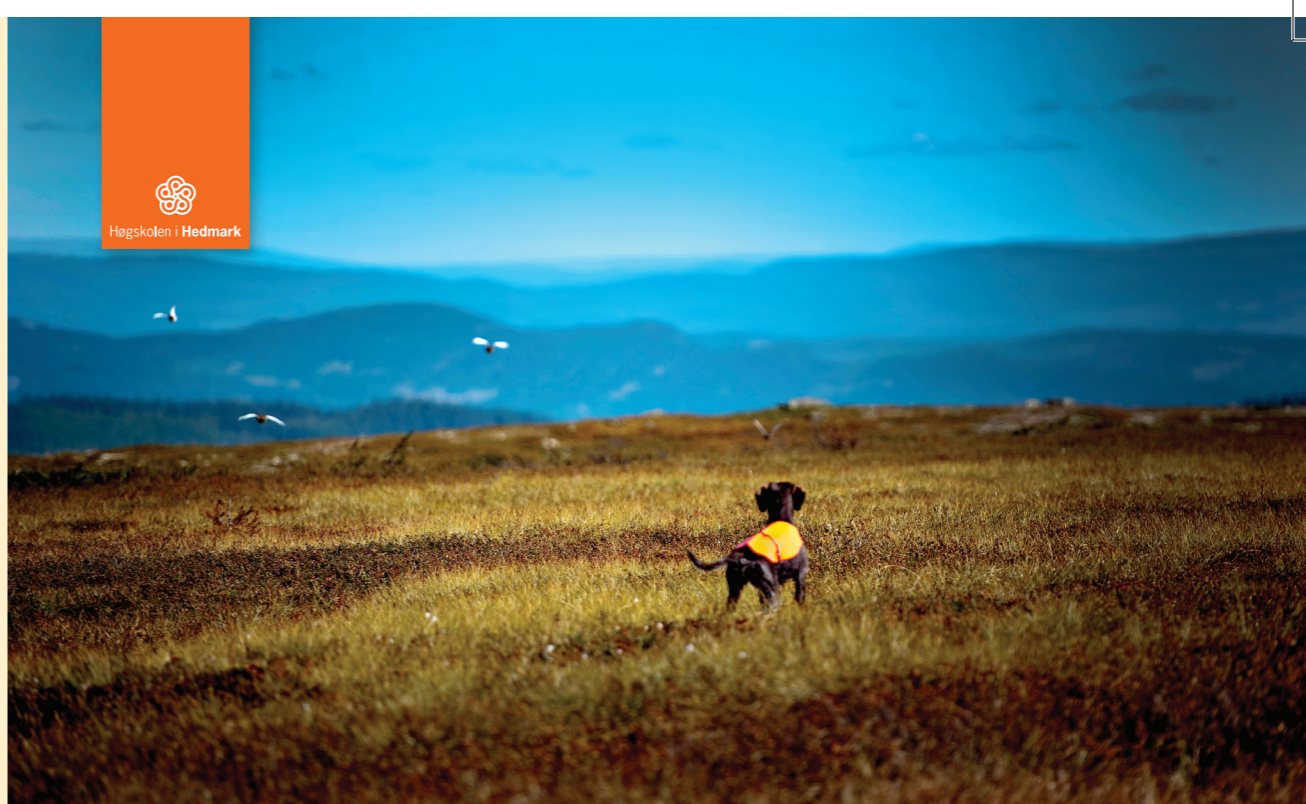




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Mikkel Andreas Jørnson Kvasnes



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Willow ptarmigan dynamics low population densities

Faculty of Applied Ecology and Agricultural Sciences

Mikkel Andreas Jørnson Kvasnes

PhD Thesis

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

PhD in Applied Ecology
2015

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Preface

I am very happy, and a little sad that my PhD-time and my life as a student is over! I am happy because I am finished with the thesis of course, and because I have learnt so much during the last five years. I am sad because I will miss the good times at Evenstad solving problems with colleagues, writing perfect sentences in English (even whole paragraphs sometimes), and I will miss all the challenges, such as statistics and major revisions of manuscripts!

I am deeply grateful to my supervisors Professor Torstein Storaas at Evenstad and Hans Christian and Erlend at the Norwegian institute of nature research (NINA) in Trondheim. You have all been incredibly patient. Torstein, first of all you helped me on to the “right track”, the *grouse track* when giving me the opportunity to work with capercaillie brood habitats in the “KONTUS” project. You rule as a professor in wildlife management and you are super-enthusiastic. Most importantly, you have the ability to spread your knowledge and enthusiasm to colleges and students as well. I will miss all the coffee breaks at the barn where we solved world problems (i.e., wildlife matters). Thank you for nagging me the last year; it really helped me to complete the thesis! Hans Christian and Erlend, thanks for letting me work with you at NINA whenever I needed it and for the interesting discussions. Hans Christian, thank you for sharing knowledge and stories from ~30 years of ptarmigan research and thanks to you and Kari for letting me stay at your home when I visited Trondheim. Erlend, you gave me a kick-start when you became my supervisor! During my PhD work, your hints, creative ideas and statistical expertise have been indispensable, and no matter how silly my questions were, you answered me fast and thorough with conscience.

