Willow ptarmigan dynamics at low population densities – the role of habitat and extrinsic environmental factors

Preface

Content

Sammendrag

Lirypa (*Lagopus lagopus*) er en økonomisk viktig og høyt yndet viltart i Skandinavia. Tettheter varierer i tid og rom, men en langsiktig bestandsnedgang i løpet av de siste tiårene har ført til bekymring i forvaltningen. En sentral forvaltningsoppgave er å implementere tiltak basert på førstehåndskunnskap for å sikre levedyktige og høstbare bestander over tid. Denne avhandlingen tar sikte på å frembringe ny kunnskap om lirypa og dens populasjonsøkologi under varierende tettheter. Tradisjonelt i Skandinavia har Lirypas økologi har som regel blitt studert i enkeltområder eller få områder i Skandinavia, men i denne studien brukte vi et omfattende datasett med linjetakseringer fra opptil 57 områder og nasjonale avskytingstall for norske hønsefugler i alle Norges fylker for å undersøke variasjon i tid og rom. Mer spesifikt; 1) beskrivelse av variasjon i tid og rom for tetthet av voksne ryper og for kyllingproduksjonen, 2) undersøke effekten av lokale forhold på tetthet av voksne og kyllingproduksjon, 3) evaluere hvilken modell for fordeling individer i en populajson som best beskriver variasjon i voksentetthet, 4) undersøke graden av synkroni inne arter og synkroni mellom arter i samme område for storfugl, orrfugl, lirype og fjellrype og 5) analysere effekten av predasjon og stor skala klimavariasjon, samt lokal klimavariasjon på kyllingproduksjonen hos lirype.

Både totaltetthet og voksentetthet var generelt lavere i denne studien enn i tidligere studier av lirype i Norge (enkelte områder samme som DF i denne studien). Voksentetthet varierte mer mellom takseringsområder enn mellom år og mellom fjellområder og enkelte takseringsområder hadde alltid høyere voksentetthet enn andre. Kyllingproduksjonene varierte imidlertid mer mellom år enn mellom takseringsområder og mellom fjellområder. Selv om det var betydelig variasjon både i vegetasjonens sammensetning og i voksentetthet fant jeg ingen klar sammenheng mellom voksentetthet og vegetasjonsvariabler. Det var imidlertid sterke indikasjoner på at privateide takseringsområder hadde høyere voksentetthet enn takseringsområder på statsgrunn. Forskjell i voksentetthet var 2,56 fugler / km^2 noe som tilsvarer hele 46% av voksentetthet på statsgrunn. Konsekvent forskjell avskytingsrater er en mulig forklaring på forskjellen. Jeg fant indikasjon for lavere kyllingproduksjon i områder med høy andel fjellbjørkeskog. Effekten var svak, men resultatet sammenfaller til en viss grad med tidligere studier på lirype. Jeg fant ingen klar seleksjon for noen vegetasjonstype i denne studien, noe

er i motsetning til tidligere studier som viser sterk seleksjon for rike myrer. Relativt lave tettheter sammenlignet med tidligere kan forklare at jeg ikke finner en klar sammenheng mellom lirype og vegetasjonstyper. Sammenlignet med perioder med høyere tetthet var det nok ressurser i forhold til antallet ryper (mat og skjul) i mitt studieområde noe som gir mindre konkurranse om ressursene.

Det var ingen sammenheng mellom voksentetthet og kyllingproduksjon. Dette er forventet hvis individene i en populasjon følger en ideell fri fordeling. Ideell fri fordeling betyr at lirypene fordeles proporsjonalt med de tilgjengelige ressursene i området. Dette fører igjen til at kyllingproduksjon blant ulike områder i en populasjon blir lik. Når individer i en populasjon er fordelt i samsvar med ideell fri fordeling forventes det også at voksentetthet blant takseringsområder innen fjellområder endrer seg proporsjonalt. Regresjonslinjen som forklarer sammenhengen mellom romlig variasjon i voksentetthet og gjennomsnittlig voksentetthet i fjellområdene var sterkt positiv. Dette tyder på at tettheten ikke endres proporsjonalt innen fjellområdene og at fugler aggregerer innenfor fjellområdene i større grad enn forventet ved ideell fri fordeling. Takseringsområder som allerede hadde høy voksentetthet økte mer enn takseringsområder med lav tetthet når den generelle tettheten økte. Det er usikkert hvilke mekanismer som fører til dette statistiske mønsteret, men basert på det vi vet om lirypas hekkebiologi er en mulig forklaring at unge ryper tiltrekkes av områder med høy tetthet ved etablering av hekkeområde om våren. Tilstedeværelsen av andre ryper (primært voksne som har overlevd og returnerer til sitt forrige hekkeområde) kan signalisere høy overlevelse og dermed kvaliteter ved området. Hvis lirypa bruker tetthet av andre ryper i et område som et signal om habitat kvalitet vil denne kunnskapen ha stor praktisk nytteverdi for forvaltningen. Forvaltere eller jegere som sparer voksne ryper i jakta kan øke kvaliteten og dermed også potensielt øke tettheten i sitt område.

Det var sterk synkroni i avskytingsstatistikkens vekstrate mellom nært beslektede arter. Styrken på synkronien mellom artene var sterkt knyttet til hvor mye de ulike artene overlappet i sin utbredelse. Dette tyder på at arter som bor i umiddelbar nærhet ofte har synkronisert dynamikk og at de er påvirket av de samme miljøfaktorene, slik som predatorregime og klima. Miljøaktorene påviker forskjellig i forskjellige deler av landet siden regioner med en lang kystlinje til både Nordsjøen og Norskehavet hadde synkroni mellom arter enn regioner med mer kontinentalt klima. Synkroni innen

de ulike artene var generelt lavere, men den var sterkere mellom fylker innen regioner definert av været enn mellom alle fylker. Synkronien avtok signifikant med avstand mellom fylker for lirype, fjellrype og storfugl. Synkronien var generelt sterkere mellom arter enn innenfor arter. Dette tyder på at ytre miljøfaktorer var viktigere faktorer for å skape synkroni enn spredning av individer mellom områdene.

Kyllingproduksjon beregnet fra linjetakseringsdata var sterk synkronisert både innen og mellom fjellområdene. Også smågnager indeksen viste sterk storskala romlig synkroni innenfor studieområdet mitt. Slik sterk synkroni tyder på de geografisk atskilte populasjonene påvirkes på samme måte av de samme miljøfaktorene.

Jeg fant en sterk positiv effekt av smågnagertetthet og den nordatlantiske oscillasjonen (NAO) for perioden mai, juni og juli på kyllingproduksjonen. Høy NAO indeks kunne relatertes til forhøyede temperaturer og nedbør i perioden før ruging, forhøyede temperaturer under rugeperioden og til fremskyndet plantevekst i fjellet. I motsetning til tidligere studier var den relative effekten av NAO sterkere enn effekten av smågnagertetthet. Dette kan forklares av kollapsen i de regulære smågnagersyklusene etter1990-tallet. Hvis lirypas populasjonsdynamikk var knyttet til smågnagersyklusen gjennom felles predatorer, kan dette båndet ha blitt svekket nå når smågnagersyklusen er mer uregelmessig. Dette kan ha ført til at andre miljøfaktorer slik som været påvirker dynamikken hos lirype sterkere nå. Gunstige klimatiske forhold i perioden før klekking slik som beskrives her kan virke som en buffer mot høy predasjon siden det kan føre til en økt andel høner som legger om etter røving. Globale klimaendringer virke indirekte lirypas populasjonsdynamikk gjennom effektene på smågnagersyklusen. Videre kan den direkte effekten av klima (dvs. NAO indeksen) føre til at klimaendringer virker positivt på lirypas kyllingproduksjon på grunn av økt mattilgang for høna og kyllingene. På den annen side er det dokumentert bestandsnedgang hos lirype de siste tiårene. Det er mulig at globale klimaendringer virker negativt lirypas overlevelse på senhøsten og vinteren siden fjærskiftet til vinterdrakt (hvit fjærdrakt) opptrer før snøfall slik at rypa blir mer utsatt for predasjon.

Abstract

Willow ptarmigan (*Lagopus lagopus*) is an economically important and highly desired game species in Scandinavia. Abundances vary considerably in time and space, but a long-term decline over recent decades has caused concern about the sustainability of current management practices. A central task of game management and conservation is to implement knowledge-based actions to ensure viable and harvestable populations over the long term. This thesis aims to add new knowledge about the ecology of willow ptarmigan populations fluctuating across a wide spectrum of equilibrium densities. Traditionally in Scandinavia, studies of willow ptarmigan have been conducted on a single or few populations, but in this study, I used an extensive survey of willow ptarmigan from up to 57 areas and national bag records for Norwegian tetraonids to investigate spatial- and temporal variation in willow ptarmigan population dynamics.

More specifically, my objectives were: 1) to describe spatial and temporal variation in density of adult birds and production of juveniles, 2) to investigate the effect of site-specific conditions on density and reproduction, 3) to evaluate which distribution model best described the observed variation in density, 4) to investigate the degree of temporal match in the dynamics of different populations of one species and between sympatric populations of four tetraonid species and 5) to analyse the effect of predation and large scale, as well as local, climate on local and regional reproductive success in willow ptarmigan.

Both total density and density of adult birds were generally lower in this study compared to historically reported densities of willow ptarmigan from south-central Norway (same areas as DF in this study). Adult density varied more between survey areas than between years and mountain regions and some survey areas consistently supported higher densities of adult ptarmigan than others. The reproductive success, however, varied more between years than between survey areas and mountain regions. Although both proportional vegetation composition and adult density varied considerably among survey areas, I was not able to detect any clear link between adult density and vegetation variables. There were, however, strong indications that privately owned survey areas supported higher

densities of adult birds than state-owned survey areas. The difference in density of adult birds was 2.56 birds/km^2, equivalent to 46 % of the adult density on state-owned land. A consistent difference in harvest rates is a possible explanation for this. I also found evidence of lower reproductive success in survey areas dominated by mountain birch forests. This effect was weak, but coincides with previous studies on willow ptarmigan. I found no clear selection for any vegetation type in this study which is in contrast to previous findings of strong selection for rich bogs. Relatively low population densities compared to earlier studies might explain the lack of a clear relationship between demographic rates and vegetation types. Hence, relative to years with higher population levels, resources (food and shelter) were plentiful in my study area and so competition was low.

There was no relationship between adult density and reproductive success. This is in accordance with the expectations of an ideal free distribution. The ideal free distribution would suggest that willow ptarmigan are distributed proportionally to the available resources, causing per capita reproductive success to be equal across the landscape. Further, when individuals are distributed in agreement with the ideal free distribution it is expected that density of adult birds among survey areas change proportionally. The steep scaling parameter of the relationship between spatial variance in adult density and mean adult density within mountain regions however, suggested that the densities did not change proportionally among survey areas. Aggregation of birds within mountain regions was stronger than expected from the ideal free distribution, and high density survey areas became increasingly crowded, relative to low density areas, when the overall density increased. The exact mechanisms causing this pattern are not clear, but based the breeding biology of willow ptarmigan I suggest that young ptarmigans are attracted to areas where densities are high during the settlement in spring. The presence of conspecifics (primarily philopatric adults) might signal high survival and thus high habitat quality. If willow ptarmigan use conspecific abundance as a cue to guide the settlement decision, it will have great practical relevance for game management. Managers who spare adult birds might increase habitat quality and hence increase the density on their land.

Synchrony in the rate of change in annual bag records was strong between ecologically close species and the degree of synchrony between species pairs was related to the distribution overlap between the

species. This suggests that species pairs living in close proximity often are synchronized in the dynamics. This result is expected if the species were affected by the same environmental factors, such as a shared predator-guild or climate. These factors worked differently in different regions since regions with a long coastline to both the North sea and the Norwegian ocean exhibited an overall stronger synchrony between species than regions with a more continental climate. Synchrony within species was generally lower for all species, but it was stronger among counties within weather-defined regions than among all counties. The synchrony faded significantly with increasing distance for willow ptarmigan, rock ptarmigan and capercaillie. Synchrony was generally stronger between species than within species, suggesting that extrinsic factors were more important than dispersal in causing synchrony.

I found strong synchrony in reproductive success both within and between mountain regions in south-central Norway. Also the rodent abundance showed strong large scale spatial synchrony in the study area. Hence, it is likely that the spatially separated populations were affected similarly by the same environmental factors.

