such a way that landscape elements having a hot spot function will not be subject to habitat destruction and fragmentation.

Tundra ecosystems in alpine/arctic regions have small rodents, in particular voles and lemmings, as their dominant herbivores in terms of biomass and ecosystem impacts (Batzli et al. 1980). Small rodents have large effects on plant communities, especially in arctic regions (Batzli et al. 1980, Oksanen & Oksanen 1981). In addition to be important herbivores, rodents also play a key role as prey for mammalian and avian predators. Habitats suitable for small rodents hence need to provide food resources, but also offer protection or refuges from predators. Vegetation cover can provide protection from especially avian predators (Tast 1966, Sonerud 1986). Hambäck (1998) found that the variation in autumn vole density in Finnmark was explained to some extent (24 % of the variation) by height of woody shrub vegetation. Another example is that root voles (*Microtus oeconomus*) usually avoid parts of open bogs harbouring plants with short stalks only (Tast 1966). In a study of the alpine region of Kilpisjärvi, Tast (1968) only caught root voles in the willow thicket subzone which were characterized by a relatively close cover of graminoids and willow shrubs. He linked this both to rich food resources, but also to the good shelter these plants provide (Tast 1968).

There are many studies analyzing habitat area and fragmentation effects on rodents, both relatively small scale experimental studies on temperate grasslands (often agricultural meadows, e.g. Ims et al. 1993, Hovland et al. 1999, Johannesen et al. 2003) and observational studies encompassing larger scales, e.g. in forests and agricultural landscapes (e.g. Bolger et al. 1997, Kozakiewicz et al. 1999). However, no previous studies have analysed the effect of variation in area and degree of fragmentation of willows on population dynamics of tundra rodents.

Here I report from an observational study aimed at analysing the effect of variation in area and degree of fragmentation of willow thickets on abundance and dynamics of rodents in coast-near south arctic tundra in eastern Finnmark. Specifically the study was designed to answer the following questions:

- I Are there any effects of willow thicket area and fragmentation on the abundance and rate of population change?
- II Are willow area and fragmentation effects spatial scale dependent?

2. MATERIALS AND METHODS

2.1 Study area

The study was carried out in two *regions* in the north-eastern part of Finnmark, northern Norway in 2005 and 2006. The two regions were the Varanger peninsula, between 70–71° N and 28–31° E and Laksefjordvidda (71° N, 27° E) about 100 km west of Varanger peninsula. At the Varanger peninsula, the selected *study sites* were situated in the main river valleys of Vestre Jakobselv and Komagdalen, whereas at Laksefjordvidda the study site was situated along the mountain pass Ifjordfjellet (Fig. 1).

The bedrock geology of the study regions consist of sedimentary rocks, mainly sandstone and mudstone. Both the Varanger peninsula and Laksefjordvidda is covered by moraines of different thickness, boulder fields and exposed bedrocks (Siedlecka & Roberts 1992, Moen 1999). According to Moen (1999), both regions are situated within an intermediate oceanic vegetation sector, the annual yearly temperature is in the range of -4° to 0°C and the annual precipitation varies between 400-1000 mm with the highest values in the geographical centre of the Varanger peninsula. The northernmost part of the Varanger peninsula is classified as a southern arctic zone with low-shrub tundra (Walker et al. 2005).

The altitudes of the study sites were in the range of 260-360 meters above sea level at Laksefjordvidda and 110-290 meters above sea level at the Varanger peninsula. These altitudes correspond to the low alpine zone (Moen 1999) where the vegetated areas are dominated by heaths mainly composed of dwarf shrubs such as *Empetrum hermaphroditum*, *Betula nana*, *Vaccinium spp.* and lichens (Oksanen & Virtanen 1995, Ims et al. 2007, Killengreen et al. 2007). The heaths are interspersed with patches of mesic and wet vegetation where dicotyledons such as *Bistorta vivipara*, *Alchemilla alpina*, *Thalictrum alpinum*, *Viola biflora* and graminoids such as *Deschampsia flexuosa*, *Nardus stricta*, *Carex bigelowii*, *Eriophorum angustifolium*, *Agrostis capillaris* and *Deschampsia cespitosa* occur along with *Salix herbacea* (Ims et al. 2007, Killengreen et al. 2007). In moist depressions and especially on sediment plains along creeks and rivers there are lush meadows interspersed with patches

of willow thickets mainly of *Salix lapponum*, *Salix phylicifolia*, *Salix lanata* and *Salix glauca*. While Varanger peninsula harbours summer pastures for reindeer and is subjected to quite intense grazing, Laksefjordvidda is mainly spring and autumn transition area and thus subjected to less grazing.