I will also thank the staff at campus Evenstad, particularly Harry P. Andreassen and Torstein Storaas for giving me the opportunity to work with the most interesting and good tasting bird in the world and Håkon Solvang for providing me with all the survey data I needed for my thesis. Thanks to all my fellow PhD students for interesting discussions, inspiration and for your good mood! Thank to my fellow PhD- (and master) students, especially the ptarmigan-enthusiasts Petter Glorvigen and Oddgeir Andersen for co- teaching, co-authoring and co-driving to Evenstad!

The thesis was greatly improved by helpful comments from Torstein Storaas, Hans Christian Pedersen, Erlend Nilsen and Jos Milner.

Thanks to my family: my parents for introducing me to the outdoor life and the interest for wildlife and my parents, sisters and in-laws for help and support to our little family during the last rather hectic years.

My beautiful, patient and caring wife Elise: You supported me when I struggled (that was quite a few times). I could not have finished this thesis without your care for our children and me. Birk, Syver and Lotta, our wonderful children, thank you for spicing up our lives, for being curious, for asking all kinds of questions – don't stop that!

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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 hønsfugler 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 populasjon 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 / km² 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 påvirker 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 smånager 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 smånagertetthet 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 smånagertetthet. Dette kan forklares av kollapsen i de regulære smånagersyklusene etter 1990-tallet. Hvis lirypas populasjonsdynamikk var knyttet til smånagersyklusen gjennom felles predatorer, kan dette båndet ha blitt svekket nå når smånagersyklusen 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 smånagersyklusen. 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/km², 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 re-nesting 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).

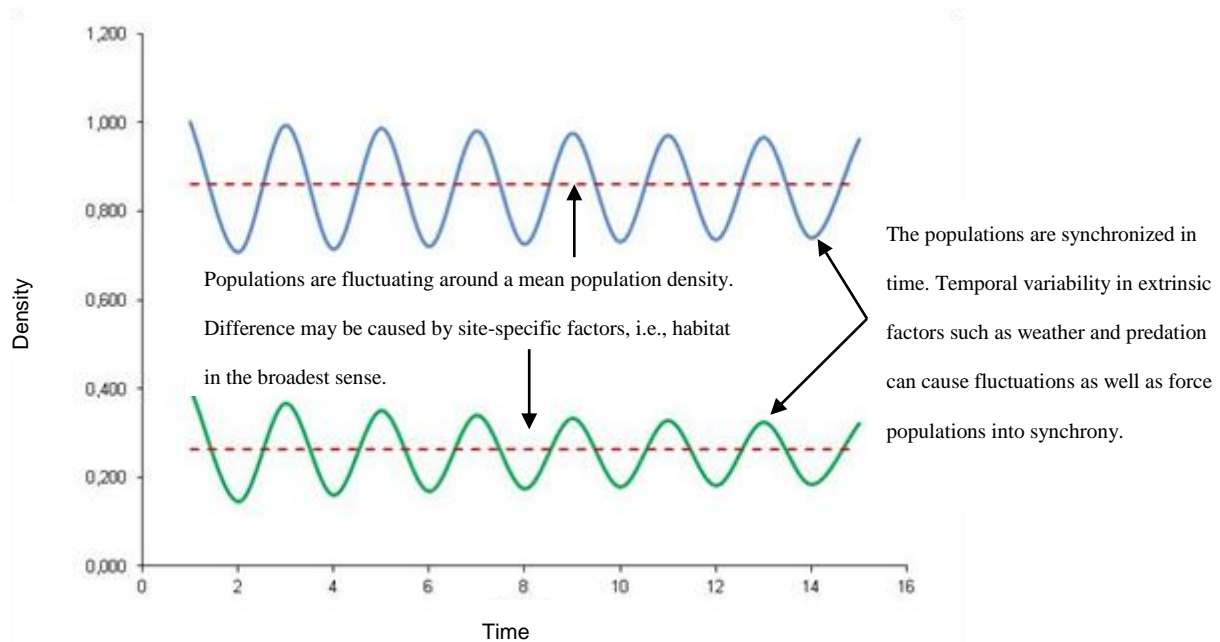


Figure 1 Illustration of two populations fluctuating in synchrony around different mean densities (*broken lines*)

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 temporarily 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, $b \rightarrow 0$ implies a uniform distribution, $b=1$ suggests a random distribution and $b \rightarrow \infty$ 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 $b \approx 2$ 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 $b \approx 2$. 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 predation 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 re-nesting can potentially increase the yearly recruitment in a population (Parker, 1985; Martin et al., 1989). The probability of re-nesting 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 re-nested had larger eggs in their first clutch than females that did not re-nest, suggesting that re-nesting probability could be related to female quality. Similarly for a larger tetraonid, the Capercaillie *Tetrao urogallus*, re-nesting increased recruitment (Storaas et al., 2000) and re-nesting 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/km² (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/km². Pedersen (1988) reported densities of territorial cocks of between 12 and 24 cocks/km² 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/km² (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 2). 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.