I found a strong positive effect of rodent abundance and the North Atlantic oscillation (NAO) during May, June and July on reproductive success. The NAO index was positively related to temperature and precipitation during the pre-incubation period and temperature during the incubation period. Positive NAO values accelerated plant growth. In contrast to previous studies, the relative effect of NAO was stronger than the effect of rodent abundance, and might be explained by the collapse in rodent cycles since the 1990s. If willow ptarmigan dynamics in the past were linked to the rodent cycle through a shared predator regime, this link may have been weakened when rodent cycles became more irregular, resulting in a more pronounced effect of environmental perturbation on the dynamics of ptarmigan. Favourable conditions during the period prior to hatching might buffer the negative effects of predation due to increased renesting frequency among hens. It is possible that global climate change will indirectly affect willow ptarmigan population dynamics through effects on the rodent cycle. Furthermore, the direct effect of climate (i.e. NAO), implies that climate change might increase reproduction in willow ptarmigan, possibly through increased food availability for hens and juveniles.

Concerning the decreasing willow ptarmigan populations in Scandinavia, it is also possible that global warming negatively affects the willow ptarmigan in late autumn and winter since the molt to white winter plumage now occurs more frequently before the onset of winter, causing an increased risk of predation.

List of papers

This thesis is based on the following original publications and submitted manuscript, indicated in the text by their roman numerals, I-IV below.

I. Kvasnes, M. A. J., Pedersen, H. C., Solvang, H., Storaas, T. & Nilsen, E. B. (2014) *Spatial distribution and settlement strategies in willow ptarmigan. Population Ecology*, **57**, 151-161.

II. Kvasnes, M. A. J., Pedersen, H. C., Storaas, T. & Nilsen, E. B. (2015) *Vegetation Type and Spatial Variation in Demography of Low Density Willow Ptarmigan Populations. (Manuscript submitted to The Journal of Wildlife Management).*

III. Kvasnes, M. A. J., Storaas, T., Pedersen, H. C., Bjork, S. & Nilsen, E. B. (2010) *Spatial dynamics of Norwegian tetraonid populations. Ecological Research,* **25,** 367-374.

IV. Kvasnes, M. A. J., Pedersen, H. C., Storaas, T. & Nilsen, E. B. (2014) *Large-scale climate variability and rodent abundance modulates recruitment rates in Willow Ptarmigan (Lagopus lagopus). Journal of Ornithology***, 155**, 891-903.

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1. Introduction

1.1. Spatial and temporal dynamics

Population sizes are driven by abiotic and biotic environmental factors through their effects on demographic rates. Populations within one species (intraspecific) or sympatric species (interspecific) might fluctuate in synchrony if the populations are influenced similarly by environmental factors (Ranta et al., 1995b; Ranta et al., 2006). Synchrony between species is not as common as synchrony within species, but the degree of overlap in distribution and similarities in life histories are assumed to be important (Cattadori et al., 2000). Synchronous population dynamics can be identified by temporal matches in the abundance, rate of change in abundance or reproduction of spatially separated populations of one species or sympatric populations of different species. In general, three factors are recognized as possible causes of synchrony: (1) Climatic perturbations (Moran, 1953; Lindstrom et al., 1996; Koenig, 2002), (2) dispersal (Ranta et al., 1995a; Lindstrom et al., 1996; Paradis et al., 1999) and (3) predation (Ims and Andreassen, 2000). While dispersal is limited to causing synchrony among populations of one species, both shared climate and predators might also cause synchrony between sympatric species. Although the effect of climate might interact with population density, climate is generally assumed to be density independent and can affect large areas similarly (Moran, 1953; Koenig, 2002; Post and Forchhammer, 2002). Dispersal can be density-dependent and has a stronger synchronizing effect locally than at large spatial scales (Lindstrom et al., 1996; Paradis et al., 1999). Predation rates may also be density dependent (Fretwell and Lucas, 1969; Martin, 1988) (but see the alternative prey hypothesis; Hagen 1952; Kjellander and Nordström 2003), and the spatial scale of its synchronizing effect is likely to be affected by the mobility of predator species.

1.2. Habitat quality

Although dispersal and shared weather or predator assemblages might synchronize rates of change in population sizes, spatial heterogeneity in habitat quality (Fretwell and Lucas, 1969; Andren, 1990; Pöysä, 2001) can cause adjacent populations to fluctuate around different equilibrium densities (figure 1). Recognition of habitat attributes that are important for the persistence of populations is central in

land use- and species management. Habitat quality is determined by the state of environmental conditions (abiotic factors such as temperature and precipitation, and biotic factors such as competitors and predators) and the amount of available resources such as food and cover (c.f. Sinclair et al., 2006). Habitat quality can be identified in many ways, but more than half of the studies reviewed by Johnson (2007) used demographic measures (e.g. density, reproduction and survival) to assess habitat quality. Hence, one assumes a positive relationship between habitat quality and demographic parameters. Very often, studies have relied on this assumption (Bock and Jones, 2004; Johnson, 2007). Van Horne (1983) however, expressed caution about this approach because she could identify several situations where animals were more abundant in low quality habitats (i.e. habitats with low reproduction and survival). Acknowledging Van Horne's view, Bock and Jones (2004) reviewed 109 studies involving 67 bird species and demonstrated that the birds usually reproduced better in high density areas (72%), implying that density in most cases is a good indicator of habitat quality. In situations where density (or other demographic rates) is used as a proxy for habitat quality, it is also useful to conduct field surveys to more precisely identify the characteristics of either high- or low quality habitats. This is especially important for land use planning as it enables management authorities to predict habitat quality beyond the study site. Using remote sensing techniques such as satellite images is a cost-efficient way to gather information about the physical habitat across large areas (Pettorelli, 2013). Combining information gathered from remote sensing, such as vegetation maps, with demographic parameters makes it possible to directly analyze the relationship between habitat and wildlife populations, and hence to identify important vegetation features that need special consideration in land-use management (Lande et al., 2013).
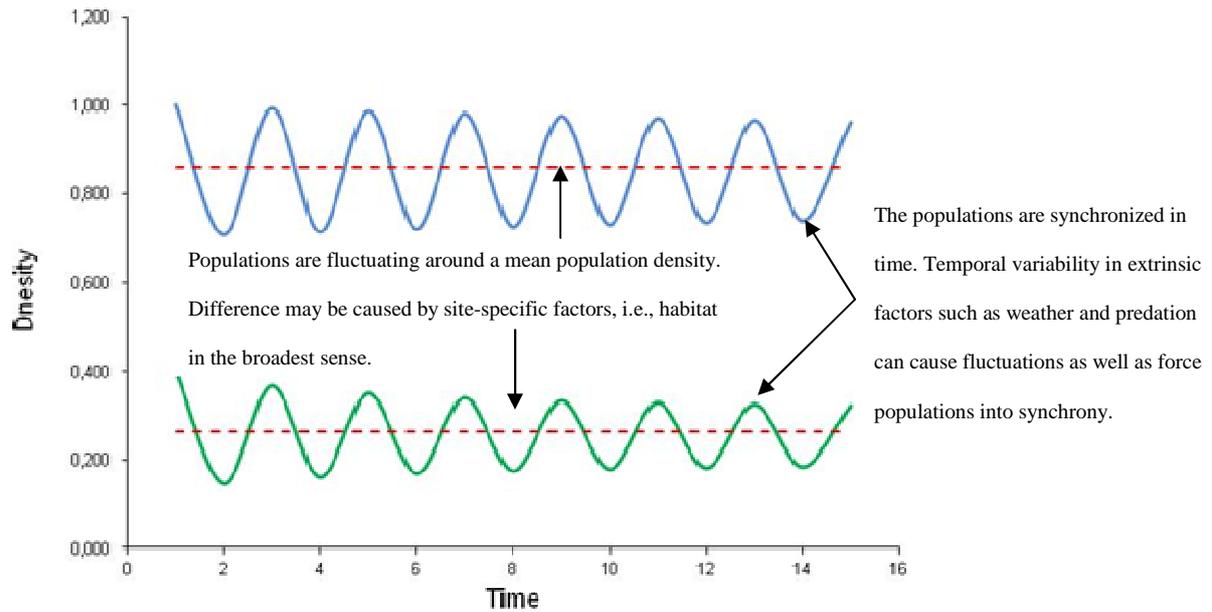
The populations are synchronized in time. Temporal variability in extrinsic factors such as weather and predation can cause fluctuations as well as force populations into synchrony.

Populations are fluctuating around a mean population density. Difference may be caused by site-specific factors, i.e., habitat in the broadest sense.

Figure 1 Illustration of two populations fluctuating in sychrony around different mean densities (*broken lines*)

1.3. Habitat selection

Besides being related to resources, habitat quality can also involve conspecifics, predators and competitors (Sinclair et al., 2006). Abundance of conspecifics, predators or other competitors might vary temporally and thus reduce the predictability of traditional habitat-wildlife analyses. When habitat quality is density dependent (density of conspecifics, predators or competitors), the per capita availability of resources will decrease as density of conspecifics, predators or competitors increase (Fretwell and Lucas, 1969). At very low population sizes it is also possible that individuals experience fitness gains rather than reductions with increasing density of conspecifics because of Allee effects (Greene and Stamps, 2001). In heterogeneous landscapes, individuals select among sites of varying quality. The fitness reward is assumed to play an important role in habitat selection. Several models have been suggested to explain how individuals are distributed in the landscape under different conditions (Fretwell and Lucas, 1969; Pulliam and Danielson, 1991; Danchin and Wagner, 1997). Applied to individual breeding-habitat selection, the ideal free distribution model (IFD) predicts that individuals should be distributed proportionally to the amount and quality of the habitat, so that all

individuals have equal access to resources, causing reproduction to be equal across all sites (Fretwell and Lucas, 1969). The ideal despotic distribution model (IDD) however, predicts that the quality of each individual's territory reflects their rank in the population (Fretwell and Lucas, 1969). Lower-ranked individuals are excluded from the best habitats, and so reproduction is expected to vary among sites (Fretwell and Lucas, 1969; Andren, 1990; Calsbeek and Sinervo, 2002). A third model, the ideal preemptive distribution model (IPD), predicts that individuals always select the best unoccupied site (Pulliam and Danielson, 1991), causing differences in reproductive rates among sites. Some authors consider IDD and IPD to cause similar distributions, but with a major difference in the mechanisms (despotism and preemption without aggressive behavior, respectively) (Holmes et al., 1996; Pöysä, 2001; Manning and Garton, 2013). All three models assume that the individuals are "ideal" in the sense that they have perfect knowledge of the options available to them and that the distribution of individuals will be related to the quality of habitat patches throughout the landscape. At the population level, the three models suggest that individuals congregate at higher densities in habitats with abundant resources. In general, when individuals are distributed according to an IFD it is predicted that there should be no relationship between density of breeding individuals and their reproductive success. In contrast, if individuals select habitats in accordance with an IDD or IPD one would expect a positive relationship between density of breeding individuals and their reproductive success. As an alternative to the negative density-dependent models of Fretwell and Lucas (1969) and Pulliam and Danielson (1991), it is possible that the presence of conspecifics attracts rather than detracts (IDD and IPD) other individuals from settling at a site (Stamps, 1988; Danchin and Wagner, 1997; Pöysä, 2001; Ward and Schlossberg, 2004; Farrell et al., 2012). Individuals might then use social cues as guides in the settlement decision, and hence select the most suitable habitats based on indirect evidence such as density of conspecifics rather than direct evidence such as vegetation communities (Stamps, 1988). When individuals are attracted to breeding sites primarily based on the presence of conspecifics, the predictability of habitat-wildlife models might be reduced if other suitable sites are undervalued due to low initial density of conspecifics (Campomizzi et al., 2008). Many studies investigating conspecific attraction have used experiments (Stamps, 1988; Danchin and Wagner, 1997; Ward and Schlossberg, 2004; Farrell et al., 2012), and this is probably the only way to actually confirm that conspecific

attraction is operating. Nonetheless, Pöysä (2001) found some indications that conspecific attraction was present in a mallard population (*Anas platyrhynchos*). When analyzing the change in habitat-specific density in relation to overall density, he found that high density lakes got increasingly crowded as overall density increased. Ducks in the rich lakes also reproduced better than ducks in poor lakes. Although other mechanisms might explain the pattern, it is evident that presence of other mallards did not repel them from settling in an occupied lake.