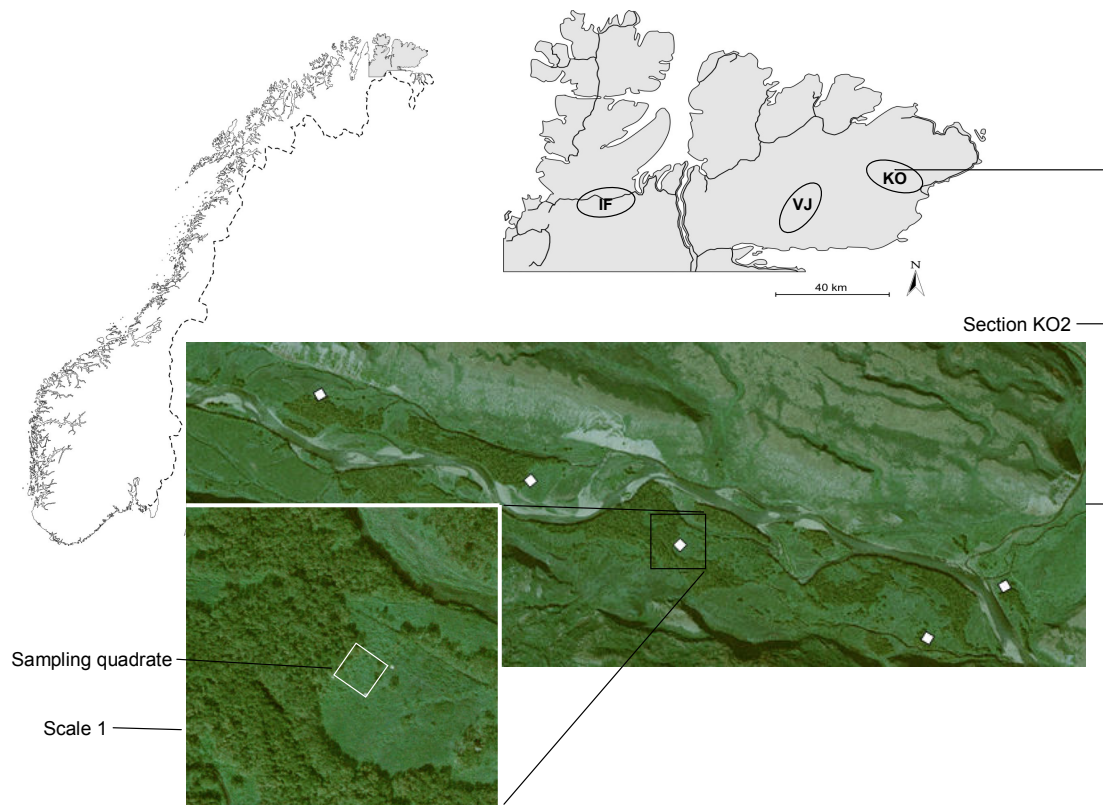


Fig.1: The study design with the three study sites (IF=Ifjordfjellet, VJ=Vestre Jakobselv, KO=Komagdalen) in eastern Finnmark and an aerial photograph with sampling quadrates in section KO2 in Komagdalen. Scale 1 (100×100 meter) is marked with a black square for one of the sampling quadrates.

2.2 Study design

2.2.1 Study sites and sampling quadrates

The study focuses on the effect of size and fragmentation of willow thickets. I strategically selected study sites in order to cover the existing variation in thicket size and degree of fragmentation. All study sites are situated on mineral soil on riparian sediment plains where the willow thickets are imbedded in lush meadow vegetation. The basic study units were 15 ×15 meters square plots, hereafter named *sampling quadrates*. A requirement for the sampling quadrates was that they should not have more than 30 % mires or be flooded. Each sampling quadrat was associated with a willow thicket so that one side of the quadrat was lining the

edge of the thicket, whereas the quadrat was extending into the surrounding meadow (Fig. 1). The distance between two adjacent sampling quadrates was minimum 164 meters and the average nearest distance was 652 meters (SD=524 meters). Since the riparian sediment plains and the associated areas with willow thickets formed distinct areas (hereafter called *section*) within the two main Varanger sites (Komagdalen and Vestre Jakobselv) and the Laksefjordvidda site (Ifjordfjellet), the sampling quadrates were clustered accordingly (Table 1). An equal number of sampling quadrates per willow thicket section were located in the adjoining heaths, approximately 20 meters from the edge of the riparian meadows.

Table 1: The number of meadow sampling quadrates in the different sections of the two study regions (Varanger peninsula and Laksefjordvidda).

<i>Region</i>	<i>Study site</i>	<i>Section</i>	<i>No. of quadrates</i>
Varanger peninsula	Komagdalen	KO 1	5
		KO 2	5
		KO 3	2
	Vestre Jakobselv	VJ 1	4
		VJ 2	5
		VJ 3	4
Laksefjordvidda	Ifjordfjellet	IF 1	5
		IF 2	1
		IF 3	4
		IF 4	2

2.2.2 Trapping methods

Small rodents were trapped according to the small quadrat method (SQM) of Myllymäki et al. (1971). According to this method 3 snap traps (baited with raisins and rolled oat) were set within radius of 2 meters from each corner of the sampling quadrat. The trapping were done over two trap nights in two trapping periods per year; i.e. summer (mid July) and autumn (early September). This amounted to a total trapping effort of 888 trap nights in the 37 willow thicket sampling quadrates each trapping period. The same trapping method and effort was applied to the heath quadrates. Heath trapping was employed to provide a comparison between the focal system (i.e. willow thicket/meadow) and the surrounding heath habitats. All animals caught were identified by species, sex, reproductive status (males: scrotal, abdominal, females: non-reproductive, pregnant or lactating) and weighted.