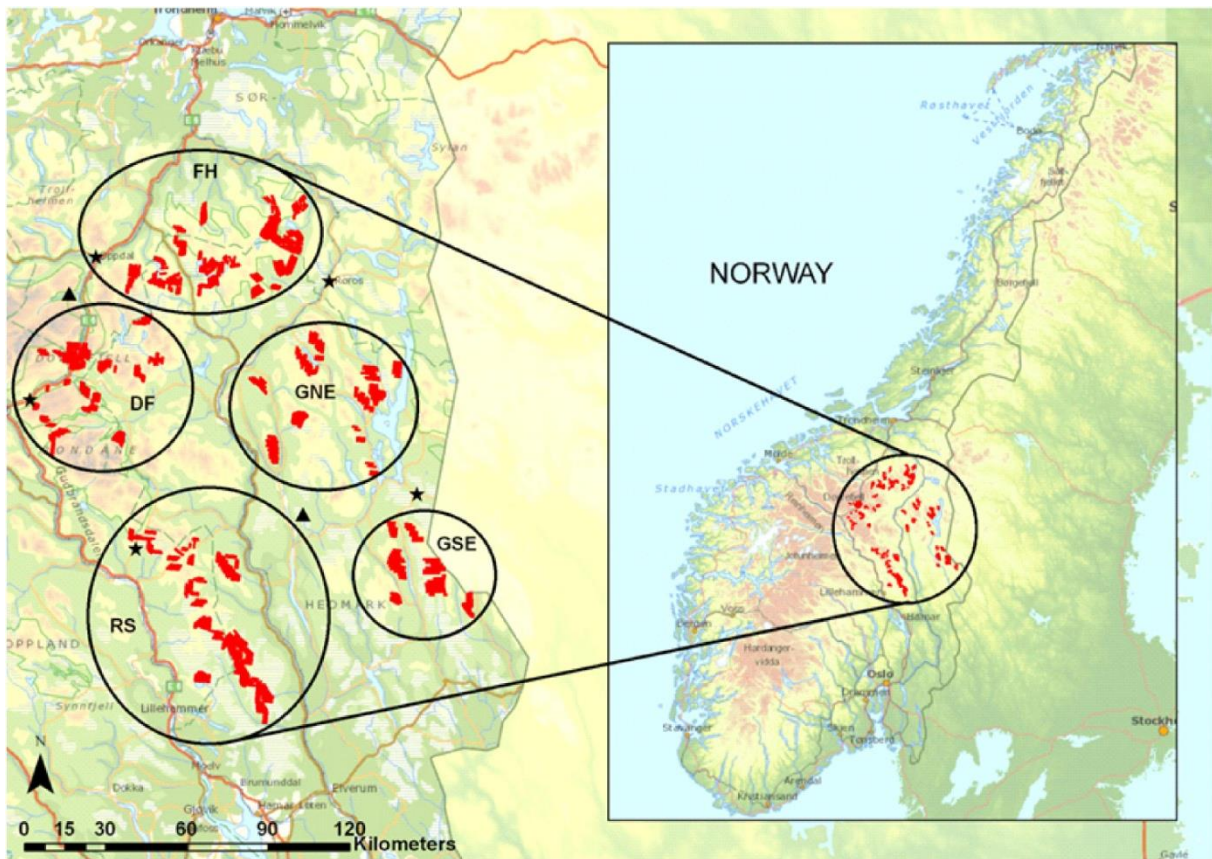


Figure 2 Study areas (*filled polygons*) within mountain regions (*open circles*) in south-central Norway used in paper I, II and IV. *RS* Rondane, *DF* Dovre and Follidal, *FH* Forrollhogna, *GNE* Glomma north-east, *GSE* Glomma south-east. The *filled stars* and *triangles* are the positions of meteorological stations and rodent trap sites used in paper IV, respectively.

Survey areas were clustered within five geographically separated mountain regions, 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/km²) 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) .