There are other statistical approaches to analyzing distribution in animal populations. For example, Taylor's spatial power law (TPL: Taylor 1961) states that spatial variance in density increases as a power function of mean density, and that the function reflects the spatial distribution of a population (Taylor 1961). On a logarithmic scale this function becomes linear and the estimated slope (*b*) can be used as an index of aggregation (Taylor, 1984; Tsai et al., 2000; Jimenez et al., 2001; Kendal, 2004; Detsis, 2009; Christel et al., 2013; Kristensen et al., 2013). In general, b → 0 implies a uniform distribution, *b*=1 suggests a random distribution and *b* → ∞ indicates higher degrees of aggregation. In Taylor's paper (1961), the *b* ranged from 0.7 to 3.1, with most values ranging from 1 to 2. Gillis et al. (1986) showed that *b*≈2 is in agreement with the predictions of an IFD, while a steeper slope (*b>2*) would indicate higher levels of aggregation than predicted by the IFD (Taylor, 1984; Tsai et al., 2000; Jimenez et al., 2001; Kendal, 2004; Detsis, 2009; Christel et al., 2013; Kristensen et al., 2013). Although *b*=2 agrees with the predictions of an IFD, the TPL is not a conclusive test as other mechanisms might also cause *b*≈2. However, according to Gillis et al. (1986), *b* = 2 should imply that density changes proportionally among sites (i.e. resource matching), whereas b>2 should indicate a disproportional change in density among sites, as Pöysä (2001) demonstrated for mallards in Finland.

1.4. Willow ptarmigan: The species and their population dynamics

Willow ptarmigan *Lagopus lagopus* is a medium-sized grouse distributed in alpine tundra habitats across the northern hemisphere (Johnsgard, 1983). Within its range, individual birds generally prefer habitats providing food and cover from predators (Erikstad, 1985a; Bergerud and Gratson, 1988; Schieck and Hannon, 1993; Hannon and Martin, 2006). In spring, males defend relatively small

breeding territories of 2-12 ha and territory size is negatively correlated with density of displaying males (Pedersen, 1984). Within these territories, 8-12 eggs are hatched by the end of June (Erikstad et al., 1985; Sandercock and Pedersen, 1994), and shortly after hatching, the male stops defending the territory. The chicks usually leave the territory accompanied by both parents (Erikstad, 1985b; Steen et al., 1985). Broods break-up from late September (Bergerud and Gratson, 1988), and at least in southern populations, adult males return to their former breeding area where they display, possibly accompanied by yearling males (Pedersen et al., 1983; Bergerud and Gratson, 1988). As winter emerges, birds in some populations move from breeding areas (i.e. summer ranges) to wintering areas, whereas in other populations the birds stay more or less in the same area but make short daily movements. The distance of any seasonal movements vary (Hornell-Willebrand et al., 2014) depending on the availability of winter forage (i.e., mountain birch *Betula pubescens czerepanovii*). Males are highly philopatric and return from wintering areas to their former breeding area in spring (Pedersen et al., 1983; Schieck and Hannon, 1989; Brøseth et al., 2005; Hornell-Willebrand et al., 2014). Females are less philopatric and are more likely to return following a successful breeding attempt (Schieck and Hannon, 1989). Although some juveniles return (Martin and Hannon, 1987; Rorvik et al., 1998), most male and female juveniles disperse from their natal area to other breeding grounds (Martin and Hannon, 1987; Brøseth et al., 2005; Hornell-Willebrand et al., 2014) in the period from brood break up in late september to the next spring. In south-central Norway, Brøseth et al. (2005) reported a mean natal dispersal distance of 3.9 km and there was no difference between juvenile females and males. Hornell-Willebrand et al. (2014) however, reported greater natal dispersal distances in birds from central Sweden and southern Norway and juvenile males were likely to settle closer to their natal area (mean 2.4 km) than females who moved much farther (mean 10.4 km). Although dispersal distances differ among studies, it is very likely that most new birds trying to establish breeding territories in an area are naïve juveniles dispersing from other breeding grounds within a radius of 20 km (Brøseth et al., 2005; Hornell-Willebrand et al., 2014).

Steen et al. (1985) compared vegetative features in willow ptarmigan territories in Norway, but could not detect any feature common to all territories. Shortly after hatching, broods left the territories and

brood movements thereafter were concentrated on habitats rich in food within the general area of the natal territory (Andersen et al., 1984; Andersen et al., 1986). It has been suggested that the breeding territories were not selected primarily to secure food for the pair, but their main function was to signal social status and quality of the males (Steen et al., 1985). Habitat selection studies of willow ptarmigan show that specific vegetation features or areas (Andersen et al., 1984; Kastdalen et al., 2003; Henden et al., 2011; Lande, 2011; Ehrich et al., 2012), including willow thickets (*Salix* spp.), bogs and dwarf birch (*Betula nana*) are important features related to willow ptarmigan occurrence (Kastdalen et al., 2003; Henden et al., 2011; Ehrich et al., 2012). Further, Erikstad (1985a) found evidence of higher brood survival in broods utilizing areas of high larvae densities and when studying the Scottish rock ptarmigan *Lagopus muta*, Moss and Watson (1984) found higher reproductive success in areas overlying base-rich bedrock. Lande (2011) however, was not able to detect any clear effect of habitat on adult density in willow ptarmigan in Sweden.

Willow ptarmigan have a short generation time and each hen may produce up to 12 chicks annually. Reproductive success, as well as numbers of breeding birds varies both in time and space (Johnsgard, 1983; Hornell-Willebrand et al., 2006). Changes in willow ptarmigan numbers are often ascribed to variation in reproductive success (Bergerud et al., 1985; Myrberget, 1988) although overwinter survival is also recognized as important (Steen and Erikstad, 1996). Most attention however is given to variation in reproductive success (Bergerud et al., 1985), probably because this rate shows more temporal variation than overwinter survival (Steen and Erikstad, 1996). The relative role of reproductive success vs. overwinter survival of chicks is, however, largely unknown because of a lack of data on the latter (Steen and Erikstad, 1996). Reproductive success is affected by environmental factors such as predation (Steen et al., 1988b; Smith and Willebrand, 1999; Sandercock et al., 2011) or weather (Slagsvold, 1975; Martin and Wiebe, 2004). Large scale synchrony in the population dynamics of willow ptarmigan in Sweden (Hornell-Willebrand et al., 2006) and other tetraonids in Europe, both between and within species (Lindstrom et al., 1996; Cattadori et al., 2000; Kerlin et al., 2007), suggests that environmental factors affecting tetraonid communities work similarly across large areas.

Predation rates on eggs and chicks are generally high in willow ptarmigan (Myrberget, 1988; Steen and Haugvold, 2009). High reproductive success (and low predations rates) often coincides with a high abundance of rodents and with the opposite holding during rodent crash years (Myrberget, 1988; Steen et al., 1988b). It is suggested that the link between willow ptarmigan and rodents is a shared predator assemblage, often referred to as the "alternative prey hypothesis" (APH). The APH predicts that a shift occurs in generalist predators' (i.e. Red fox *Vulpes vulpes,* Marten *Martes martes* and Stoat *Mustela ermine*) diet, from main prey species (voles *Microtus* spp.and Norwegian lemmings *Lemmus lemmus*) to alternative prey species (e.g. ptarmigan *Lagopus* spp. and Mountain hares *Lepus timidus.*) during rodent crash years (Hagen, 1952; Kjellander and Nordstrom, 2003). Steen et al. (1988b) found that the crash in rodent abundance had a regular 4-year cycle that was coherent with the breeding success of willow ptarmigan. Ims et al. (2008) and Kausrud et al. (2008) showed that the historically regular cycles in rodents collapsed during the 1990s and they linked the collapse to unfavourable climatic conditions during winter. It is thus possible that reproductive success in willow ptarmigan is indirectly affected by climate change through rodents and predation. Climatic conditions may also influence reproductive success in willow ptarmigan, and a general held view is that early snowmelt and onset of plant growth positively affect quality of eggs and chicks thorough enhanced female nutrition (Slagsvold, 1975; Steen et al., 1988a; Steen et al., 1988b; Martin and Wiebe, 2004) (i.e. maternal effects). Willow ptarmigan might lay a second clutch if the first one is predated, and renesting can potentially increase the yearly recruitment in a population (Parker, 1985; Martin et al., 1989). The probability of renesting in a North American willow ptarmigan population was higher in a year with normal weather conditions compared to a year with harsh weather (Martin and Wiebe 2004). Furthermore, Sandercock and Pedersen (1994) found that females that renested had larger eggs in their first clutch than females that did not renest, suggesting that renesting probability could be related to female quality. Similarly for a larger tetraonid, the Capercaillie *Tatrao urogallus*, renesting increased recruitment (Storaas et al., 2000) and renesting probability was greatest for heavy hens. It is also possible that weather effects on plant growth influence the availability of food for chicks (Erikstad and Spidso, 1982; Erikstad, 1985a; Steen et al., 1988a) as important insect prey feed on vegetation (Erikstad and Spidso, 1982).

Large scale spatial synchrony in the dynamics of willow ptarmigan populations has been reported in Finland (Ranta et al., 1995a) and Sweden (Hornell-Willebrand et al., 2006) and for other tetraonids in Europe (Small et al., 1993; Lindstrom et al., 1996; Cattadori et al., 2000; Kerlin et al., 2007). Climate and predation are extrinsic factors that can potentially drive the population dynamics of any species into synchrony if either of them are correlated in space (climate: Ranta et al., 1995a; Lindstrom et al., 1996; Koenig, 2002; and predation: Ims and Andreassen, 2000). Hence, as both climate and predation might influence the reproduction of willow ptarmigan (Slagsvold, 1975; Steen et al., 1988b; Martin and Wiebe, 2004), it is likely that both spatially-correlated climate and predation are causing the observed synchrony among willow ptarmigan populations.

Population densities, which are the result of environmental forcing on demographic rates (as described earlier) vary greatly across the distributional range and across time. In Canada, local spring densities varied between less than 1 to more than 200 ptarmigan/km^2 (Hannon et al., 1998) and on an island in northern Norway, Myrberget (1988) reported spring densities of adult birds in the period 1960-1988, of 19 to 172 pairs/km^2. Pedersen (1988) reported densities of territorial cocks of between 12 and 24 cocks/km^2 in south-central Norway during 1979 to 1986 (same area is within DF in this study). Typical autumn densities in Swedish mountain areas over the last 10 to 15 years range from 1 to 50 birds/km^2 (Hornell-Willebrand, 2005). There has been a significant decline in willow ptarmigan densities in Fennoscandia over the last 10 years (Lehikoinen et al., 2014) and in Norway this coincides with a marked reduction in national harvest bags (Statistics Norway, 2013)

2. Objectives

Management of willow ptarmigan in Norway has traditionally been based on local beliefs and assumptions, rather than scientific knowledge (Pedersen and Storaas, 2013). There is however an interesting change underway in willow ptarmigan management, and probably other game species as well: when a crisis becomes apparent and populations are declining, managers seek firsthand knowledge-based advice to sustain their populations. Willow ptarmigan and several other mountain birds are declining in Northern Europe in concert with climate change (Lehikoinen et al., 2014).

Similarly, rock ptarmigan populations in the Italian Alps might have an uncertain future under various climate change scenarios (Imperio et al., 2013). Environmental factors such as climate might drive populations of one or several species into synchrony. Thus, it is also possible that populations of one species across large areas or whole communities are negatively affected simultaneously if this environmental factor has a long term negative trend (Robinson et al., 2013). Climate change through increases in temperature and precipitation in Northern regions is, by now, well documented (Stocker, 2013), and thus there is a directional trend in climatic conditions, potentially influencing all living organisms in some way. The worst case scenario is that whole communities or ecosystems synchronously pass a tipping point where a shift to a contrasting dynamic regime occurs (Scheffer et al., 2009).

With declining populations, it is obvious that there has been a mismatch between increasing and decreasing demographic rates causing this decline. Hence, for management and conservation, it is important to assess the influence of factors causing variation in ptarmigan populations, both temporally and spatially. Only then is it possible to apply adequate mitigation measures.