2.2.3 Local vegetation variables

Willow shrub density and height was measured at four points along the side of the sampling quadrat lining the thicket. Shrub density was assessed by a modified point frequency method,

placing a telescopic stick vertically 1 meter inside the thicket and counting number of hits with secondary stems and branches. Thicket height was measured as the highest willow branch inside a circle with 20 cm radius surrounding the telescopic stick. The sampling quadrature score for the height and shrub density variables was the mean of the four measurements. Willow shrub density was corrected for height, i.e. dividing on willow height and multiplied by hundred to get a robust measure. As part of a companion study analysing plant diversity in the same sampling quadrates, different vegetation variables describing cover and biomass of dominant plant species in the meadow, were measured (Ravolainen et. al. unpublished).

2.2.4 Quantifying willow thicket area and fragmentation

Willow thicket areas and fragmentation variables were derived from 1:15000 ortho-rectified aerial photographs taken summer 2006 in raster tiff-format. The resolution of these layers was 0.20 meter. For converting aerial photographs from tiff-format to img-format ARC GIS-software, version 9.1 (Environmental systems research institute 2002) was used. All willow thickets within the different sections were digitized in GRASS, version 6.1 (Grass development team 2006) and the appropriate raw data files were made by the same software. The raw data were further analysed with FRAGSTATS, version 3.3 (McGarigal & Marks 1995), quantifying willow thicket area and two variables describing the degree of fragmentation, which are straightforward to interpret in terms of biological significance for small mammals. The two fragmentation variables were patch density (PD) and edge density (ED) and their proper definitions are given in Appendix I: Table I.1. Increasing values for both of the variables indicate increasing fragmentation. The willow thicket area variable was taken as the percentage of area (PLAND) covered by willows. For all analyses, we defined a willow patch as consisting of an aggregation of pixels that are spatially connected using the eight neighbours rule (McGarigal & Marks 1995) (see Appendix I: Table I.1 for interpretation of the landscape metrics).

2.2.5 Scale considerations

Animal population processes are generally thought to be affected by habitat heterogeneity in a spatial scale dependent fashion (Senft et al. 1987, Wiens et al. 1993). Which scales are relevant (most influential) can rarely be determined a priori, because of lack of knowledge of the focal system, and this also applies to the present study. For this reason, the willow thicket area and fragmentation variables were quantified somewhat exploratory at three different

scales in addition to the scale of the sampling quadrat (15×15 meter, hereafter named the local scale). Scale 1 was a 100×100 meter quadrat centred on the middle of the sampling quadrat side lining the thicket (Fig. 1). This scale corresponds to the size of a local population of small mammals in many live-trapping studies (Stenseth & Lidicker 1992). Scale 2 was a 200×200 meter quadrat with the same center as scale 1. This scale was the largest scale allowing for non-overlapping measurements of area and fragmentation variables, when sampling quadrats were treated as study units (except for the distance between two sampling quadrats in section KO1 at the Varanger peninsula, which was 164 meters). The largest scale (i.e. scale 3) corresponded to the average size of the willow thicket sections. For quantification of thicket area and fragmentation at this scale, a quadrat of 2.2×2.2 km (corresponding to the average length of willow thicket sections) was centred on the middle point of the sections. Because such large quadrats included large areas of heaths, two additional variables than PLAND, PD and ED were quantified at this scale. One variable, Psediment3, measured the proportion of the 2.2×2.2 km square covered by the riparian sediment plain (i.e. the potential habitat for willow thickets and meadows). The other variable, PWsediment3, quantified the proportion of willow thicket area of the sediment plain area (Appendix I: Table I.1).

2.3 Statistical analysis

2.3.1 Exploratory analysis of variables

The empirical distributions of the variables, including their degree of confounding with other variables (also vegetation variables from Ravolainen et al, unpublished), were assessed graphically and by mean of a multivariate method (i.e. PCA). The purpose of this exploratory analysis was to identify a set of predictor variables and spatial scales which was not strongly correlated. Local vegetation variables from Ravolainen et al. (unpublished) were assessed in order to rule out such vegetation variables that could account for the potential effects of variation in landscape variables. The small mammal trapping data were assessed to establish for which species and regions there were a sufficiently large material (number of trapped individuals) to perform statistical analyses of abundance and population rate of change at the levels of sampling quadrats and sections.

2.3.2 Modelling small rodent abundance and dynamics

Habitat selection within sampling quadrats (local scale) was analysed with logistic regression using the proportion individuals trapped along the willow thicket edge, i.e. testing for

selection of thicket edge versus open meadow. Five sampling quadrates on study site Ifjordfjellet had no rodents trapped at all and these quadrates were excluded from the statistical analysis. Study site was considered as a covariate. For simple proportions 95 % confidence intervals were calculated according to Wilson's method (Agresti & Coull 1998). For model parameter estimation, I relied on using quasi-likelihood approach since overdispersion was present (McCullagh & Nelder 1989). Abundance and rate of population change (between 2005 and 2006) were modelled with general linear models. The adequacy of potential predictor variables for the linear models were assessed based on a corrected Akaike's Information Criterion, AIC_c and for the logistic regression quasi- AIC_c was assessed (Burnham & Anderson 2002). AIC_c is used when the number of fitted parameters constitute a too large fraction of the sample size (Sugiura 1978, Hurvich & Tsai 1989). Models with $\Delta AIC_c < 2$ were considered to be indistinguishable (i.e. equally supported) and the simplest model was chosen. Vole abundance was log transformed ($\log + 1$) before analysis and the results were interpreted by evaluating estimates with 95% confidence intervals (CI). All statistical analyses were carried out in R (R Development Core Team 2005).

