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1 01 Declining willow ptarmigan populations: The role of habitat structure 2 and community dynamics

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5 Abstract

6
7 The recent range contractions and population declines of many grouse species worldwide have been attributed to loss and
8 fragmentation of their habitats, although the empirical evidence for the actual drivers is often weak. In case of the willow
9 ptarmigan *Lagopus lagopus* in Fennoscandia, ungulate overbrowsing of willows has been hypothesized to exert such negative
10 habitat-related impacts. Moreover, a steep population decline of willow ptarmigan in southern Fennoscandia has recently been
11 attributed to community interactions linking the fate of the willow ptarmigan to a change in keystone tundra rodent populations.
12 Community and habitat factors may also interact in their impact on willow ptarmigan abundance. Here we assess whether
13 willow thicket structural characteristics sensitive to ungulate browsing impacted willow ptarmigan habitat occupancy and
14 whether such impacts depended on small rodent population dynamics. We employed an extensive survey approach spatially
15 encompassing three riparian tundra regions and covering the phases of increase, peak and crash of the small rodent cycle. Willow
16 ptarmigan habitat occupancy increased with the areal extent of willow thickets, whereas it decreased with increasing degree
17 of thicket fragmentation (i.e. habitat shredding). Both of these effects were consistent with ungulate over-browsing impacting
18 willow ptarmigan abundance negatively. Over the 4-year study period, willow ptarmigan habitat occupancy declined steeply
19 independently of spatial variation in willow thicket areal extent and fragmentation. Moreover, the expected increase in ptarmigan
20 populations during the increase/peak phase of the rodent cycle was not observed. Thus although our study provides support
21 for the hypothesis that intense ungulate browsing negatively impacts willow ptarmigan, our study also suggests that causes
22 of the current steep decline of ptarmigan populations in northern Fennoscandia should be sought in factors other than habitat
23 fragmentation and changed rodent population dynamics.

24 Zusammenfassung

25 Die derzeitigen Verkleinerungen der Verbreitungsgebiete und die Populationsabnahme bei vielen Arten der Raufußhühner
26 weltweit wurden auf den Verlust und die Fragmentierung ihrer Habitate zurückgeführt, auch wenn die empirischen Belege für
27 die tatsächlichen Ursachen häufig schwach sind. Im Falle des Moorschneehuhns *Lagopus lagopus* in Fennoskandien wurde
28 vermutet, dass die Überbeweidung durch Ungulaten einen solchen negativen habitatgebundenen Einfluss hat. Darüber hinaus
29 wurde eine aktuelle steile Abnahme der Populationsgröße von Moorschneehühnern im südlichen Fennoskandien mit Interak-
30 tionen in der Lebensgemeinschaft in Verbindung gebracht, die das Schicksal der Moorschneehühner mit Veränderungen in den
31 Populationen der Schlüsselarten der Nagetiere in der Tundra verbinden. Lebensgemeinschafts- und Habitatfaktoren können
32 auch in ihrem Einfluss auf die Häufigkeit der Moorschneehühner interagieren. An dieser Stelle schätzen wir ab, ob die struk-
33 turellen Eigenschaften der Weidengebüsche, die empfindlich für die Beweidung durch Ungulaten sind, die Habitatbesetzung
34 durch Moorschneehühner beeinflussen und ob dieser Einfluss von den Populationsdynamiken kleiner Nagetiere abhängt. Wir

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verwendeten einen extensiven Erfassungsansatz, der drei Regionen flussbegleitender Tundra räumlich abdeckte und die Phasen der Zunahme, die Spitzenphase und den Zusammenbruch im Zyklus der kleinen Nagetiere erfasste. Die Habitatbesetzung der Moorschneehühner nahm mit der räumlichen Ausdehnung der Weidengebüsche zu, während sie mit einem zunehmenden Grad der Fragmentierung der Gebüsch abnahm (d.h. ‘habitat shredding’). Beide Effekte stimmten damit überein, dass eine Überbeweidung durch Ungulaten die Häufigkeit der Moorschneehühner negativ beeinflusst. Über die vierjährige Untersuchungsperiode nahm die Habitatbesetzung der Moorschneehühner unabhängig von der räumlichen Variation in der Ausdehnung und Fragmentierung der Weidengebüsche steil ab. Darüber hinaus konnte die erwartete Zunahme der Raufußhuhnpopulation während der Zunahme und Spitzenphase im Nagetierzyklus nicht beobachtet werden. Obwohl unsere Untersuchung die Hypothese unterstützt, dass eine intensive Beweidung durch Ungulaten die Moorschneehühner negativ beeinflusst, lässt unsere Untersuchung auch vermuten, dass die Gründe für die steile Abnahme der Moorschneehuhnpopulationen im nördlichen Fennoskandien in anderen Faktoren als der Habitatfragmentierung und den veränderten Populationsdynamiken der Nagetiere gesucht werden sollten.