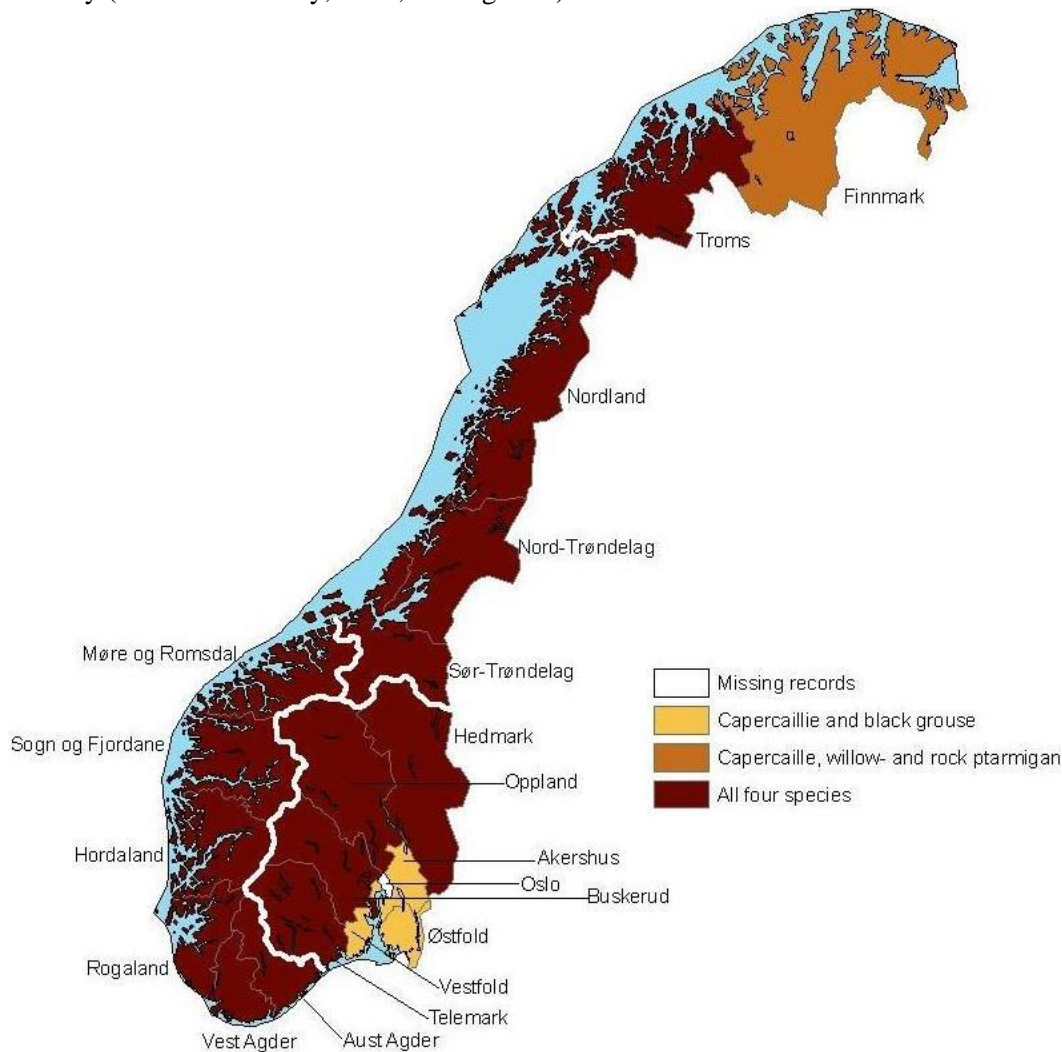


Figure 3 Map of the study area used in paper III. Colors indicate the species with hunting records included in the analysis. Thin white lines depict borders between counties. Solid white lines depict borders between regions (region east at the right, region west at the left, centre region in the middle 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