3. RESULTS

3.1 Exploratory analyses

PCA analyses showed that habitat variables at scale 1 were strongly correlated with habitat variables at scale 2, whereas variables at scale 1 and 2 were little correlated with scale 3. Since scale 1 and 2 were highly correlated, only one of them was used in the statistical analyses. Scale 1 was chosen as this scale (i.e. 1 ha) corresponds to many other studies of small rodents (Stenseth & Lidicker 1992). At both scales patch density (PD) and edge density (ED) were strongly correlated (scale 1, $R^2=0.52$, scale 3, $R^2=0.71$) and I chose to keep edge density as this variable somewhat corresponds to potential edge preference at a smaller scale. At scale 3 the proportion of willow thicket area of the sediment plain area, PWsediment3 was correlated with the proportion willow thicket area of the whole 2.2×2.2 km square, PLAND3 ($R^2=0.42$). PLAND3 was chosen because it corresponds to PLAND1 at scale 1. The other variables at both scales were kept in the statistical analyses. Vegetation variables at the level of sampling quadrates from Ravolainen et al (unpublished) were not correlated with any of the landscape variables and therefore not used in the further statistical analyses. Edge density (ED) in one section at Ifjordfjellet (IF3) had much higher values than all other sections and appeared as strong outliers when included in the statistical models. Thus I excluded this

section from the statistical analyses on abundance at scale 3. See table 2 for mean value and range of willow thicket variables used in the statistical analyses.

Table 2: Mean value and range of the willow thicket/habitat variables used in modelling small rodent abundance and population rate of change.

Variable	Ifjordfjellet		Komagdalen		Vestre Jakobselv	
	Mean	[min,max]	Mean	[min,max]	Mean	[min,max]
PLAND 1	31.15	[6.01,58.89]	24.09	[7.33,57.40]	26.01	[5.41,46.19]
PLAND 3	1.66	[0.57,3.45]	1.82	[0.68,2.47]	1.65	[0.56,3.02]
ED 1	824.70	[401.61,1839.30]	520.75	[250.90,965.07]	641.29	[263.33,1290.78]
ED 3*	28.17	[17.81,43.65]	36.51	[23.61,45.10]	27.68	[19.95,31.77]
Psediment3	4.74	[1.54,8.71]	15.65	[11.90,21.60]	5.2	[3.01,8.32]
Wheight	117.3	[77.50, 220.00]	210.63	[145.00,270.00]	154.62	[110.00,220]
Wdensity	2.71	[1.36,3.61]	1.25	[0.45,2.97]	1.35	[0.14,2.54]

* Section IF3 excluded because of outliers.

3.2 Small rodent abundance

Of a total 175 rodents caught in heath quadrates, grey sided voles (*Clethrionomys rufocanus*) dominated numerically (89 %), followed by Norwegian lemmings (*Lemmus lemmus*) (6 %) and root voles (5 %). In the meadow quadrates root voles dominated numerically (85 %) among the 291 rodents caught, second most abundant were grey sided voles (12 %) and there were fewest Norwegian lemmings (3 %). Thus there was only sufficient material for root voles to be considered further in the analyses of the meadow quadrate data. Abundance varied greatly between seasons and years and in both habitats (Fig. 2). The two dominant vole species were in the increase phase of the cycle at all study sites, but the abundances were clearly higher at the two sites at the Varanger peninsula (especially Komagdalen), than at Ifjordfjellet. Because of the low abundance at Ifjordfjellet there were only sufficient data for analyzing rate of population change at the two sites on the Varanger peninsula. To obtain sufficient number of voles to do robust analyses on rate of change from 2005 to 2006, I added summer- and autumn catches within year and for abundance I added catches over both years and included study site Ifjordfjellet in the analyses.

3.3 Modelling abundance and dynamics of root voles

3.3.1 Habitat selection within sampling quadrate

In the logistic regression modelling of local scale habitat selection, a constant model was chosen, as the two models (constant and with study site as covariat) were considered to be equally supported (quasi-AICc: constant model: 42.0; study site as covariat: 40.7; the

overdispersion parameter c_{hat} was estimated as 2.44). There was a significant higher probability of catching root voles at the willow edge versus out in the open meadow in the sampling quadrates (estimated probability: 68.0 %, CI: 62.0, 73.5).