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Keywords: Willow ptarmigan; Willow thickets; Habitat fragmentation; Over-browsing; Ungulates; Small rodent cycle; Population decline

Introduction

Grouse species, especially of the genus *Lagopus*, are among the most intensively studied birds worldwide (Storch 2007; Moss, Storch, & Muller 2010). Their historic attractiveness to research can both be explained by their role as important game species (Aanes, Engen, Saether, Willebrand, & Marcström 2002), both for recreation and subsistence, and their fascinating population dynamics, often characterized by multiannual density cycles (Moss & Watson 2001). However, during the last decades many species and populations of grouse have been declining and some are even threatened with extinction (Connelly & Braun 1997; Storch 2007; Aldridge et al. 2008). While this has been particularly evident in landscapes densely populated and intensively used by humans, some grouse species have been declining even in remote northern areas of both North America and Eurasia (Storch 2007). For instance, while Storch (2007) refers to willow ptarmigan as a “non-problem” species, national hunting bag statistics show that numbers of willow ptarmigan have dramatically decreased during the last decades in Norway (Kausrud et al. 2008; SSB 2010). While habitat degradation, loss and fragmentation, resulting from increasing exploitation of their habitats, have been put forward as the major threats to ptarmigan populations worldwide (Storch 2007; Watson & Moss 2008), the empirical evidence for what drives these changes is often weak.

In the case of the willow ptarmigan *Lagopus lagopus*, ungulate overabundance (*sensu* Coté, Rooney, Tremblay, Dussault, & Waller 2004) has been hypothesized to exert negative impacts mediated by overbrowsing on willow shrubs (den Herder, Virtanen, & Roininen 2004; den Herder, Virtanen, & Roininen 2008; Ims et al. 2007). This hypothesis is in line with the pervasive effect ungulate overabundance has been shown to exert in many ecosystems in terms of dramatic reduction of palatable shrubs (Coté et al. 2004; Beschta & Ripple 2007). In Finnmark, northern Norway, ungulate (i.e. reindeer *Rangifer tarandus*, moose *Alces alces*) populations have increased substantially over the last decades, reaching

densities deemed by some authors to represent an “ecological disaster” (Moen & Danell 2003). Willows are highly palatable to many ungulate species and several studies have shown that ungulate browsing is capable of reducing the cover and height of willows (Olofsson, Kitti, Rautiainen, Stark, & Oksanen 2001; Ripple & Beschta 2004; den Herder et al. 2008; Pajunen, Virtanen, & Roininen 2008; Kitti, Forbes, & Oksanen 2009; Olofsson et al. 2009). Moreover, the results of Ravolainen (2009) indicated that abundant reindeer could be responsible for fragmentation of tall thickets through a shredding effect (Feinsinger 1994). Habitat shredding is a form of habitat fragmentation that increases the amount of edges, but not necessarily the number and distances between the patches. den Herder et al. (2004) predicted the willow ptarmigan to be among the game species most sensitive to high reindeer densities owing to the willow ptarmigan’s strong reliance on willow shrubs as food and cover (Weeden 1969; Moss 1973; Hakkarainen, Virtanen, Honkanen, & Roininen 2007; Watson & Moss 2008; Tape, Lord, Marshall, & Ruess 2010). Indeed Ims et al. (2007) found lower prevalence of willow ptarmigan in regions with high reindeer densities. However, in lack of adequate data on willows they were not able to provide an explicit link between willow characteristics, such as areal extent, and ptarmigan prevalence.