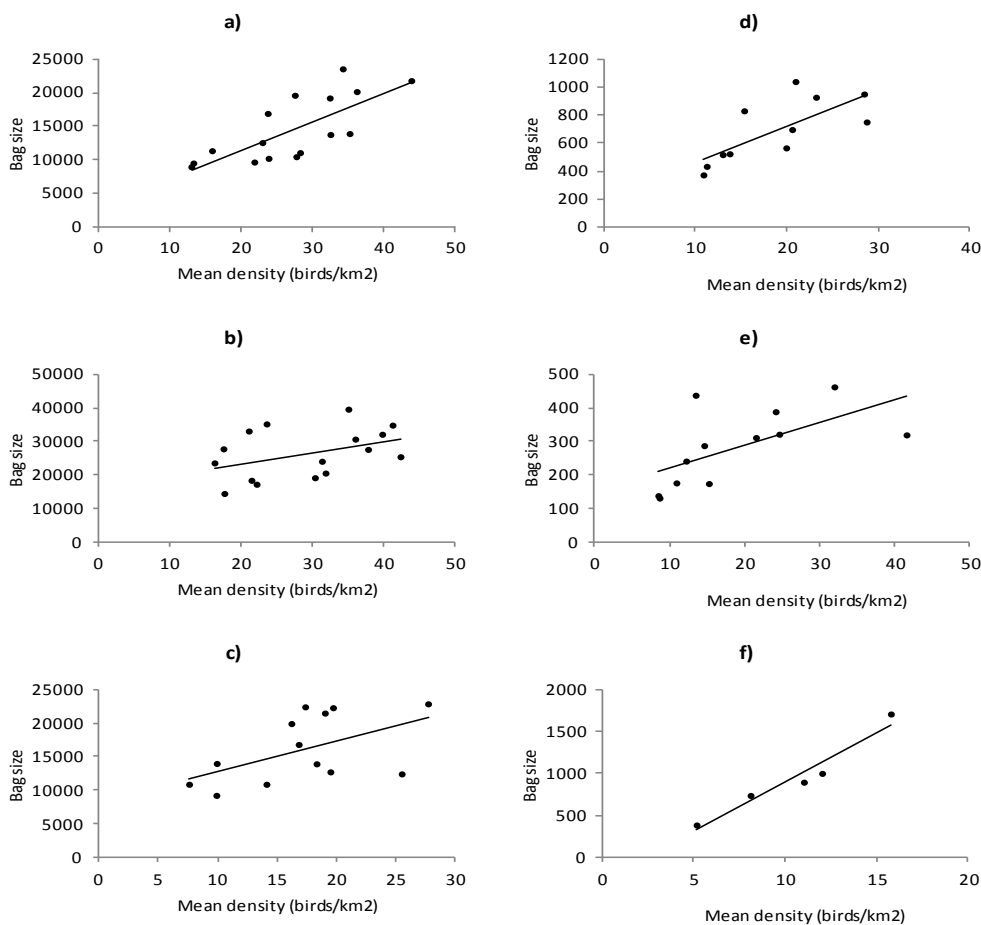


Figure 4 Hunting bag size as a function of mean density. *a – c* county-wise bag statistics and mean density from line transect surveys in *a* Hedmark county, *b* Sør-Trøndelag county, *c* Oppland county. *d* Bag statistics from Trysil fellesforening and line transect survey data from four areas within 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 transect 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 ± 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 ± 8.00 , $F_{1,9} = 10.37$, $p = 0.01$, Ringsaker: slope \pm SE 6.83 ± 2.77 , $F_{1,10} = 6.09$, $p = 0.03$, Ringebu: slope \pm SE 117.12 ± 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 (Table 1).

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 Snowbeds (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.

<i>Original vegetation type (classification nr)</i>	<i>Mean (median)</i>	<i>Pooled vegetation types</i>	<i>Mean (min-max)</i>
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)		
<i>Lowland forest (1-5)</i>			<i>0.043 (0.000-0.190)</i>
<i>Other (21-25)</i>			<i>0.005 (0.000-0.056)</i>

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/km², with the highest survey-area mean density being 91.8 birds/km² and the lowest being 8.2 birds/km². The mean density of adult birds and reproductive success were 7.8 adults/km² (highest mean: 25.3 adults/km², lowest mean: 2.2 adults/km²) and 4.8 juveniles/pair (highest mean: 6.4 juveniles/pair, lowest mean: 3.0 juveniles/pair), respectively (Figure 5).