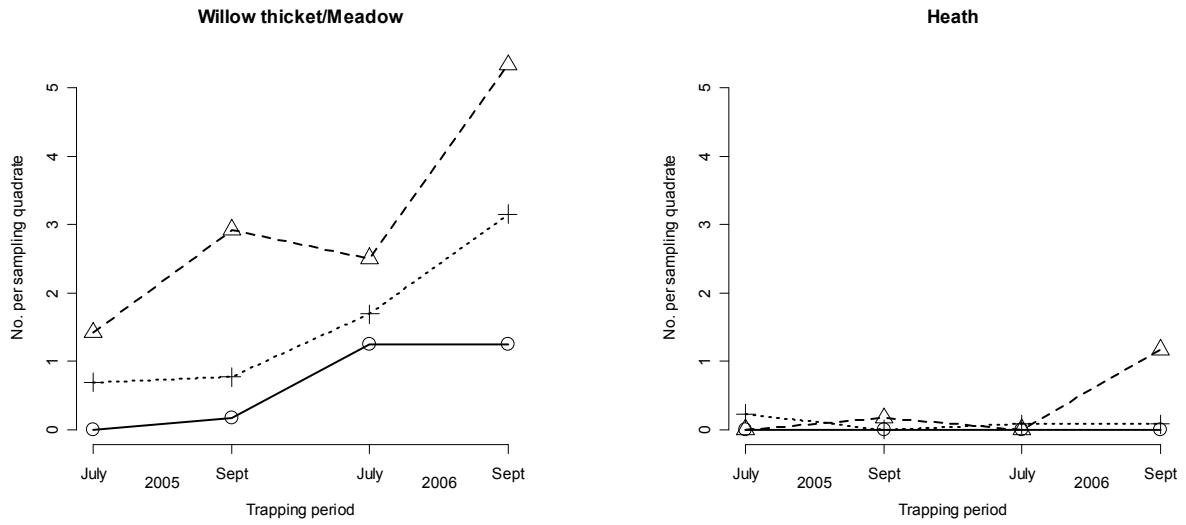
3.3.2 *Variation in abundance*

At the scale of 100×100 meter (i.e. scale 1) the best model of root vole abundance included an interaction between proportion area with willow thickets (PLAND) and study site (Appendix II: Table II.1). The interaction term was due to shifting sign of the effect of PLAND between the study sites; the effect was positive in Komagdalen, while it was negative in Vestre Jakobselv and at Ifjordfjellet (Fig. 3, Table 3). At scale 3 the best model included only study site (Table 3).

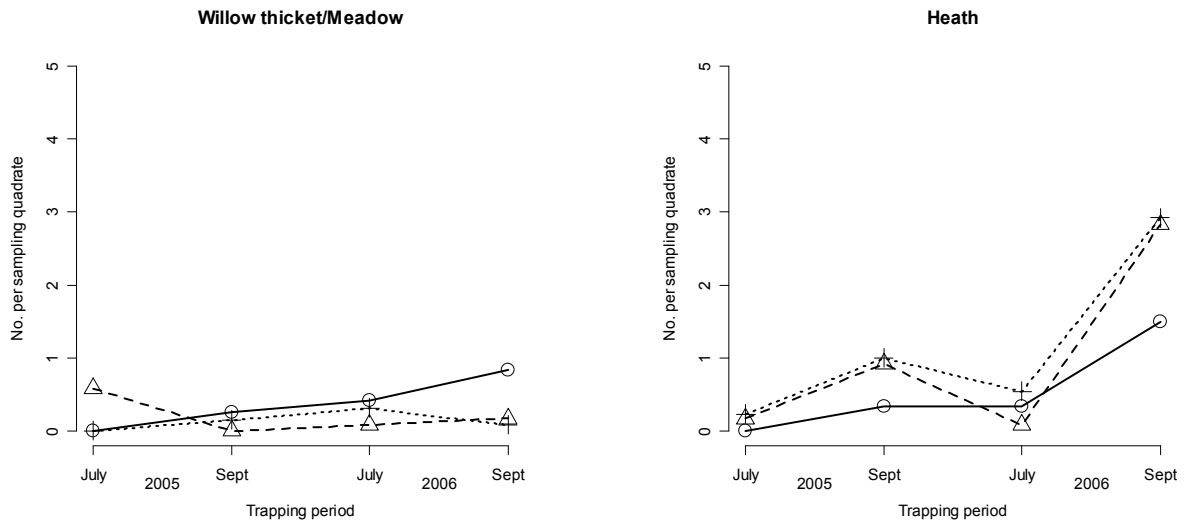
3.3.3 *Variation in growth rate*

At scale 1 the best model of yearly growth rate included an interaction between willow shrub density (Wdensity) and study site (Appendix II: Table II.1). The interaction term was due to shifting sign of the effect of Wdensity between the study sites; the effect was positive in Komagdalen and negative in Vestre Jakobselv (Fig. 4, Table 4). At scale 3 I did not find any effects on growth rate (the best model is a constant model, Appendix II: Table II.1).

Root voles



Grey sided voles



—○— Ifjordfjellet
--△-- Komagdalen
...+... Vestre Jakobselv

Fig. 2: Mean number of root voles and grey sided voles trapped per sampling quadrates in willow thickets/meadows and heaths for the various study sites.

Table 3: Parameter estimates from the most appropriate model of root vole abundance at a) scale 1 and b) scale 3. Intercept is the mean (log + 1) root voles trapped per sampling quadrat in Komagdalen, while PLAND1 is the slope for the proportion willow in Komagdalen. The other coefficients are differences in means and slopes. Statistically significant coefficients are bolded.

	Coefficient	[95% CI]
a) Scale 1		
Intercept(Komagdalen)	1.70	[1.05,2.35]
PLAND1(Komagdalen)	0.03	[0.01,0.05]
Study site Ifjordfjellet	-0.51	[-1.51,0.48]
Study site Vestre Jakobselv	0.79	[-0.20,1.77]
PLAND1: Study site Ifjordfjellet	-0.05	[-0.08,-0.01]
PLAND1: Study site Vestre Jakobselv	-0.06	[-0.10,-0.02]
b) Scale 3		
Intercept(Komagdalen)	2.51	[1.73,3.30]
Study site Ifjordfjellet	-1.78	[-2.81,-0.75]
Study site Vestre Jakobselv	-0.54	[-1.65,0.56]

Table 4: Parameter estimates from the most appropriate model of root vole population rate of change (yearly growth rate) at scale 1. Intercept is the mean (log + 1) growth rate per sampling quadrat in Komagdalen, while Wdensity is the slope for the willow shrub density in Komagdalen. The other coefficients are differences in mean and slope. Statistically significant coefficients are bolded.