This thesis aims to add new knowledge about the spatial and temporal dynamics of willow ptarmigan populations fluctuating across a wide spectrum of equilibrium densities. Traditionally, studies of willow ptarmigan have focused on a single or a few populations, and often at high population densities. Much of my thesis is based on several years of line transect survey data (<= 15 yrs) from up to 57 willow ptarmigan survey areas from across the whole spectrum of densities from almost zero to relatively dense populations. The main objective of this study is to use this extensive survey of willow ptarmigan, together with national bag records for Norwegian tetraonids, to investigate spatial variation (distribution, synchrony and vegetation features) and temporal variation (climate and predation) in population dynamics. The main objectives are addressed in four different papers where the aim of each was:

Paper I: In this paper I used autumn survey data of willow ptarmigan from Norway to: 1) describe the spatial and temporal patterns of variation in density of adult birds (representing density of breeding

birds in spring) and reproductive success (juveniles/pair) within and among ptarmigan populations in heterogeneous mountain landscapes in south-central Norway, and 2) to evaluate which distribution model best describes the spatial variation in abundance within mountain region populations.

Paper II: In this study I investigated the relationship between site-specific conditions (availability of different vegetation classes and management regime) and both adult density and reproductive success in willow ptarmigan from 40 survey areas across south-central Norway in the years 1996-2011.

Paper III: Here I used hunting-bag statistics to examine the patterns of synchrony in Norwegian tetraonid populations, to ask the following broad questions: 1) do ecologically related tetraonid species show interspecific synchronous population fluctuations? and 2) does the intraspecific synchrony decrease with increasing distance between the populations?

Paper IV: Here I used survey data from 2000 to 2011 in a large number of survey areas in south-central Norway to: 1) investigate the degree of synchrony in reproduction within and among mountain region populations, and 2) investigate the effect of predation and large scale as well as local climate on local and regional reproductive success in willow ptarmigan.

3. Methods

3.1. Survey areas and data collection

3.1.1. Line transect surveys (paper I, II and IV)

In papers I, II and IV, I used an extensive line-transect survey of willow ptarmigan. The surveys were conducted from 1996-2011 in up to 60 survey areas across south-central Norway (Figure 3). Only four areas were surveyed from 1996, but new areas were added throughout the period. Since the questions raised in the various papers were very different, I used different inclusion criteria in the different papers. Hence, I used data from 42 survey areas in paper I, 40 survey areas in paper II and 57 survey areas in paper IV.
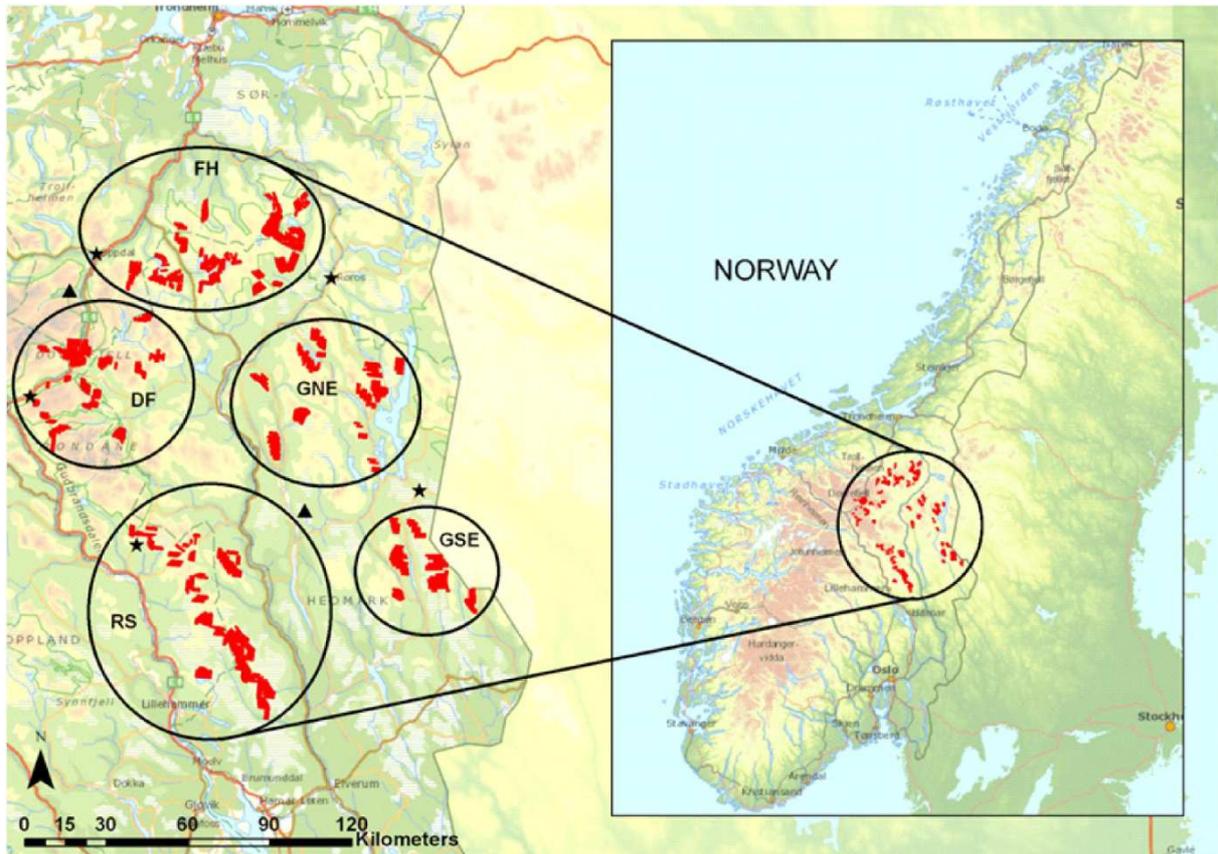
Figure 2 Study areas (*filled polygons*) within mountain regions (*open circles*) in south-central Norway used in paper I, II and IV. *RS* Rondane, *DF* Dovre and Folldal, *FH* Forrolhogna, *GNE* Glomma north-east, *GSE* Glomma south-east. The *filled stars* and *triangles* are the positions of meterological stations and rodent trap sites used in paper IV, respectively.

Survey areas were clustered within five geographically separated mountain regions (Figure 3), and were assigned accordingly to a mountain region (n=5, Figure 2). The transect lines in a survey area were usually placed 500 meters apart, orientated either north-south or east-west, although there was some variation (cf. Pedersen et al. 1999 and Solvang et al. 2007). At least two volunteers, one dog handler and one keeping track of the transect line, walked along predetermined transect-lines with one free-running pointing dog searching the area on both sides of the line following the procedure of distance sampling (Buckland et al. 2001; Pedersen et al. 2004; Pedersen et al. 1999; Warren and Baines 2011). At each ptarmigan encounter, the volunteer dog handlers recorded the number of birds observed (chicks, adult males, adult females and birds of unknown age/sex) and their perpendicular distance from the transect line (m). Pedersen et al. (2004) and Pedersen et al. (1999) provide detailed descriptions of the sampling protocol.

Based on data from the line transect surveys described above, I used multiple covariate distance sampling (MCDS) in the program Distance 6.0 (Thomas et al., 2010) to estimate half- normal detection functions and cluster density (DS) in all survey areas and years (668 survey area-year combinations). I used year as a factor covariate to account for possible variation in detection probability between years (Marques et al., 2007; Pedersen et al., 2012). Following Buckland et al. (2001), I estimated the cluster size (ES, which is the average number of birds in each encounter) separately for all survey areas and years as a function of distance from the line using regression. This is likely to result in unbiased estimates when larger clusters of birds are more likely to be detected at greater distances (Pedersen et al., 1999; Pedersen et al., 2004).

To obtain estimates of reproductive success (juveniles/pair) and density of adult birds (adults/km^2) I estimated the proportion of chicks and adults in each survey area and year (Paper I, II and IV). In addition for the analyses in paper IV, I pooled data from survey areas to estimate proportion of chicks and adults at the scale of mountain regions (c.f. figure 2).

I used mixed effect models to estimate the proportion of chicks in the samples (Crawley, 2007). I fitted a variable linking survey areas to year (called survey area-year) and a variable linking mountain regions to year (called mountain region-year) as random intercepts in the models. This allowed me to estimate the proportion of chicks (PC) from each encounter for each year in all survey areas or mountain regions separately. The survey area-year specific reproductive success (juveniles/pair) was estimated as:

$$R_{(i,j)} = PC / \left[\frac{1-PC}{2} \right],$$

Where $R_{(i,j)}$ is the reproductive success in area i, in year j and finally, density of adult birds was estimated as:

$$AD_{(i,j)} = DS * ES * [1 - PC],$$

where $AD_{(i,j)}$ is adult density in area i in year j and $DS * ES$ is the total density.

3.1.2. Tetraonid hunting statistics (Paper III)

In paper III, I used county-level hunting bags for willow ptarmigan, rock ptarmigan, black grouse *Tetrao tetrix* and capercaillie from 1982 to 2006 obtained from the open-access database at Statistics Norway (Statistics Norway, 2013, c.f. Figure 3) .
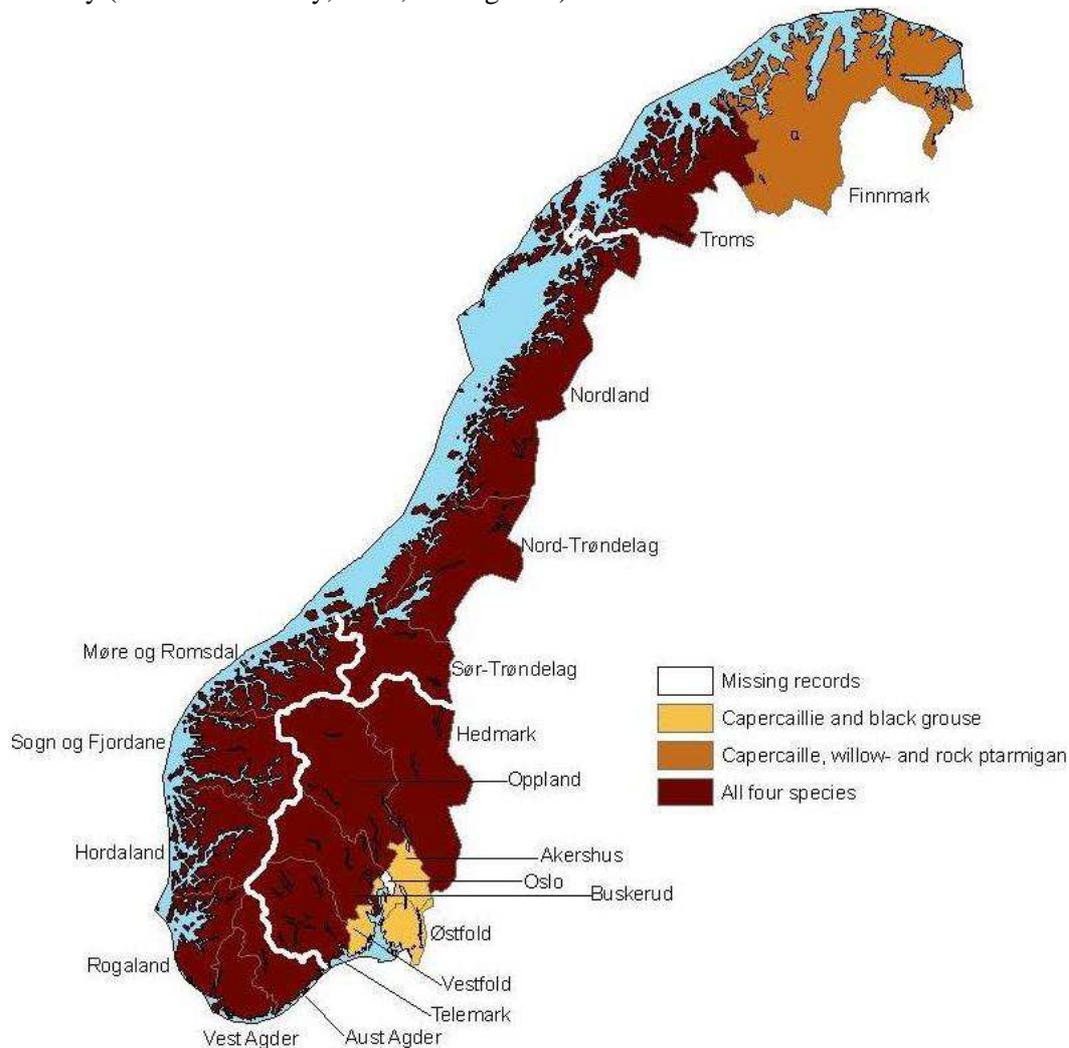

Figure 3 Map of the study area used in paper III. *Colors* indicate the species with hunting records included in the analysis. *Thin white lines* depict borders between counties. *Solid white lines* depict borders between regions (region east at the *right*, region west at the *left*, centre region in the *middle* and region north at the *top*). Regions are defined on the basis of similarities in precipitation between counties.