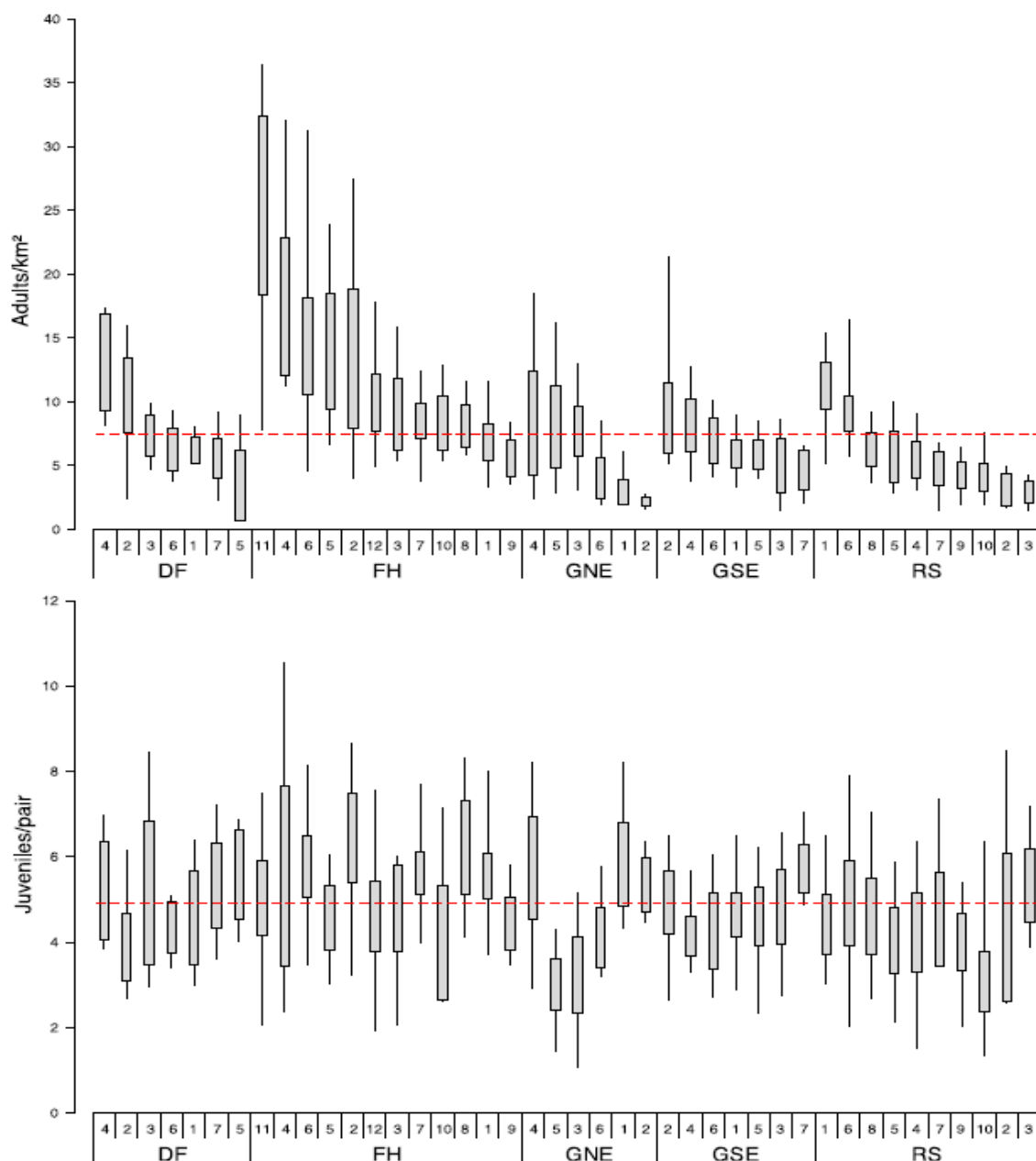


Figure 5 Boxplots of density of adult birds (*top*) and reproductive success (*bottom*) in the survey areas in south-central Norway. Survey areas are ranked within mountain regions by density of adults from left to right. *Boxes* represent the 95 % confidence intervals of the mean with upper and lower 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

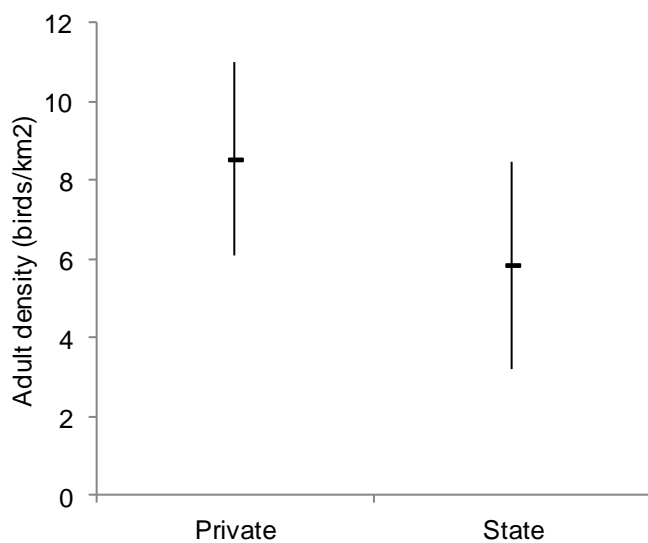


Figure 6 Mean adult density and 95 % confidence intervals for survey areas managed by private landowners (*Private*) or survey areas managed as common land (*State*).

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 Δ AICc units, Table 2a) explaining adult

density included 1) a model with the effect of land ownership where private

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/km², 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 Δ AICc 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 Δ AICc 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

<i>Variables</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	Δ <i>AICc</i>	<i>AICc weight</i>
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

<i>Variables</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	Δ <i>AICc</i>	<i>AICc weight</i>
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