Like several other grouse species (e.g. Moss & Watson 2001; Williams, Ives, Applegate, & Ripa 2004) willow ptarmigan populations have exhibited multi-annual cycles (Myrberget 1984; Steen & Erikstad 1996; Moss & Watson 2001). In Fennoscandia the ptarmigan cycle period has typically been 3–4 years and synchronous with the population cycles of small rodents (Myrberget 1984; Steen, Steen, Stenseth, Myrberget, & Marcström 1988). The willow ptarmigan cycles have been assumed to be driven by the small rodent cycle, where the link between rodents and ptarmigans is mediated by predators partly shifting their diet from small rodents to ptarmigan (mostly eggs and chicks) in small rodent crash years (termed the alternative prey mechanism; Moss & Watson 2001; Valkama et al. 2005). In fact the rodent cycle has been forwarded as a key community level pro-

cess underlying the synchronous cyclic dynamics classically found within the community of small to medium-sized vertebrates in boreal and arctic ecosystems (Elton 1942; Hörnfeldt, Löfgren, & Carlsson 1986; Hansson & Henttonen 1988; Gauthier, Bety, Giroux, & Rochefort 2004; Ims & Fuglei 2005; Gilg & Yoccoz 2010). However, in parts of Fennoscandia the classical small rodent population cycle with high amplitude peak densities has recently collapsed into non-cyclic low amplitude dynamics (Ims, Henden, & Killengreen 2008). Kausrud et al. (2008) have recently shown for an alpine region in southern Norway that willow ptarmigan populations rapidly declined and cyclicity was lost simultaneously with the sudden collapse of the small rodent cycle in this region. They attributed the fate of the willow ptarmigan to increased predation impact when the rodent population reaches low levels.

Thus in case of declining willow ptarmigan populations in Fennoscandia there may be two processes at work: (1) habitat loss and fragmentation due to ungulate overbrowsing of willow shrubs, which is likely to be a slow process that has taken place over many decades of ungulate overabundance (Moen & Danell 2003), and (2) fast community processes related to the rapid dynamics of small rodent population. Moreover, synergetic impacts of the two processes (i.e. an interaction) may also be expected. Specifically, predation on alternative prey mediated by crashing rodent populations is expected to become enhanced in landscapes that are in an advanced stage of loss and fragmentation of refuge habitat (Ims, Rolstad, & Wege 1993).

In the present paper we use a large-scale survey approach to quantify the dependence of willow ptarmigan habitat occupancy on willow thicket characteristics. We focused on willow thicket characteristics that are likely to be affected by ungulate overbrowsing and expected to affect predation risk. The study was conducted in sub- and low-Arctic tundra in northern Norway, where riparian willow thickets appear to be in different stages of fragmentation and loss due to ungulate browsing (Ravolainen 2009). This enabled us to design our survey so as to strategically include distinct spatial contrasts in willow variables. The survey was extended over a period of four years which included distinctly different phases of rodent population dynamics that could be expected to influence predation risk on alternative prey. We could thereby assess whether the expected temporal change in predation pressure associated with rodent dynamics had any impact on the temporal dynamics of willow ptarmigan habitat occupancy depending on spatial willow thicket characteristics.

Methods

Study area

The study was carried out during the years 2005–2008 in three riparian regions in north-eastern Finnmark, north-

ern Norway. Two of the regions were situated on Varanger peninsula (70–71°N and 28–31°E), while the third was situated about 100 km to the west, at Ifjord (71°N, 27°E). In Varanger peninsula the two study regions were situated along the main river valleys of Vestre Jakobselv (VJ) and Komag (KO), whereas the study region Ifjord (IF) was situated along several smaller rivers and creeks, mostly tributaries to the river Storelva. While the region at Ifjord constitutes sub-arctic alpine tundra, the northernmost part of the Varanger peninsula is classified as erect low-shrub tundra belonging to the southern Arctic zone (Walker et al. 2005). However, the three regions hold the same main vegetation characteristics (Killengreen et al. 2007), with the landscape dominated by heaths (Fig. 1) mainly composed of dwarf shrubs such as *Empetrum hermaphroditum*, *Betula nana* and *Vaccinium* spp. Erect, thicket forming willows (mainly a mix of *Salix phylicifolia*, *Salix lanata*, *Salix glauca*, *Salix lapponium* and hybrids) are found almost exclusively in moist depressions on sediment plains along creeks and rivers where the thickets are found as patches imbedded in meadows dominated by graminoids and herbs (Fig. 1). The patches of willow thickets form sharp edges against the surrounding meadows and are easily delineated in high resolution aerial photographs (Fig. 1). Since willow thickets are mainly restricted to riparian sediment plains in the tundra landscape the study regions were selected to harbour such landscape elements. The two study regions in Varanger peninsula (i.e. KO and VJ) are situated within a summer herding district, whereas the region IF constitutes mainly a transition area for reindeer herds in spring and autumn.