Hunting bag records are widely used as population size indices in population studies, and it is assumed that such indices reflect the actual fluctuations in population size (Small et al., 1993; Cattadori et al., 2000; Cattadori et al., 2003; Kerlin et al., 2007; Willebrand et al., 2011). Although there are known problems related to the use of hunting statistics as population indices (Hornell-Willebrand, 2005; Ranta et al., 2008; Willebrand et al., 2011), there are often temporal matches in the fluctuations when

comparing line transect data and hunting data for willow ptarmigan (Box 1), hence I assumed that the long-term hunting statistics would provide an acceptable index of fluctuations in abundance in tetraonid populations.

From the hunting bag statistics, I calculated population growth rates as: $r_t = n_{t+1} - n_t,$ Where *n* is the log of bag size year *t*. This operation directed the data from expressing fluctuations in number of birds shot to fluctuations in rate of change in bag size between years.

3.1. Variation in willow ptarmigan population dynamics (Paper I)

Spatial and temporal variation in adult density and reproductive success was analysed with mixed effect models that were fitted with either adult density or reproductive success as the dependent variable and mountain region, survey area, and year nested within mountain region as random intercepts. The amount of variation attributable to each random factor was then estimated in a variance components analysis (Crawley, 2007; Nilsen et al., 2008).

If individuals follow an ideal free distribution, it is predicted that there should be no correlation between density of adult birds and reproductive success (Fretwell and Lucas, 1969; Danchin and Wagner, 1997; Skagen and Adams, 2011). If individuals form an ideal despotic distribution or an ideal preemptive distribution however, it is expected that individuals would aggregate at higher densities in high quality habitats and achieve higher reproductive success rates than individuals settling in low quality habitats at lower densities. This would generally result in a positive relationship between density of adult birds and reproductive success (Fretwell and Lucas, 1969; Holmes et al., 1996; Calsbeek and Sinervo, 2002; but see: Van Horne 1983 and Skagen and Adams 2011).
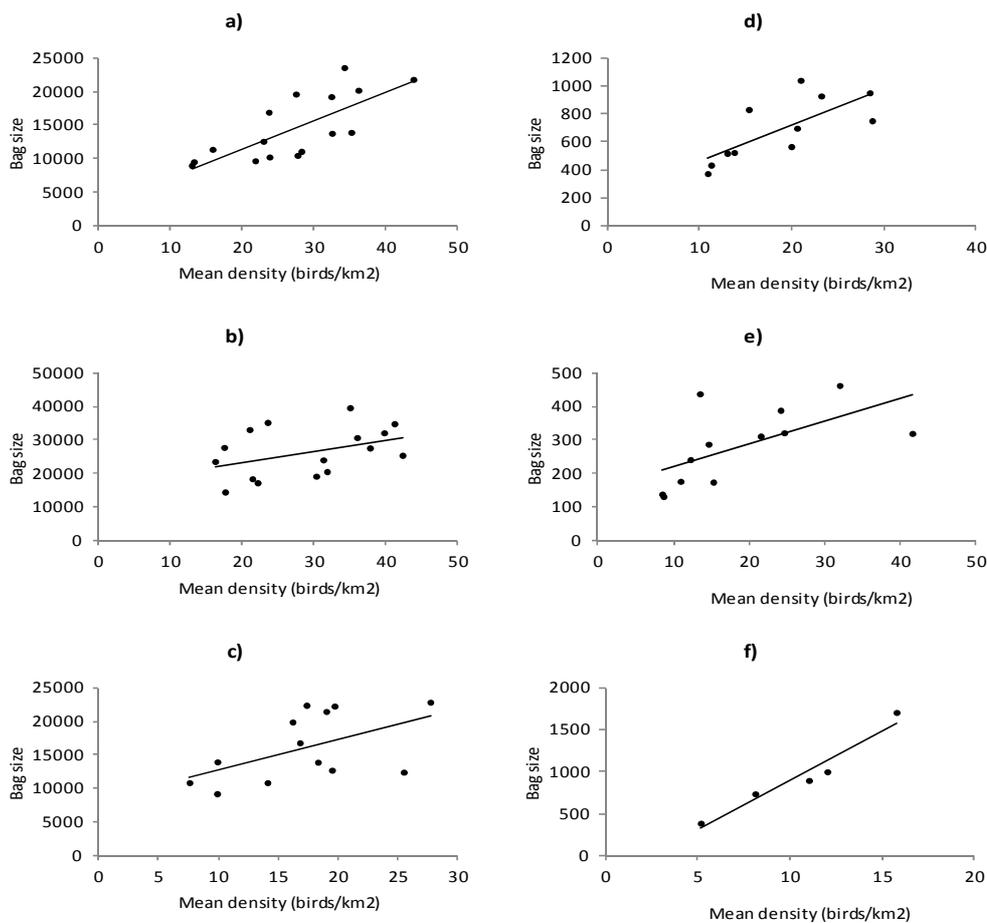
Box 1

a)

Bag size vs Mean density (birds/km2)

d)

Bag size vs Mean density (birds/km2)

b)

Bag size vs Mean density (birds/km2)

e)

Bag size vs Mean density (birds/km2)

c)

Bag size vs Mean density (birds/km2)

f)

Bag size vs Mean density (birds/km2)

Figure 4 Hunting bag size as a fuction of mean density. *a – c* county-wise bag statistics and mean density from line transect surveys in *a* Hedmark county, *b* Sør-Trøndelag county, *c* Oppland county. *d* Bag statistics from Trysil fellesforening and line transect survey data from four areas within Trysil fellesforening (same areas are in mountain region *GSE* c.f. paper I, II and IV). *e* bag statistics from Ringsaker jakt- og fiskeområde (www.rjfo.no) and line trasect surveys from one area within Ringsaker jakt- og fiskeområde (survey area is within mountain region *RS*, c.f. paper I, II and IV). *f* bag statistics from Ringebu fjellstyre (www.ringebu-fjellstyre.org) and line transect surveys from three areas within Ringebu fjellstyre (same areas are in mountain region *RS* in paper I, II and IV).

I used linear regression to analyze the relationship between bag size and density estimates from areas where both variables were available. I did the analysis at two scales; county and local management units. I used the counties Hedmark, Sør-Trøndelag and Oppland and the local areas were Trysil, Ringsaker and Ringebu (see legend of Figure 4). Hunting bag size was either based on national county-level statistics (counties) (Statistics Norway, www.ssb.no) or local reports (local areas). Density was either the mean density among survey areas within counties or mean density among a limited number of survey areas within the local report area. There was a clear significant relationship between bag size and mean density for Hedmark county (slope $\pm$ SE 420.76 $\pm$ 101.80, $F_{1,14} =$ 17.10, p = 0.001), but not for Sør-Trøndelag (p = 0.11) or Oppland (P = 0.06) (figure 4 a – c). It is worth noticing that the line transect surveys are mean densities from a limited part of each county while the bag statistics represent the whole county. In addition, the number of survey areas has increased over time. Hedmark county has the highest number of survey areas. It may explain why the relationship is stronger there. At the local scale, there was a clear positive and significant relationship for all areas (Trysil: slope$\pm$SE 25.78$\pm$8.00, $F_{1,9} =$ 10.37, p = 0.01, Ringsaker: slope$\pm$SE 6.83$\pm$2.77, $F_{1,10} =$ 6.09, p = 0.03, Ringebu: slope$\pm$SE 117.12$\pm$17.19, $F_{1,3} =$ 46.4, p = 0.006).

To test the predictions of different habitat selection models (Fretwell and Lucas, 1969; Pulliam and Danielson, 1991; Skagen and Adams, 2011), I used a linear mixed effect model to assess the relationship between reproductive success (dependent variable) and adult density (independent variable). In this analysis, I used the same random structure as described above.

To assess the level of aggregation of birds within mountain regions, I used Taylor's power law (TPL: Taylor 1961). First, to ensure that variances and means in the TPL were estimated across a sufficient number of survey areas I made a rule to maximize the number survey areas, but to have at least 5 survey areas in each mountain region and to have at least 5 years of data from each mountain region. This resulted in a new dataset of 28 survey areas covering five years in four mountain regions. Second, I calculated the spatial variance in density among survey areas within mountain regions (variance among samples) and mean adult density among the same samples for each year. Third, I estimated the slope (b) (i.e, the aggregation index described in the Introduction above (Taylor, 1961; Tsai et al., 2000; Jimenez et al., 2001; Kendal, 2004; Detsis, 2009; Christel et al., 2013; Kristensen et al., 2013)) of the relationship between spatial variance and mean density. Due to the low sample size (only four mountain regions) I estimated b in both an ordinary regression model with mountain region as a fixed effect and in two mixed effect models with mountain region either as a random intercept or as both a random slope and a random intercept.

3.2. Vegetation data and management regime (Paper II)

I estimated the proportion of different vegetation classes in the survey areas from a satellite based vegetation map (Johansen, 2009). There were initially 25 vegetation classes within the survey areas, but these were simplified by pooling together classes based on similarities in features that can be linked to willow ptarmigan food availability and cover from avian predators.

The survey areas were either managed as private land or as state owned land. There is a general assumption that hunting pressure is higher on state-owned than on private land in Norway (Pedersen and Storaas, 2013). A consistent spatial variation in harvest rate might cause spatial variation in

densities (Smith and Willebrand, 1999; Pedersen et al., 2004; Sandercock et al., 2011). I used

landownership as a crude indicator of the harvest rate in the survey areas.

I used generalized mixed effect models to analyze the effect of vegetation on adult density and

reproductive success. The models were fitted with survey area, mountain region, and year nested

within mountain region as random effects. I considered a number of candidate models with different

plausible combinations of the explanatory variables (both vegetation and management regime), but

confounded vegetation variables were analyzed separately (variables were considered confounded if

the correlation coefficient between them was > 0.4). I took the same approach for reproductive

success, but did not include terms for hunting pressure.

Table 1 Summary of vegetation types within the survey areas. The first column from left shows the *Original vegetation types* and classification numbers defined in Johansen et al. (2009). *Pooled vegetation types* is the simplification of the *Original vegetation classes* into 6 broader vegetation types (see methods for details). In the analysis I used Mountain birch forest (MB), Swamps and bogs with sparse field layer (BSF), Bogs with dense field layer (BDF), Open areas with sparse field layer (OSF), Open areas with dense field layer (ODF) and Snow-beds (SB). Mean and median values are proportional cover calculated across all survey areas. Note: there are no cities or built-up areas present in the study areas.

Original vegetation type (classification nr)	Mean (median)	Pooled vegetation types	Mean (min-max)
Bilberry- low fern birch forest (6)	0.026 (0.021)	Mountain birch forests (MB)	0.062 (0.000-0.289)
Crowberry birch forest (7)	0.013 (0.003)		
Lichen-rich birch forest (8)	0.023 (0.003)		
Wet mires, sedge swamps and reed beds (11)	0.008 (0.004)	Bogs with sparse field layer (BSF)	0.008 (0.000-0.041)
Ombrotrophic bog and low-grown lawn vegetation (9)	0.116 (0.110)	Bogs with dense field layer (BDF)	0.161 (0.000-0.465)
Tall-grown lawn vegetation (10)	0.044 (0.032)		
Exposed alpine ridges, scree and rock complex (12)	0.004 (0.000)	Open areas with sparse field layer (OSF)	0.319 (0.001-0.754)
Graminoid alpine ridge vegetation (13)	0.026 (0.006)		
Heather-rich alpine ridge vegetation (14)	0.233 (0.247)		
Lichen-rich heathland (15)	0.057 (0.043)		
Heather- and grass-rich early snow patch community (16)	0.050 (0.025)	Open areas with dense field layer (ODF)	0.384 (0.127-0.811)
Fresh heather and dwarf-shrub communities (17)	0.293 (0.252)		
Herb-rich meadows (18)	0.041 (0.031)		
Grass and dwarf willow snow-patch vegetation (19)	0.009 (0.003)	Snowbeds (SB)	0.017 (0.000-0.112)
Bryophyte late snow patch vegetation (20)	0.008 (0.003)		
Lowland forest (1-5)			*0.043 (0.000-0.190)*
Other (21-25)			*0.005 (0.000-0.056)*

3.3. Inter- and intraspecific synchrony (Paper III and IV)

I estimated spatial intraspecific synchrony (paper III and IV) by constructing matrices of pairwise Pearson correlation coefficients between pairs of time series for the bag records of willow ptarmigan, rock ptarmigan, black grouse and capercaillie (paper III) and for willow ptarmigan reproduction (paper IV). In paper III the correlations were calculated among all counties and among counties within regions that were predefined by similarities in weather. In Paper IV, I estimated correlations both among survey areas within mountain regions and among mountain regions. To assess the spatial scaling of the synchrony for the species in paper III, I analyzed the relationship between pairwise correlations at the county scale and distances between counties (Lindstrom et al., 1996; Kerlin et al., 2007).