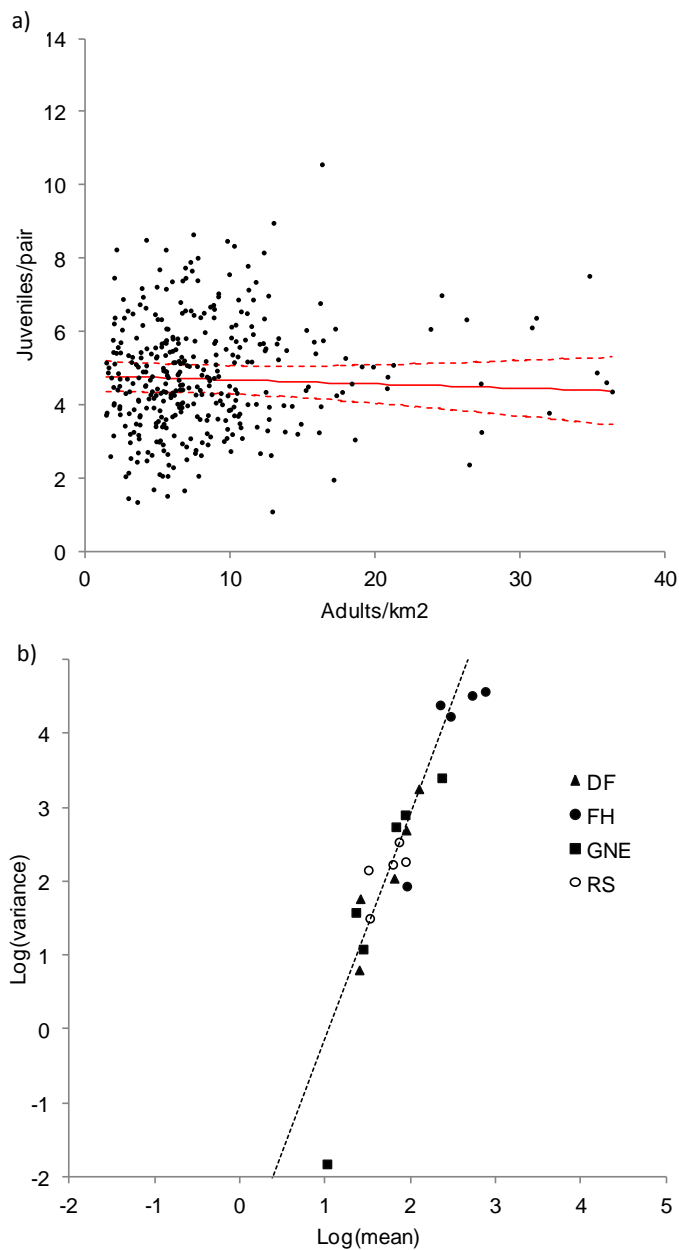


Figure 7 a) The relationship between survey area densities of adult birds and reproductive success. The *solid* and *broken lines* represent the estimated slope and 95 % confidence intervals. b) Logarithm of spatial variance in density of adult birds within mountain regions. The *solid line* is fitted 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 where 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