Fig. 1. Structural characteristics of riparian landscape elements and willow thickets in tundra. Large aerial photograph: A small section of region V. Jakobselv (VJ) showing how willow thickets (outlined by coarse grey tracing) form narrow belts along creeks and rivers. The willow thickets are surrounded by a narrow meadow zone (~15–30 m). The rest (majority) of the landscape constitutes heath vegetation. Ground photograph (inset left lower corner): The typical sharp edge of willow thickets towards the surrounding meadow (flat open ground) and heath (slopes).

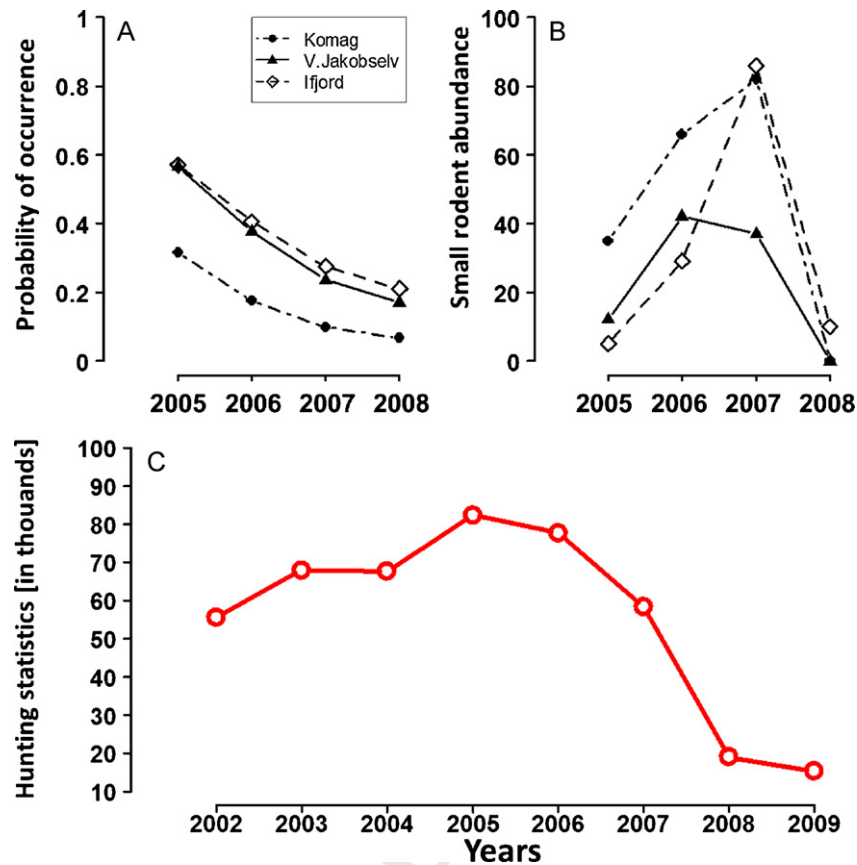


Fig. 2. Temporal dynamics of willow ptarmigan habitat occupancy, hunting statistics and small rodent population dynamics. Panel (A) shows the predicted habitat occupancy (i.e. from the statistical model) of willow ptarmigan in autumn for each study region (Komag, V. Jakobselv and Ifjord) and year (2005–2008). Panel (B) depicts the total number of small rodents caught in autumn for each region and in all small quadrats where willow ptarmigan pellet counts were conducted (see Henden et al. 2011 for more details on the rodent trapping and dynamics). Panel (C) depicts the temporal trend in the hunting statistics for Finnmark (number of willow ptarmigan shot during 2002–2009 (SSB 2010)). Note that the figure legend is the same for panels (A) and (B).

Small rodent populations in all study regions exhibit a spatially synchronous 5-year density cycle (Killengreen et al. 2007). The last peak before the current study commenced was in 2002. The dynamics of the small rodent population in the three study regions were censused during the study period by means of snap-trapping as described in Henden, Ims, Yoccoz, Sørensen, and Killengreen (2011). The first year of the study (2005) had low small rodent densities in all regions (Fig. 2B). The small rodents increased to reach a peak over the years 2006–2007, although with some deviations in timing and amplitude between the regions. The population in all regions had crashed to very low levels by spring of 2008 (Fig. 2B).