Interspecific synchrony in growth rate (paper III) was analyzed at three spatial scales; national, regional (defined by weather) and county by constructing pairwise Pearson correlation coefficients between the species (Ranta et al., 1995b; Cattadori et al., 2000).

3.4. Synchrony and distribution overlap (paper III)

Species with overlapping distributions and similar life histories is likely to be affected similarly by environmental factors and thus fluctuate in synchrony (Cattadori et al., 2000). To test this prediction, I analysed the relationship between the estimated interspecific synchrony (correlation coefficient as dependent variable) and a distribution overlap-index (independent variable). I used a correlation test at the national level and mixed effect models at the regional and county levels. The mixed models were fit with region or county, respectively and species pair as random effects. The amount of variation attributable to each random factor was assessed in a variance component analysis (Crawley, 2007; Nilsen et al., 2008).

3.5. The effect of climatic conditions and predation on reproductive success (paper IV)

Local weather data (Paper IV): I used local meteorological data (Figure 2) for mean daily temperature (°C) and daily precipitation (mm) from three predefined periods during the breeding season; Pre-

incubation (PRE-INC, 1st May – 2nd June), Incubation (INC, 3rd -24th June) and Brooding (BROOD,

25th June to 15th July). The measure of temperature was the mean of all daily mean temperatures in the

periods and precipitation was the sum of all daily precipitation in millimetres. Willow ptarmigan

reproduction data at the survey area scale and mountain region scale were linked to the data from the

nearest meteorological station. *Large scale climate variation (Paper IV)*: The North Atlantic

oscillation (NAO) is known to impact on population dynamics in birds (Forchhammer and Post 2000;

Stenseth et al. 2002; Barnagaud et al. 2011). Here I used a seasonal station-based NAO-index from the

period May, June and July (NAO$_{MJJ}$) (Hurrell et al. 2013) obtained from an open-access database at:

https://climatedataguide.ucar.edu/guidance/%20hurrell-north-atlantic-oscillation-nao-index-station-

based. Timing of the onset of plant growth (OPG) in spring is related to weather conditions such as

snow-cover and temperature (Wielgolaski et al. 2011; Odland 2011), hence variation in the OPG could

affect reproduction through its effects on maternal nutrition and prey availability (Steen et al. 1988a;

Moss and Watson 1984; Erikstad and Spidso 1982). I used estimates of OPG, from MODIS satellite

data from 2000 to 2011 for each mountain region.

Steen et al. (1988b) demonstrated that reproductive success was strongly related to variation in rodent

abundance. Abundance of rodents can function as an index of predation rates if the alternative prey

hypothesis (Kjellander and Nordstrom 2003; Hagen 1952) is valid. I obtained long term rodent trap

data from two sites within the study area (Figure 2). As with the local weather data, I linked willow

ptarmigan data from survey areas and mountain regions to the nearest rodent trapping site. I modelled

the effect of climatic conditions (large to local scale) and predation (indexed by rodent abundance) on

reproductive success with linear mixed effect models. I only considered additive effects and did not

combine confounded variables, and local and regional climatic conditions were modelled separately.

At the survey area scale I included area, mountain region and year nested within mountain region as

random intercepts, and at the mountain region scale I included mountain region and year as random

intercepts. I also used mixed effect models to investigate the relationship between local conditions

(weather and onset of plant growth) and large scale climate variability (NAO index) (paper IV). One

model was fitted for each local and regional variable, with year as a random intercept.

4. Results and discussion

4.1. Spatial and temporal variation in breeding density and reproduction

In the 42 survey areas used in paper I, the mean total density was 26.5 birds/km^2, with the highest survey-area mean density being 91.8 birds/km^2 and the lowest being 8.2 birds/km^2. The mean density of adult birds and reproductive success were 7.8 adults/km^2 (highest mean: 25.3 adults/km^2, lowest mean: 2.2 adults/km^2) and 4.8 juveniles/pair (highest mean: 6.4 juveniles/pair, lowest mean: 3.0 juveniles/pair), respectively (Figure 5).
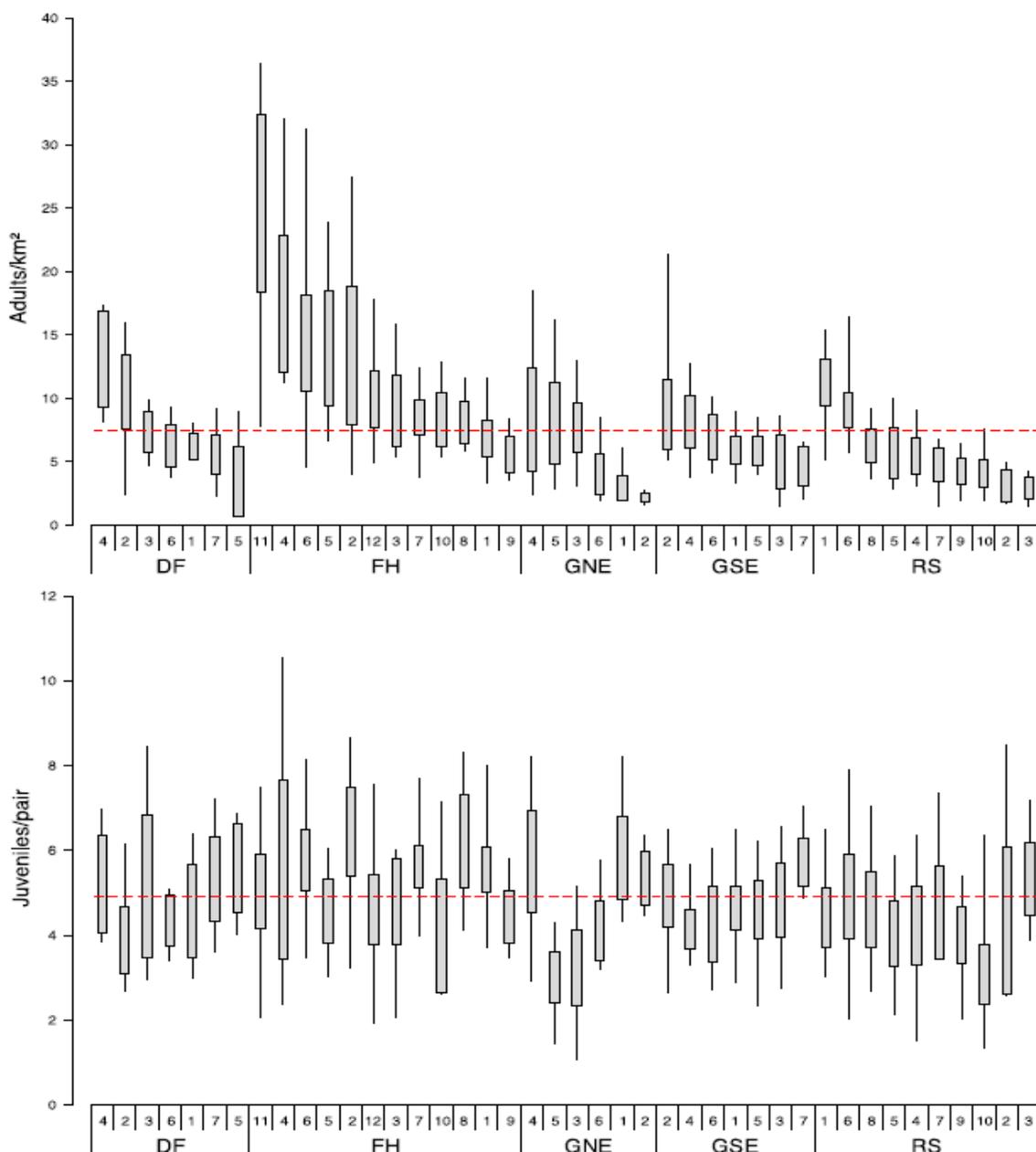

Figure 5 Boxplots of density of adult birds (*top*) and reproductive success (*bottom*) in the survey areas in south-central Norway. Survey areas are ranked within mountan regions by density of adults from left to roght. *Boxes* represent the 95 % confidence intervals of the mean with upper and lower ends of the *vertical lines* representing maximum and minimum values, respectively. The *horizontal broken lines* represent the overall mean adult density and reproductive success, respectively. *RS* Rondane, *DF* Dovre and Folldal, *FH* Forolhogna, *GNE* Glomma north-east, *GSE* Glomma south-east.

Density of adult birds varied more between survey areas than between years and mountain regions with some survey areas consistently supporting higher densities of adult ptarmigan than others (Figure 5). Reproductive success (juveniles/pair) however, varied more between years than between survey areas and mountain regions.

If the dynamics in the survey areas were mainly driven by survival and reproductive success, then these patterns might arise because of spatial variation in survival or reproduction. There was however only a small amount of spatial variation in reproductive success, suggesting that variation in reproductive success is not a key factor determining the consistent variation in adult densities among survey areas. Survival rates might vary spatially as a consequence of local variation in harvest mortality (Smith and Willebrand, 1999; Pedersen et al., 2004; Sandercock et al., 2011) or spatial variation in predation rates (Marcstrom et al., 1988). Human activities might also facilitate medium sized generalist predators (e.g., Kurki et al. 1998; Støen et al. 2010), which may increase predation and thus affect local demographic rates (Marcstrom et al., 1988). Spacing behavior during settlement could possibly also cause variation in densities of breeding birds because young birds select to settle in specific areas. Spatial variation in reproductive success was obviously present, but much lower than the temporal variation caused by differences between years. This could not be explained by site-specific conditions as there was no clear connection between reproductive success and vegetation types (paper II). Large temporal variation in reproductive success of willow ptarmigan is expected given that reproduction is known to be sensitive to environmental variability such as climate and predation (Steen et al., 1988b; Martin and Wiebe, 2004). These factors did indeed also affect the reproductive success in my study areas (paper IV).

4.2. Effect of vegetation features and management regime on breeding density and reproduction

Although both the proportional vegetation composition (paper II) and the adult density (paper I) varied considerably among all survey areas (Figure. 5), I was not able to detect a clear link between adult density and vegetation variables (paper II). I considered six aggregated vegetation types as well as

land ownership (private or state) in the analyses in paper II. Vegetation classes covered the whole range of the willow ptarmigan distribution in south central Norway, from the lowest elevations with
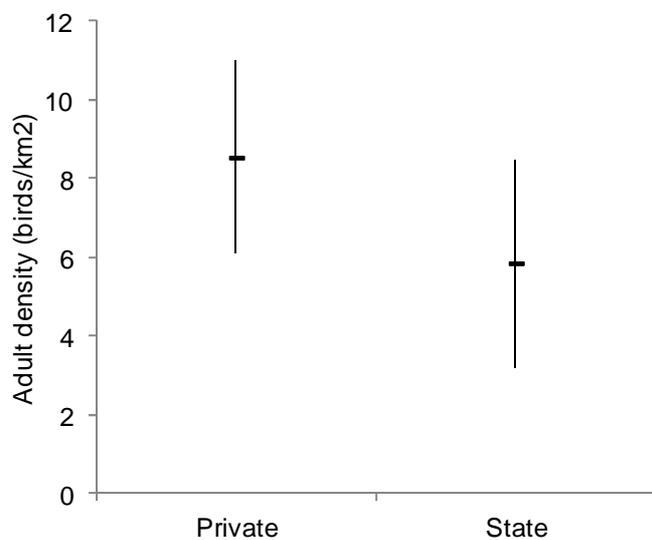

sub-alpine mountain birch forests to the higher elevations with snow-bed vegetation, open sparsely vegetated areas, densely vegetated open areas, bogs with sparse field layer and densely vegetated bogs (detailed description in paper II). The highest ranked models (all within 2 ΔAICc units, Table 2a) explaining adult density included 1) a model with the effect of land ownership where private

Figure 6 Mean adult density and 95 % confidence intervals for survey areas managed by private landowners (*Private*) or survey areas managed as common land (*State*).

survey areas had generally higher densities than state-owned survey areas (Figure 6), 2) the null model, 3) a model with land ownership and a negative effect of snow-bed cover, 4) a model with land ownership and a positive effect of open areas with dense field layer and 5) a model with land ownership and a negative effect of mountain birch cover. All models were equally supported by the data (Burnham and Anderson, 2002), and the principle of parsimony suggests selecting the simplest model, i.e., the null model. There were however strong indications that there was an effect of landownership. Firstly, the model accounted for 37 % of the AICc model weights compared to only 18 % for the second and third ranked models (Table 2a). Secondly, the bootstrapped confidence intervals for effect of state-owned land in the model with land ownership did not overlap zero (-5.61 and -0.09, 2.5 and 97.5% percentiles). Thirdly, the difference in effect size was substantial, 2.56 birds/km^2, which correspond to 46 % of the average density found on state-owned land (Figure 6).