	Coefficient	[95% CI]
Intercept (Komagdalen)	0.28	[-0.61,1.16]
Wdensity (Komagdalen)	0.37	[-0.21,0.95]
Study site Vestre Jakobselv	1.95	[0.55,3.36]
Wdensity: Study site Vestre Jakobselv	-1.41	[-2.34,-0.49]

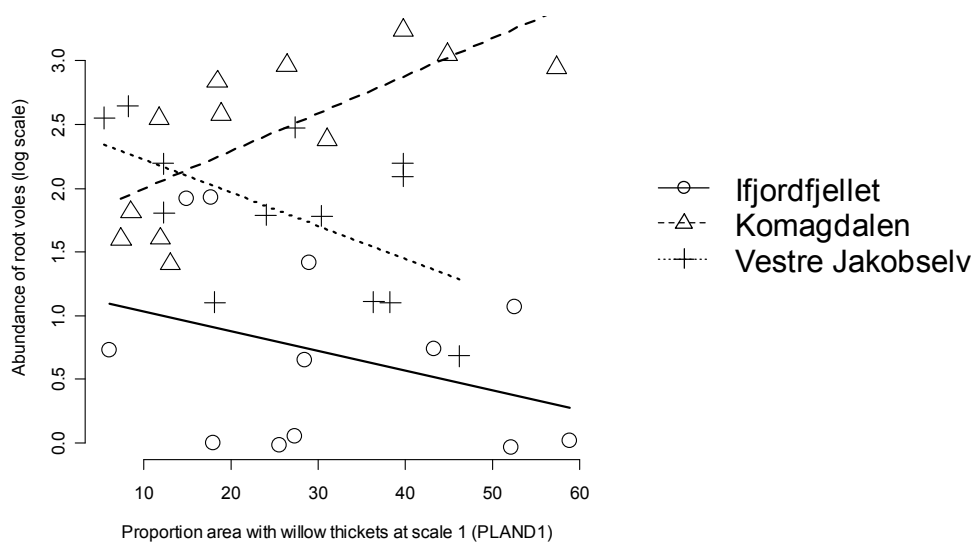


Fig. 3: Abundance of root voles (log scale) at the various study sites as a function of proportion area with willow thickets (PLAND) at scale 1. The lines are the site specific predictions obtained from the linear model described in table 3.

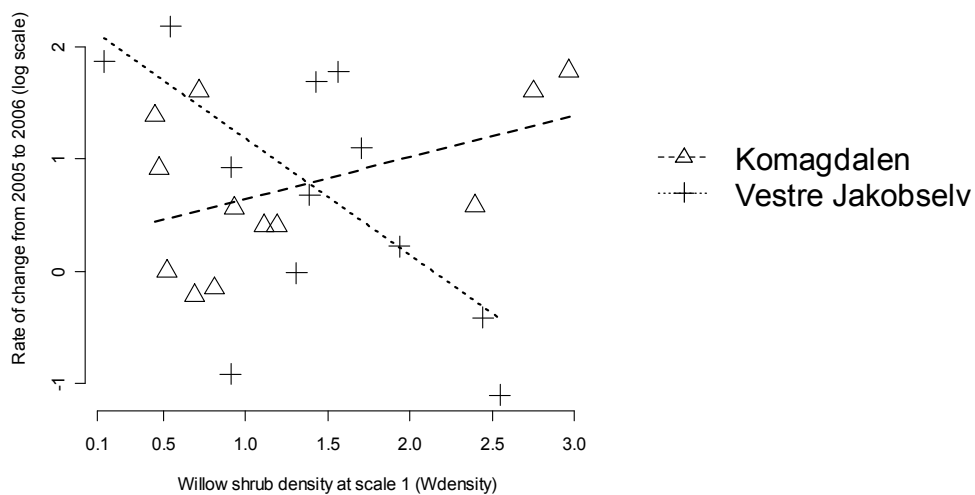


Fig. 4: Rate of population change (log scale) from 2005 to 2006, based on a total catch per year, at the various study sites as a function of willow shrub density (Wdensity) at scale 1. The lines are the site specific predictions obtained from the linear models described in table 4.

4. DISCUSSION

This study was set out to evaluate the effect of variation in size and degree of fragmentation of willow thickets on the abundance and population dynamics of small rodents. As expected from previous studies (Tast 1966), the root vole was the dominant small rodent species present in such habitats. Although root voles to some extent were caught in the open meadow parts of the sampling quadrates, they showed a clear and consistent preference for the willow edge lining the sampling quadrates in all study sites. Based on this habitat preference at a local scale, one could expect consistent positive effects of willow thicket area and amount of willow thicket edge on abundance and/or population growth at larger scales. However, surprisingly the effect of willow area at the scale of 1 ha changed sign among the different study sites, whereas the edge related variable was unimportant. Also, unexpectedly I found willow shrub density to explain a significant part of the root vole population rate of change at this scale. This relationship also differed strongly between the study sites.