Study design

Within each study region we selected study sites in riparian sediment plains covering the existing variation in the configuration of willow thickets. Each study site was represented by two nested square sampling units: (1) a central 15 m × 15 m square (hereafter called small quadrat) for estimating ptarmigan occurrence using faecal pellet counts and willow vertical structure using measurements on the ground,

and (2) centred on the 15 m × 15 m square, a 100 m × 100 m square (large quadrat) for measurements of willow area extent and fragmentation from aerial photographs. Further requirements for the exact positioning of the small quadrats were that they should be situated on mineral soils, the willow thickets should be imbedded in meadow vegetation (Fig. 1) and that the quadrats should not show any sign of flooding (flooding could wash away ptarmigan faecal pellets). The small quadrats were placed so that one side of the quadrat bordered on the edge of the thicket with the quadrat extending into the surrounding meadow. The average nearest neighbour distance between small quadrats was 652 m (SD = 524 m) with a minimum distance of 164 m (i.e. no overlap between the large quadrats). We placed 12 study sites in each of the regions KO and IF, while there were 13 study sites in region VJ (i.e. in total $N = 37$ study sites).

Recording willow ptarmigan site occupancy

Our large-scale survey in remote tundra regions demanded a ptarmigan census method that required little time per study site and worked equally well in early summer and

autumn. For these reasons we used “faecal pellet counts” to record site-specific occupancy of ptarmigan. Several studies have demonstrated that this method gives a suitable relative index for abundance or habitat use (hare: Krebs et al. 2001; ptarmigan: Evans, Mougéot, Redpath, & Leckie 2007; deer: Forsyth, Barker, Morriss, & Scroggie 2007; reindeer: Ims et al. 2007). In each small quadrat we deployed eight 50 cm × 50 cm plots for recording faecal pellets so that one plot was placed in each corner and one midway on each side of the small quadrat. Because number of pellets at the level of individual plots was low, we will use presence/absence of pellets at the level of small quadrats for the analysis of occurrence (see statistical analysis). Faeces were recorded in two census periods per year, one in early summer (early July) and one in autumn (early September). As all faecal pellets were removed from the small quadrats after each census, counts reflect the seasonal activity (early summer = mainly winter period and autumn = summer activity) of ptarmigan. Note that in 2005 only data from the autumn is included since counts in spring 2005 (i.e. start of study) could represent faeces accumulated over more than one season. In all study regions we also recorded ptarmigan pellets in an equal number of small quadrats in the adjacent heath habitat. However, as the number of faeces was very low (3 times lower than in the willow thicket quadrats) these data will not be considered further in this paper.

Quantifying willow thicket configuration

To quantify the areal extent and degree of fragmentation of willow thickets we used ortho-rectified aerial photographs (ground resolution of 0.20 m) taken in the summer of 2006. All willow thickets within the three regions were digitized in GRASS, version 6.1 (Grass Development Team 2006) and the appropriate raw data files were imported in FRAGSTAT, version 3.3 (McGarigal & Marks 1995). We used FRAGSTAT to obtain area-based variables quantifying areal extent and degree of fragmentation of willow thickets within the large quadrats of 100 m × 100 m (see above). The areal extent of willow thickets was measured as the percent cover of thickets within each large quadrat. To describe the degree of fragmentation or shredding of willow thickets in terms of variables likely to reflect reindeer browsing effects on thickets (Ravolainen 2009) we extracted *edge density* (metres of edge per large quadrat) and *patch density* (number of distinct patches per large quadrat). Increasing values of these variables indicate increased shredding or fragmentation of thickets. Note, however, that edge density was highly correlated with patch density ($r = 0.72$, see Appendix A: Table 3), whereas cover and edge density were only moderately correlated ($r = 0.34$, see Appendix A: Table 3).

Reindeer browsing has been shown to also affect the vertical structure of willow thickets (den Herder et al. 2004; Pajunen et al. 2008; Kitti et al. 2009). Accordingly, we measured the *height* and *density* of the thickets in the field at four

points along the side of the small quadrat lining the thicket. Willow density was measured by point frequency, placing a telescopic stick vertically 1 m 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 willow height and density was taken as the mean of the four measurements. Although the mean of the thicket variables differed somewhat between the three regions (Table 3, Appendix) their ranges were highly overlapping, meaning that regional effects due to some other factors could be statistically separated from the effect of willow thicket variables. Also note that reindeer impact on tall willow thickets, and in particular those areal characteristics measured in the large quadrats, is likely to induce changes that are so slow that the single recording made in this study (i.e. 2006) will be representative for the whole 4-year period.