Also when considering reproductive success, five models were within 2 ΔAICc and a negative effect of mountain birch cover was included in all these models (Table 2b). The simplest, and hence the most parsimonious model explaining reproductive success was a univariate model with mountain birch. The effect size of mountain birch on reproductive success in the simplest model was -4.85 with

bootstrapped confidence intervals not overlapping zero (-7.87 and -1.71, 2.5 and 97.5% percentiles).

This suggests that the negative effect of mountain birch on reproductive success was significant.

Table 2: Model selection tables based on AICc selection criteria for adult density (*a*) and reproduction (juveniles/pair) (*b*). Only models within 2 ΔAICc units considered. (+), (-) and (Private +) shows the direction of the effects. See Table 1 for definitions of vegetation variables (*BSF, MB, ODF, SB*).

a) *Adult density*

Variables	df	logLik	AICc	ΔAICc	AICc weight
Area (-), Landownership (Private +)	7	-990.96	1996.20	0.00	0.37
Area (-)	6	-992.72	1997.70	1.44	0.18
Area (-), Landownership (Private +), SB (-)	8	-990.64	1997.70	1.47	0.18
Area (-), Landownership (Private +), ODF (+)	8	-990.89	1998.20	1.96	0.14
Area (-), Landownership (Private +), MB (-)	8	-990.90	1998.20	1.98	0.14

b) *Juveniles/pair*

Variables	df	logLik	AICc	ΔAICc	AICc weight
BSF (-), MB (-)	7	-566.92	1148.20	0.00	0.28
MB (-)	6	-568.01	1148.30	0.09	0.27
MB (-), SB (+)	7	-567.26	1148.90	0.68	0.20
BSF (-), MB (-), SB (+)	8	-566.58	1149.60	1.41	0.14
MB (-), OSF (+)	7	-567.78	1149.90	1.72	0.12

The results of this study differ from other studies where individual ptarmigan selected special vegetation classes or features (Kastdalen et al., 2003; Henden et al., 2011; Ehrich et al., 2012). However, such individual scale selection, did not affect the density at the population scale in this study. Although the negative effect of mountain birch cover on reproductive success was weak, it did agree with the findings of Andersen et al. (1984) who demonstrated that willow ptarmigan broods avoided mountain birch during the first three weeks after hatching. Instead, Andersen et al. (1984) found selection for rich bogs in central Norway.

One possible explanation for the lack of a clear relationship between vegetation composition and either adult density or reproductive success in this study was that willow ptarmigan populations in most survey areas were well below carrying capacity (c.f. Myrberget 1988, Pedersen 1988, Lehikoinen et al. 2014). Hence, relative to years with higher population levels, resources (food and shelter) were plentiful and there was little competition. Theoretically the effect of vegetation would be clearer at

higher densities because of increased competition for optimal habitats (Fretwell and Lucas, 1969). Kastdalen et al. (2003) found that willow ptarmigan selected willow thickets at relatively high bird densities. However, Henden et al. (2011) also found the same at very low ptarmigan densities indicating that we should expect evidence for habitat selection in our study too. Over-browsing and trampling by domestic reindeer *Rangifer tarandus* in Henden et al.'s study area in northern Norway might explain this discrepancy. Earlier studies (e.g. Andersen et al. 1984 and Steen et al. 1985) have also shown that willows are important habitat components for willow ptarmigan. In our study, willows occurred in several of the considered vegetation types (Johansen et al., 2009).

The only factor able to distinguish the areas in terms of adult density was landownership. Since private and state-owned areas have similar vegetation composition I suggest that the most plausible explanation for this is that hunting pressure varies. As I suggest in paper I, it is possible that higher numbers of dispersing ptarmigan are attracted to private land due to higher survival of adults in such areas.

4.3. Spatial distribution of adult breeding birds within mountain regions

I tested the predictions of the ideal free distribution (IFD, Fretwell and Lucas 1969), ideal despotic distribution (IDD, Fretwell and Lucas 1969) and the ideal preemptive distribution (IPD, Pulliam and Danielson 1988) and found no clear relationship between adult density and reproductive success (Figure 7a). This suggests that willow ptarmigan are distributed according to an IFD within the mountain regions (Fretwell and Lucas, 1969; Danchin and Wagner, 1997; Skagen and Adams, 2011). In practice this implies that willow ptarmigan are distributed proportionally to the available resources, causing per capita reproductive success to be equal across the landscape. In a two patch system the density of birds would be higher in the patch with the highest intrinsic quality, but the minority who settle in the lower quality patch would have access to the same amount of resources. Further, when individuals are distributed in agreement with the IFD it is expected that all survey areas would have an equal proportional increase or reduction in density of adult birds (Gillis et al., 1986). I tested this prediction with Taylor's power law; a precise IFD should generate an exponent (*b*) of 2.0 for the
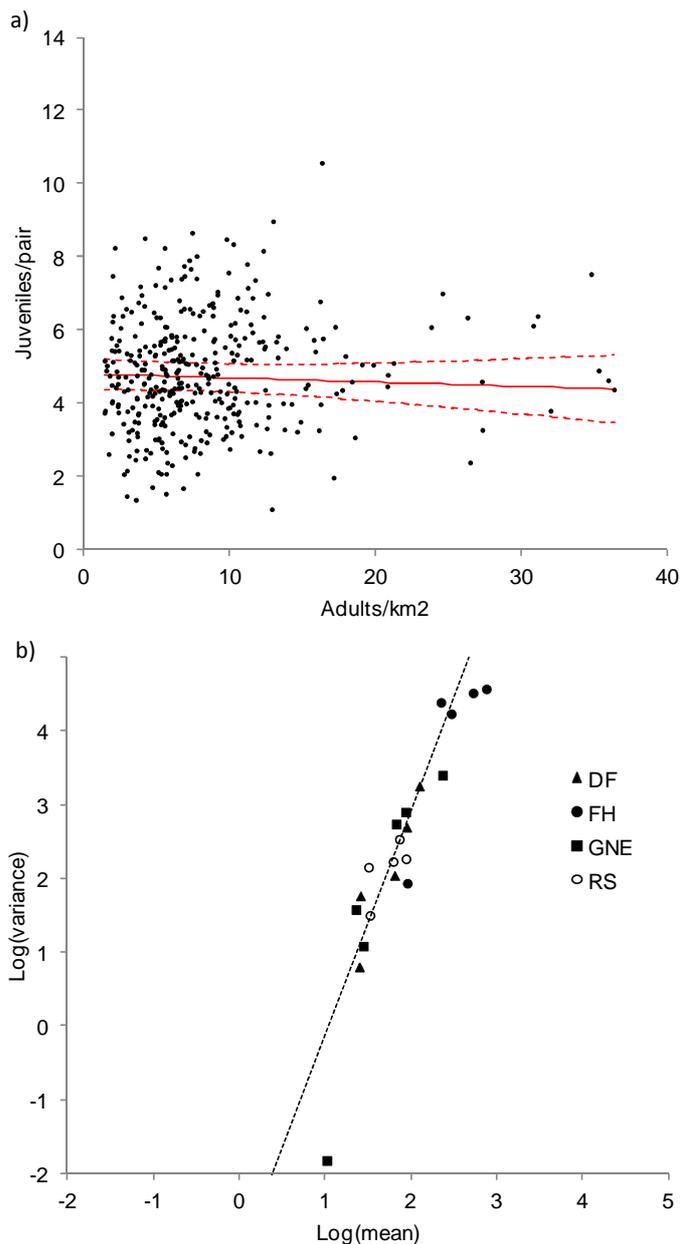
a)

b)

Figure 7 a)The relationship between survey area densities of adult birds and reproductive success. The *solid* and *broken lines* represent the estimated slope and 95 % confidence intervals. b) Logarithm of spatial variance in density of adult birds within mountain regions. The *solid line* is fitted from the linear regression model (for details see the methods section) with slope (*b*).

relationship between logarithm of spatial variance and mean density of adult birds (Gillis et al. 1986). My analysis showed that the slope (*b*) was significantly steeper than 2 (lower 95 % confidence limit of *b*; mixed effect model 2.3 and linear regression: 2.2, Figure 7b). When interpreted as an aggregation index (Taylor, 1984; Gillis et al., 1986; Tsai et al., 2000; Jimenez et al., 2001; Kendal, 2004; Detsis, 2009; Christel et al., 2013; Kristensen et al., 2013) the steep scaling parameter indicated stronger aggregation of breeding adult willow ptarmigan within mountain regions than expected under the IFD, and that high density survey areas became increasingly crowded, relative to low density areas, when the overall density increased (Gillis et al., 1986).

Aggregations of breeding birds in certain sites or areas might arise by different mechanisms. Individuals might be able track intrinsic habitat quality and then settle at higher rates in the best areas, or alternatively individuals might settle in breeding areas using abundance of philopatric adults as a guide in the settlement decision. In the first case, breeding aggregations could occur if there was a contemporary change in intrinsic habitat quality causing high quality survey areas to be relatively more suitable compared to low quality survey areas. However, I have no reason to suspect that a disproportional

change in habitat quality has occurred during this study. In relation to the second option, Pöysä (2001) found similar breeding aggregations in mallards were high quality areas became increasingly crowded when overall density increased and he further suggested that the birds probably used presence of conspecifics as a cue when selecting habitats. In the case of willow ptarmigan, juveniles are accompanied by the adult male and female throughout the breeding season from hatching in June to the brood's break up in late September. In the following period, juveniles disperse and most of them will settle in a breeding area within their natal mountain region (mountain region as defined in this study, cf. the scale of Figure 2) (Brøseth et al., 2005; Hornell-Willebrand et al., 2014). Stamps (1988) suggested that the presence of conspecifics could provide valuable information about habitat quality. If territory selection among juvenile birds occurs in spring they might have few opportunities to assess intrinsic habitat quality since the vegetation at that time is usually covered by snow. Further, the majority of new breeders are naïve (one year old) and may thus use the abundance of philopatric adults surviving from last year as a cue to assess habitat quality. Due to high levels of philopatry in adults, the density of adults in a survey area might signal high survival probability or good reproductive prospects (Schieck and Hannon, 1989). For naïve one year old birds, conspecific cuing may be a cost-effective strategy as they have a short life expectancy and thus few opportunities to acquire personal information through trial and error tactics (Danchin et al., 2004).

Generally, when individuals settle in a given area, both the competition for limited resources and predation rates may increase with density, resulting in reduced quality (Fretwell and Lucas, 1969; Martin, 1988; Sergio and Newton, 2003). On the other hand, Greene and Stamps (2001) proposed that individuals at low densities might have fitness gains rather than reductions with increasing density, thus causing positive effects of conspecific interactions at low densities due to Allee effects. They further demonstrated that Allee effects could generate aggregated distributions even if all habitat patches had the same intrinsic quality. Since the present study took place during a period of generally low population densities (c.f., Myrberget 1988 and Pedersen 1988), this might partly explain the distribution in my study areas.