4.1 Local scale habitat selection.

The presence of shelter and food are two of the main features determining habitat quality in microtines (Tast 1966, Rose & Birney 1985). Predation is a major cause of death (Hanski et al. 1991, Steen 1994, 1995) and it is likely that the willow thickets provide more shelter, especially against avian predators, than the meadow habitat. Thus, the less vegetative cover in the meadow may explain the preference for willow edge found in my study. The first study analysing individual feeding events in root voles (Hovland et al. 1999) reported root voles to never avoid edges and to feed more than expected along edges in small fragments. Finally, these preferences for edges may result from the fact that the individuals' foraging decisions involve a trade-off between obtaining resources and avoiding predators (Myserud & Ims 1998). Such a trade-off situation may be likely where the root voles need for cover is found inside the willow thicket and their food requirement is located out in the meadow.

Root voles prefer nutrient rich vegetation dominated by graminoids since such plants constitute their main food items (Tast 1966). Although I do not have quantitative estimates of the amount of potential food plants of root voles inside the willow thickets, it is clear that the biomass of graminoids is less in the very shaded conditions under the willow canopy. However, there is still a possibility that the smaller biomass of shaded understorey plants may have higher nutrient quality (Sipura & Tahvanainen 2000) than plants exposed to more light.

If such attractive plants inhabit edges, this could be part of the edge preference seen in this study.

4.2 Variation in abundance and population dynamics

According to Bowers & Matters (1997), studies that examine density-area relationships in patchy habitats have yielded inconsistent results. They suggested on these grounds that density-area relationships appear to be scale dependent. My results support this, as local scale habitat selection did not predict large-scale abundance patterns and as the relations at the scale of 1 ha were not evident at the scale of willow thicket sections. Even more, inconsistent effects were also found within scale 1 (1ha), with a shifting sign among the study sites of both the effect of willow area on abundance and the effect of willow shrub density on population growth rate. There is no obvious explanation why the positive area- and shrub density effect in Komagdalen is contrary to the negative effects in Vestre Jakobselv and at Ifjordfjellet (only abundance). However, I suspect that there may be a different relation between the amount of willow and meadow areas in the different study sites. The topography in Vestre Jakobselv and Komagdalen are rather different, with more narrow valleys and steeper valley sides in Vestre Jakobselv. The topography at Ifjordfjellet is also dominated by narrow valleys compared with Komagdalen. Although I had no precise information on the amount of meadow area surrounding the willow thickets, I speculate that smaller sediment plains in Vestre Jakobselv and at Ifjordfjellet lead to decreasing meadow area when the area of willow thicket increases. If meadow is of great importance for instance as a source of food resources, this could be a reason for the different abundance and growth rate effects of increasing willow thicket area and shrub density. The trade-off situation due to two habitat types with different functions (Mysterud & Ims 1998) may thus also be involved in determining the patterns at scale 1. The negative growth rate in Vestre Jakobselv could be explained by increasing willow shrub density, leading to less food at the edge and inside the willow thickets and thus root voles consequently have to forage out in smaller meadows compared to Komagdalen.

Responses in population dynamics may be complex and thus difficult to predict because the growth rate of a population reflects the combination of several parameters, each possibly exhibiting a different response to fragmentation (Johannesen et al. 2003). Habitat fragmentation and connectivity have been shown to affect individual space use and spatio-social organization in experimental root vole populations (Andreassen et al. 1998, Bjørnstad et al. 1998), but responses in demographic parameters and population dynamics has been

found to be relatively unaffected by relatively small-scale habitat fragmentation (Ims & Andreassen 1999, Johannesen et al. 2003). However, the previous experimental studies of habitat fragmentation effects on root vole populations have been mainly restricted to analysing the dynamics over the summer season. The dynamics and the underlying demographic mechanisms may differ much between winter and summer (Aars & Ims 2002). Due to low densities and insufficient data I could not reliably analyse summer and winter dynamics separately. However, the long winter in sub-arctic Finnmark naturally has a significant effect on the yearly growth rate.

Voles and lemming populations in Finnmark exhibit 4-5 year population density cycles (Ekerholm et al. 2001) and accordingly the abundance and growth rate in a particular year will depend on cyclic phase (Ims et al. 2007). The contrasting abundances and growth among the study sites in this study may indicate that the different study sites are in various cyclic phases. For example predation is assumed to influence mortality differently in the various phases of the cycle (Hanski & Korpimäki 1995, Norrdahl & Korpimäki 1995, Steen 1995). Thus, different trophic interactions may have shaped the population processes differently among my study sites, although the effect mechanism is difficult to identify.

In a general sense, the shifting sign of the effects of willow area and shrub density on abundance and growth rate might be an example of context dependency (Power et al. 1996, Wellnitz & Poff 2001). Context dependency refers to how species functional roles in communities can change in different parts of the environmental ranges where they occur. Specifically, I suggest that differences in topography and different cyclic phases could be the context responsible for the inconsistent results among study sites in this study.