Statistical analyses

We analysed the data using generalized linear mixed-effects models (GLMM) applied to a binary response variable (site-specific presence or absence of faecal pellets) with a logit-link function and a binomial distribution. The predictions from this model thus give probabilities of site-specific ptarmigan occurrence as indexed by presence of faecal pellets. Fixed effects in the model were the four willow configuration variables, year (2005–2008), season (spring and autumn) and region (VJ, KO and IF). GLMM's were fitted using site identity as random effects (Pinheiro & Bates 2000) thus taking into account the repeated census within sites. Willow configuration variables were standardized (i.e. scaled with mean = 0 and SD = 1) to ease comparison of their effects. GLMMs were fitted using the lme4 package (Bates et al. 2008) in the software R (R Development Core Team 2009).

Model selection started from four pre-defined candidate models (c.f. Burnham & Anderson 2002), one baseline model containing only additive effects and three with interactions between the four continuous configuration variables and the categorical variables year, region and season, respectively (see Appendix A: Table 1). Year is considered a focal variable in the analysis because it represents different phases of the small rodent population dynamics and thus possibly different levels of predation pressure affecting ptarmigan habitat occupancy. The interaction between year and the willow configuration variables are also focal terms in the models as they provide assessments of whether temporally changing predation pressures have spatially variable impacts depending on willow configuration variables. As edge density and cover have a potential suppressor relationship (i.e. opposite qualitative effects and a positive correlation, c.f. Smith, Koper, Francis, & Fahrig 2009), removing one will underestimate the effects of the remaining predictor (c.f. Smith et al. 2009). Consequently, the four willow configuration variables were

retained in all candidate models. Log-Likelihood ratio tests (LRT) were used to compare candidate models and to subsequently identify the best model. GLMM's were fitted using the Laplace approximation (Bates et al. 2008) and models were checked for constant variance of the residuals and presence of outliers and approximate normality of the predicted random effects.

Results

The best model for ptarmigan site occupancy (see Appendix A: Tables 1 and 2) was a model without any interactions between the willow configuration variables and the variables year, region and season. The effect of willow configuration could therefore be assessed independently for these variables. Both spatial configuration variables had strong effects on ptarmigan site occupancy (Fig. 3). Occupancy decreased with degree of thicket shredding (i.e. edge density, logit scale: -0.53 , 95% CI: $[-0.88, -0.18]$), whereas it increased with the areal extent of willow thickets (i.e. cover, logit scale: 0.49 , 95% CI: $[0.14, 0.83]$). There was no evidence for an effect of the two variables describing vertical structure of the thickets (see Appendix A: Table 2).

One study region (KO) had significantly lower average mean occupancy than the two other regions (odds ratio VJ vs. KO: 3.43, CI: $[1.49, 7.87]$, odds ratio IF vs. KO: 4.49, CI: $[1.50, 13.45]$), which could not be attributed to willow variables in the study sites (see Appendix A: Tables 1 and 2). Occupancy was estimated to be generally higher in early summer than in the autumn (odds ratio; early summer vs. autumn: 4.64, CI: $[2.44, 8.83]$). Finally, there was a strong monotonous declining trend in ptarmigan occupancy in all regions over the four year census period (Fig. 2A); the odds

for ptarmigan site occupancy was on average 2.17 (CI: $[0.87, 5.45]$) times higher in 2005 than in 2006 (rodent increase), 4.29 (CI: $[1.64, 11.21]$) higher than in 2007 (rodent peak) and 6.46 (CI: $[2.41, 17.34]$) higher than in 2008 (rodent crash).

Discussion

Synthesis of results

In the present study we employed a large-scale study design, which enabled us to demonstrate that willow ptarmigan occurrence is likely to be greatly affected by changes in the areal extent and fragmentation of willow thickets, i.e. habitat features likely to be affected by intense browsing by ungulates. Moreover, the relations we found were highly consistent over time and over a large spatial scale, meaning that willow thicket–willow ptarmigan relations did not depend on seasonal habitat use or multiannual changes in willow ptarmigan abundance in the different study regions. The lack of any temporal changes in habitat choice, that in our analyses would have been evident as significant interactions between year and habitat variables, indicate that our occupancy estimates did reflect temporal changes in willow ptarmigan population abundance both within and between the study regions. Surprisingly, the sharp decrease in ptarmigan populations (i.e. occupancy) took place independently of the rise and fall of the small rodent populations in the same riparian regions (Fig. 2), i.e. there was no apparent impact of the cyclic phases on decline rate. Thus the decline of the willow ptarmigan in the study regions cannot be explained by the alternative prey hypothesis nor by a collapse of the rodent cycle (c.f. Kausrud et al. 2008). The small rodent cycle is clearly still present in north-eastern Fennoscandia (Fig. 2B