4.4. Synchrony in population dynamics

Different spatial patterns were observed when analyzing the intraspecific spatial synchrony within all species in paper III. Cross-correlations between counties showed a generally weak synchrony; median correlation [2.5%, 97.5% percentiles]: capercaillie 0.09 [0.05, 0.13], rock ptarmigan 0.12 [0.07, 0.16]), black grouse 0.19 [0.15, 0.24] and willow ptarmigan 0.21[0.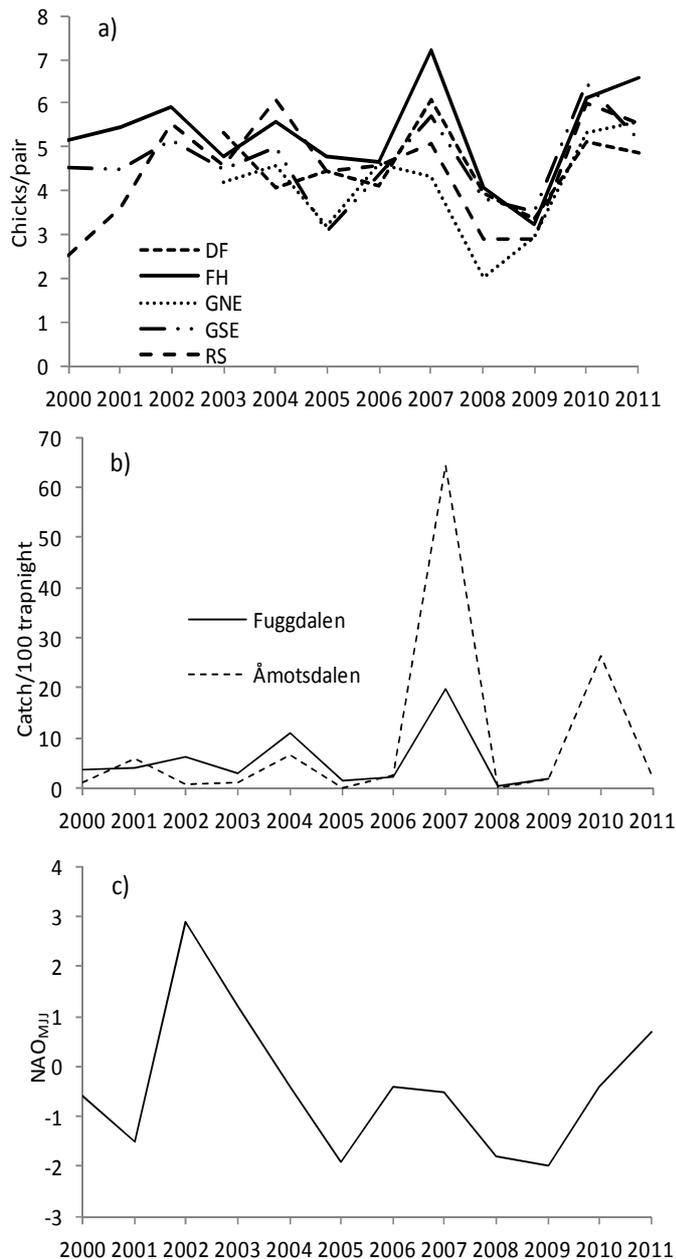16, 0.27]). The synchrony was stronger between neighbouring counties and between counties within precipitation-defined regions. It decreased significantly with distance for willow ptarmigan, rock ptarmigan and capercaillie (median correlation [2.5%, 97.5% percentiles]: -0.69 [-0.74, -0.64], -0.34 [-0.44, -0.24], -0.14 [-0.23, -0.05], respectively). Synchrony in reproductive success (paper IV) was generally strong, both between mountain regions (Figure 8) and all areas in south-central Norway. The spatial structuring of the study areas suggested significant synchrony within 96.5 km. Also the rodent abundance indices showed strong large scale spatial synchrony with a correlation coefficient (95% cl) of 0.89 (0.60-0.97) (distance 118 km).

The strong correlation in reproductive success among mountain regions and the strong correlation in abundance indices

Figure 8 a) Reproduction (juveniles/pair) in mountain regions, b) standardized rodent abundance indices from Åmotsdalen and Fuggdalen (c.f. figure 2) and c) the seasonal NAO index for May, June and July, all in the period 2000 – 2011. In a) *RS* Rondane, *DF* Dovre and Folldal, *FH* Forrolhogna, *GNE* Glomma north-east, *GSE* Glomma south-east.

between rodent trap sites suggest that spatially separated populations were affected by the same environmental factors such as shared predator-guild (Ims and Andreassen, 2000) or climate (Moran, 1953).The spatial scaling of the synchrony further suggests that environmental forces work similarly across large regions. However, there was some variation in synchrony, even at short distances (paper III) and between neighbouring survey areas (paper IV). This indicate that local factors also play a role in shaping the dynamics (Tavecchia et al., 2008).

Dispersal is also a possible cause of synchrony among populations (Lindstrom et al., 1996; Paradis et al., 1999), but Lindstrom et al. (1996) proposed that synchrony caused by dispersal would generate a stronger negative relationship between synchrony and distance than synchrony mainly caused by environmental factors. We found a relatively strong relationship for willow ptarmigan, but weak for the other species. The overall weak intraspecific synchrony compared to the strong interspecific synchrony (see next paragraph) suggests that extrinsic environmental factors are more important than dispersal in causing synchrony at the spatial scales studied in paper III. In paper IV, intraspecific synchrony was much stronger and it is possible that dispersal was more important at that scale.

The analysis of interspecific synchrony in tetraonids (paper III) showed that ecologically related species were highly synchronous across Norway, and the synchrony was closely related to distribution overlap between species. Also within precipitation-defined reg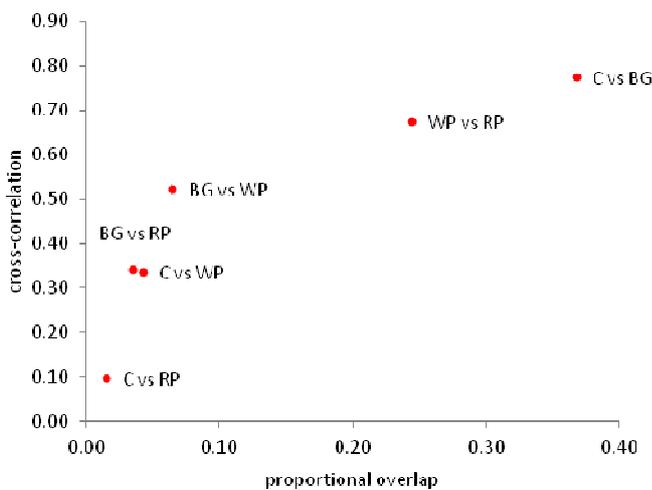ions and within counties, I found strong mean synchrony between ecologically related species with a high overlap in distribution. When accounting for the fact that species pairs with a high distribution overlap were synchronized, more of the remaining variation in synchrony was caused by differences between areas (i.e., counties or regions) than by differences between species pairs. This suggests that species pairs living in

Figure 9 Synchrony plotted against distribution overlap index between tetraonid species in Norway. *C* capercaillie, *BG* black grouse, *WP* willow ptarmigan, *RP* rock ptarmigan.

close proximity were often synchronized in their dynamics and that proximity is more important than differences between species' life histories and body sizes. This result also corresponds to what would be expected if the different species were affected by the same environmental factors such as shared predator-guilds (Ims and Andreassen, 2000) or climate (Moran, 1953). There was a stronger interspecific synchrony among species in the western and center regions than in the eastern and northern regions. One explanation for this difference is that environmental factors are important and work differently among regions. The western and central regions have long coastlines and inland areas are only a short distance from the coast, whereas the eastern and northern regions have shorter coastlines and include more continental/inland areas.

4.5. Effect of climate and predation on reproductive success

In paper IV, I found strong evidence of environmental factors playing an important role in shaping the dynamics of willow ptarmigan. I modelled reproductive success as a function of climatic variables and predation (indexed by rodent abundance) and found strong positive effects of both the large scale climatic variability (NAO_{MJJ}) and rodent abundance (Slope±SE; mountain region scale: NAO_{MJJ} = 0.53±0.10, Rodent = 0.03±0.01 and survey area scale: NAO_{MJJ} = 0.54±0.08, Rodent = 0.03±0.01, c.f., Figure 8).

A sensitivity analysis to compare the two factors revealed that NAO_{MJJ} had a greater influence on reproductive success than rodent abundance in this study area. The effect of NAO_{MJJ} has little practical use unless it can be related to local climatic conditions. In my study, NAO_{MJJ} was correlated positively with local temperatures and precipitation during the pre-incubation period and with temperature during the incubation period. In addition, high NAO_{MJJ} values were related to an early onset of plant growth in the mountain regions.

I suggest that the positive effect of rodent abundance was related to lower predation rates in years of high rodent abundance (Steen et al., 1988b), as predicted by the alternative prey hypothesis (Hagen, 1952; Kjellander and Nordstrom, 2003). High abundance of rodents during the breeding season may indirectly reduce predation on ptarmigan eggs and chicks if generalist predators prefer easily caught

rodent prey. It is interesting however, that my models explained a similar amount of variation in reproductive success as the models of Steen et al. (1988b), but contrary to that study, more of the variation in my models was explained by weather conditions (NAO_{MJJ}) than rodent abundance. A possible explanation for this is that climatic forcing of ptarmigan population dynamics has become more pronounced in recent years due to the collapse in small rodent population cycles (Ims et al., 2008; Kausrud et al., 2008). Other species, such as ptarmigan and hares were entrained in the rodent cycle by their shared predators when regular population fluctuations existed (Hagen, 1952; Kjellander and Nordstrom, 2003). This link may have weakened as small rodent fluctuations became more irregular (Ims et al., 2008; Kausrud et al., 2008) and the effects of environmental perturbations and climatic variation became more pronounced in the dynamics of ptarmigan.

NAO_{MJJ} was related to conditions that contribute to an acceleration of spring (i.e., early snowmelt and onset of the growing season). A possible mechanism behind this might be that NAO and an early onset of spring influence maternal nutrition (Moss and Watson, 1984), food availability for chicks (Erikstad and Spidso, 1982; Erikstad and Andersen, 1983; Erikstad et al., 1985) and the timing of laying (Erikstad et al., 1985), all which are important for reproduction in willow ptarmigan. Adequate maternal nutrition is especially important since it affects the quality of eggs (i.e., also newly hatched chicks) and it may increase the probabillity of renesting in tetraonids (Sandercock and Pedersen, 1994; Storaas et al., 2000). In North American willow ptarmigan, renesting probability was higher in years with normal conditions than in years with harsh weather and since renesting has the potential to increase yearly reproduction in a population (Parker, 1985; Martin et al., 1989), it is possible that favourable conditions in spring may buffer some of the negative effects of egg predation through increased renesting frequency.

5. Concluding remarks

Willow ptarmigan select habitat at the individual level, but differences in habitat composition did not explain consistent differences in adult density among survey areas. Nor was there any relationship between reproductive success and adult density. This might be explained by relatively low densities in

the survey areas and consequently little competition for resources. It is thus unlikely that habitat management will have any effect on willow ptarmigan population sizes in Norway during periods of relatively low densities. I propose that the disproportional change in adult density among survey areas within mountain regions is caused by spacing behavior during settlement, with abundance of conspecifics positively affecting settlement decisions, i.e., conspecific attraction. For young dispersing willow ptarmigan, high abundance of philopatric adults in an area might signal high survival and good reproductive prospects, hence abundance signals habitat quality. Habitat composition was similar, but adult density was higher on private than state-owned land, suggesting differences in survival rates. It is possible that private hunting units with lower harvest rates and higher survival rates attracted dispersing juvenile ptarmigan from neighboring hunting units with higher adult harvest rates.

Ecologically related species fluctuated in synchrony at national, regional and county levels, but the strength of the correlations varied between regions/counties. My results suggest that environmental conditions are affecting tetraonid species similarly and cause the observed patterns of synchrony. Both the North Atlantic oscillation in the period before laying to the early juvenile stages and rodent abundance positively affect reproduction and are therefore possible drivers of the observed spatial synchrony across populations in south central Norway. I suggest that global climate change indirectly affects willow ptarmigan population dynamics through effects on the rodent cycle. Furthermore, the direct effect of climate (i.e NAO_{MJJ}) suggests that climate change might accelerate snow melt and plant growth during spring, and hence increase reproduction, possibly through food availability for the hen and juveniles. However, in the light of decreasing willow ptarmigan populations in Scandinavia, it is possible that climate change works the other way around in the period of transition from autumn to winter (Imperio et al., 2013). Timing of the molt into white winter plumage is related to day length, not climatic conditions and a delayed onset of winter caused by climate change might therefore increase the risk of predation due to a mismatch in timing of the molt.

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