5. CONCLUSION

I have not been able to show consistent habitat area or fragmentation effects on root vole populations in this study, but my results showed a kind of scale dependency as local scale habitat selection did not predict more large scale patterns of abundance and population growth rate. I suggest that shifting sign effects of willow area and shrub density on abundance and growth rate among different study sites might be due to context dependency. One limitation of the study was that I did not have quantitative estimates of the meadow area at each scale. Future studies need to explore how important the surrounding meadow area is for root vole populations and to get a better knowledge of population level responses, winter dynamics

should be analysed. This study also shows the importance of setting up studies on large and multiple scales. Results are scale and context dependent and working in only one of three study sites would have shown different results dependent on which study site was chosen.

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APPENDIX I: LANDSCAPE / HABITAT VARIABLES

Table I.1: Description of landscape metrics measured. For details on the computation of PLAND, PD and ED, see McGarigal & Marks (1995) and the FRAGSTATS 3.3 Software.

Landscape metric	Scale	Range	Unit	Interpretation
Percentage of landscape, PLAND1	1	0 < PLAND1 ≤ 100	%	PLAND1 = 0 if willow does not occur in the landscape. PLAND1 = 100 if the entire landscape is comprised of willow
Percentage of landscape, PLAND2	2	0 < PLAND2 ≤ 100	%	PLAND2 = 0 if willow does not occur in the landscape. PLAND2 = 100 if the entire landscape is comprised of willow.
Percentage of landscape, PLAND3	3	0 < PLAND3 ≤ 100	%	PLAND3 = 0 if willow does not occur in the landscape. PLAND3 = 100 if the entire landscape is comprised of willow.
Patch density, PD1	1	0 < PD1 ≤ maximum number of patches per 100 hectar		PD1 = number of patches per 100 hectar on scale 1.
Patch density, PD2	2	0 < PD2 ≤ maximum number of patches per 100 hectar		PD2 = number of patches per 100 hectar on scale 2.
Patch density, PD3	3	0 < PD3 ≤ maximum number of patches per 100 hectar		PD3 = number of patches per 100 hectar on scale 3.
Edge density, ED1	1	0 < ED1 ≤ maximum number of meters edge per hectar		ED1 = meters edge per hectar on scale 1.
Edge density, ED2	2	0 < ED2 ≤ maximum number of meters edge per hectar		ED2 = meters edge per hectar on scale 2.
Edge density, ED3	3	0 < ED2 ≤ maximum number of meters edge per hectar		ED3 = meters edge per hectar on scale 3.
Psediment3	3	0 < Psediment3 ≤ 100	%	Psediment3 = 0 if sediment plains does not occur in the landscape. Psediment3 = 100 if the entire scale 3 is comprised of sediment plains.
PWsediment3	3	0 < PWsediment3 ≤ 100	%	Pwsediment3 = 0 if willow does not occur at the sediment plain. Pwsediment3 = 100 if the entire sediment plain is comprised of willow.
Wheight	local	0 < maximum height	cm	Mean of 4 high measures per sampling quadrat.
Wdensity	local	0 < maximum number of hits	hits	Mean of 4 shrub density measures per sampling quadrat corrected for willow high (Wdensity/Wheight*100).

APPENDIX II: MODEL SELECTION

Table II.1: Results of the model selection of root vole abundance and rate of population change from 2005 to 2006 based on total catches per year at a) scale 1 and b) scale 3. The different models are ranked according to the corrected Akaike's Information Criterion (AICc). $\Delta AICc$ is the difference between the model with minimum AICc (i.e. the best model, $\Delta AICc=0$) and the other models. Models with $\Delta AICc < 2$ are considered to be equally supported (bolded). Terms included in different models are indicated with X. Np = Number of parameters in the model.

Response variable	PLAND1	ED1	Wdensity	Wheight	Study site	PLAND1:study site	ED1:Study site	Wdensity:Study site	Wheight:study site	constant	Np	$\Delta AICc$	
<i>a) Scale 1</i>													
<i>Abundance</i>	X				X	X					6	0.00	
	X	X			X	X					7	1.54	
	X			X	X	X					7	2.70	
	X		X		X	X					7	2.82	
	X	X		X	X	X					8	3.65	
	X	X	X		X	X					8	3.96	
	X	X	X		X	X	X				6	4.08	
			X	X	X	X		X			6	5.25	
			X	X	X	X					3	5.32	
		X	X	X	X	X	X				7	5.44	
	<i>Rate of population change, year</i>												
				X		X			X			4	0.00
				X	X	X			X			5	1.32
	X			X		X			X	X		1	2.60
	X		X	X	X			X			5	3.05	
		X	X	X	X			X			5	3.08	
X			X								2	3.72	
											2	4.43	
X			X	X	X			X			2	4.43	
		X	X	X	X			X			6	4.72	
			X	X	X			X			6	4.79	

Table II.1: continued

Response variable	PLAND3	ED3	PDELTA3	Study site	PLAND3:Study site	ED3:Study site	PDELTA3:Study site	constant	Np	Δ AICc
<i>b) Scale 3</i>										
<i>Abundance</i>										
				X					3	0.00
			X						2	6.01
								X	1	7.02
		X							2	9.60
	X			X					2	10.30
		X		X		X			6	34.24
	X			X					6	36.58
			X	X			X		6	42.35
<i>Rate of population change, year</i>										
								X	1	0.00
		X			X				2	2.08
									2	3.37
				X					2	4.56
	X								2	5.00
	X			X		X			4	40.90
		X		X				X	4	41.66
			X	X			X		4	41.77