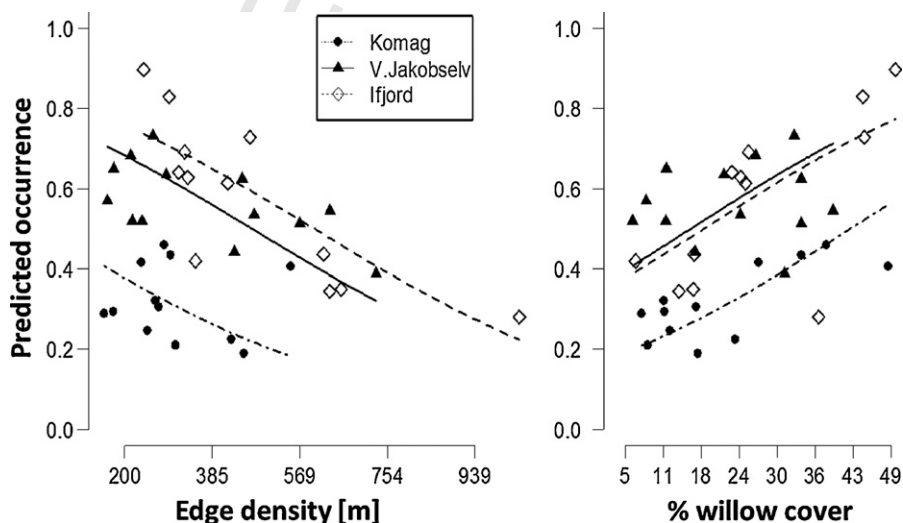


Fig. 3. Relationship between willow thicket characteristics (edge density and percent cover) and predicted probability of occurrence (i.e. from the statistical model) of ptarmigan in relation to study region (Komag, V. Jakobselv and Ifjord). While the graphs show predicted values for autumn 2005, the slopes of the predictions (i.e. the curves) and the relative positions of the regions (i.e. the intercepts) were the same for both seasons (spring and autumn) and all years (2005–2008).

and Ims et al. 2008). The strong synchronous decrease in ptarmigan habitat occupancy (Fig. 2A) over the 4 years in the three riparian regions is reflective of a population decrease taking place at a larger scale. The hunting statistics (i.e. the reported number of ptarmiganshot) for Finnmark county (covering an area of 46,000 km²) showed a similar decrease over the years 2005–2008 (Fig. 2C). Even at the scale of the country of Norway (SSB 2010) there has been a long-term decline in hunting bags (e.g. from ~500,000 birds in 2002 to 150,000 in 2009).

Effects of willow configuration on willow ptarmigan

In all three study regions willow ptarmigan patch occupancy decreased with edge density and increased with the percent cover of willow thickets. The positive effect of increased areal extent of thickets was expected based on the importance of tall willow thickets both as refuges from predators, breeding habitat and forage (Watson & Moss 2008; Wilson & Martin 2008). In general, both theoretical and empirical studies have found that habitat area is an important predictor of the occurrence of many species in fragmented landscapes, with its effect consistently positive and strong across regions, habitats and taxa (Rosenzweig 1995; Fahrig 2003; Ewers & Didham 2006; Smith, Fahrig, & Francis 2010). Large thicket complexes likely support more breeding pairs, since they provide ptarmigan with more forage and cover against predators. Large willow thickets may especially be important in winter when willow ptarmigans aggregate in flocks and when tall thicket forming shrubs are the only available forage and cover (Weeden 1969; Moss 1973; Andreev 1988; Hakkarainen et al. 2007; Watson & Moss 2008). On the other hand, small patches of thickets may fall below willow ptarmigan's requirements for cover (Schmiegelow & Mönkkönen 2002; Aldridge & Boyce 2007) and movements between small patches across open habitat may be associated with enhanced predation risk (Ims et al. 1993). Furthermore, the simultaneous strong negative effect of edge density indicates that even at a high percent cover of thickets, increased shredding or fragmentation of willow thickets reduce ptarmigan patch occupancy. This means that the effects of willow configuration variables found in this study are not entirely an effect of habitat area, but also of the spatial configuration in terms of the degree of shredding of the willow thickets (i.e. a fragmentation measure). These results are in accordance with previous studies where fragmented habitat have been shown to support lower average densities of ptarmigan than more continuous habitats (Watson & Moss 2008, and references therein).

In terms of mechanisms, the negative effect of edge density in our study is likely related to predation, the primary agent of avian nest mortality (Chalfoun, Ratnaswamy, & Thompson 2002a; Chalfoun, Thompson, & Ratnaswamy 2002b) and/or natural mortality of adult ptarmigans (Smith

& Willebrand 1999). In our study areas, several ptarmigan predators, both avian (e.g. golden eagle *Aquila chrysaetos* and gyrfalcon *Falco rusticolus*) and mammalian (e.g. red fox *Vulpes vulpes*, stoat *Mustela erminea* and least weasel *Mustela putorius*), are present year round. Thus, a constantly high predation pressure, both during summer and winter, might promote an increased aggregation of ptarmigan in larger and more homogenous patches. Large homogeneous patches of willows are likely to reduce the accessibility to patch interiors of especially avian, but also mammalian, predators. This conjecture is in accordance with several studies reporting elevated rates of predation in fragmented landscapes, small habitat remnants and along habitat edges (Chalfoun et al. 2002a, 2002b). Further, some studies (Kroodsmas 1984; Wilcove 1985; Chalfoun et al. 2002a; Chalfoun et al. 2002a, 2002b) have found that avian predators were more common along habitat edges than in the habitat interior. Among potential mammalian predators some, such as stoats and foxes, have been shown to occur at higher densities (Bider 1968), and concentrate their hunting, along habitat edges (Ford, Barrett, Saunders, & Recher 2001 and references therein; Phillips et al. 2003). These mammalian predators are, however, known to respond strongly, both numerically and functionally, to cyclic small rodent populations (Lindström & Hörnfeldt 1994; Gilg, Hanski, & Sittler 2003). Thus the lack of any "effect" of small rodent dynamics on willow ptarmigan habitat occupancy indicates that these rodent-dependent predators do not play an important role for the spatial and temporal patterns of willow ptarmigan habitat occupancy.

Our study provides further support to the hypothesis that large herbivores may impact willow ptarmigan populations negatively by providing an explicit link between willow thicket structural characteristics and ptarmigan habitat occupancy (c.f. den Herder et al. 2004; Ims et al. 2007). However, although overbrowsing of willow thickets by large herbivores is likely to affect such structural characteristics (e.g. Ripple & Beschta 2004; Ravolainen 2009), new studies should be conducted to verify this. Emphasis should then be shifted from the current focus on small-scale, ground-based measures mostly reflecting thicket vertical structure (e.g. Olofsson et al. 2001; den Herder et al. 2008; Pajunen et al. 2008; Kitti et al. 2009; Olofsson et al. 2009; Forbes, Fauria, & Zetterberg 2010) to larger-scale areal metrics found to be related to ptarmigan habitat occupancy in the present study. Indeed, extracting such measures from aerial photographs or high resolution satellite images may be a relatively inexpensive and efficient means of both monitoring willow ptarmigan habitat suitability and the impacts of large herbivores.

The steep and spatially synchronous decline in willow ptarmigan habitat occupancy, that took place in all three study regions independently of willow thicket structural characteristics, indicates that this rapid decline cannot be attributed to management of semi-domestic reindeer. The impact of reindeer overabundance on willow ptarmigan through browsing effects on willow thicket areal extent and fragmentation is likely to be a much slower process acting on the time-scale

of decades rather than years. Moreover, in contrast to the results of Kausrud et al. (2008), the recent decline in willow ptarmigan in Finnmark cannot be attributed to altered small rodent dynamics and therefore those predators that have been assumed to link ptarmigan and small rodent population dynamics through an alternative prey mechanism (reviewed in Moss & Watson 2001). This implies that research and management need to consider other mechanisms (e.g. Aldridge & Boyce 2007) presently unexplored/unknown in tundra ecosystems, when attempting to identify and eventually manage factors that cause the current decline in Fennoscandian ptarmigan populations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.05.006.

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