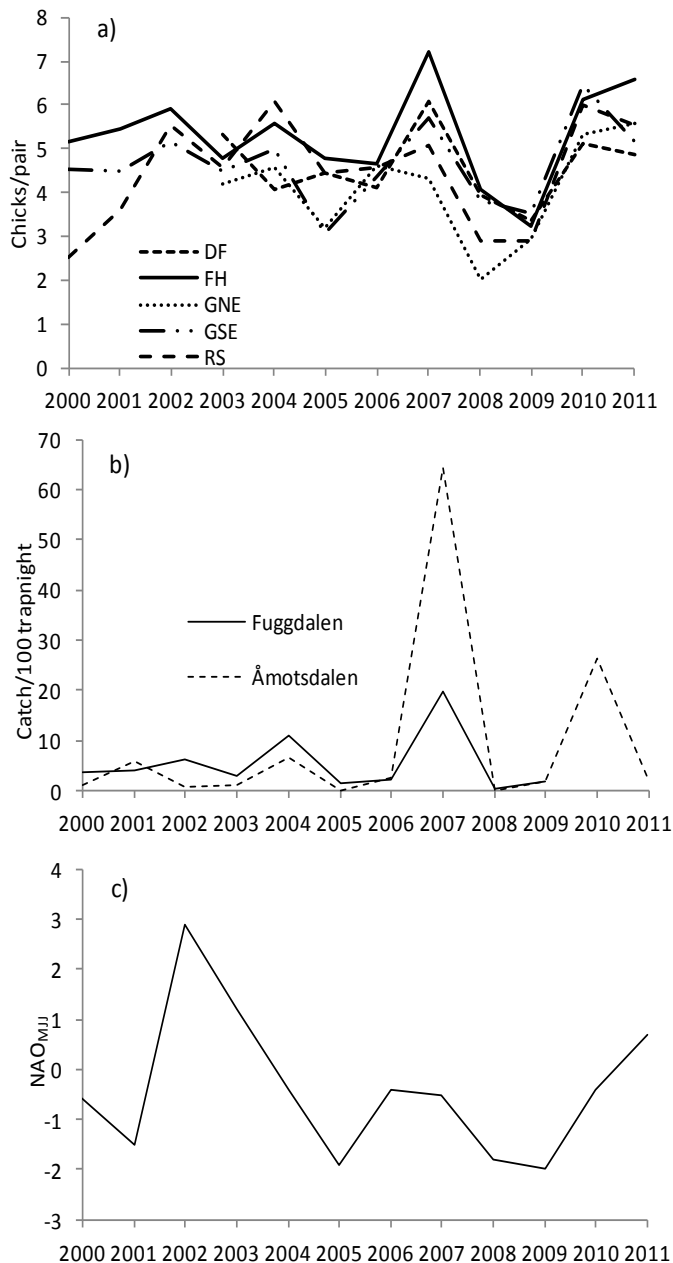


Figure 8 a) Reproduction (juveniles/pair) in mountain regions, b) standardized rodent abundance indices from Åmotsdalen and Fuggdalen (c.f. figure 2) and c) the seasonal NAO index for May, June and July, all in the period 2000 – 2011. In a) RS Rondane, DF Dovre and Follidal, FH Forrollhogna, GNE Glomma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

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 8a) 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

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 indicates 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 (Figure 9). Also within precipitation-defined regions and within counties, I

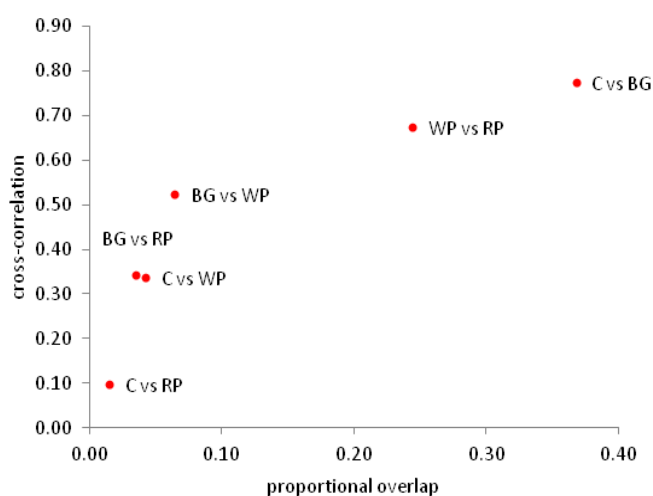


Figure 9 Synchrony plotted against distribution overlap index between tetraonid species in Norway. *C* capercaillie, *BG* black grouse, *WP* willow ptarmigan, *RP* rock ptarmigan.

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

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 \pm SE; mountain region scale: $NAO_{MJJ} = 0.53\pm 0.10$, Rodent = 0.03 ± 0.01 and survey area scale: $NAO_{MJJ} = 0.54\pm 0.08$, Rodent = 0.03 ± 0.01 , c.f., Figure 8b and 8c).

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 probability 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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Paper I

Spatial distribution and settlement strategies in willow ptarmigan

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Abstract In heterogeneous landscapes individuals select among several habitat patches. The fitness rewards of these choices are assumed to play an important role in the distribution of individuals across landscapes. Individuals can either use environmental cues to directly assess the quality of breeding sites, or rely on social cues to guide the settlement decision. We estimated the density of adult birds and per capita reproductive success of willow ptarmigan over 5–15 years in 42 survey areas, nested within 5 spatially separated populations in south-central Norway. Our aims were to (1) examine spatial and temporal patterns of variation in densities of adult birds (i.e., the breeding densities) and reproductive success (juveniles/pair) measured in autumn and (2) evaluate which habitat distribution model best described the distribution of willow ptarmigan across heterogeneous

mountain landscapes. Variation in density of adult birds was primarily attributable to variation between survey areas which could arise from spatial heterogeneity in adult survival or as a consequence of spacing behavior of juveniles during the settlement stage. In contrast, reproductive success was more variable between years and did not vary consistently between survey areas once year effects were accounted for. The lack of any relationship between the density of adult birds and reproductive success supported the predictions of an ideal free distribution (IFD), implying that within years, the mean reproductive success was approximately equal across survey areas. However, analysis based on Taylor's power law (i.e., the relationship between logarithms of spatial variance and mean density of adult birds) suggested that aggregation was stronger than expected under IFD. This implies that the relative change in density of adult birds was larger in areas with high mean densities than in areas with low densities. The exact mechanisms causing this statistical pattern are unclear, but based on the breeding biology of willow ptarmigan we suggest that yearlings are attracted to areas of high densities during the settlement period in spring. Our study was conducted during a period of low overall density and we suggest that this pattern might be particular to such situations. This implies that the presence of conspecifics might represent a cue signaling high adult survival and thus high habitat quality.

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Introduction

Spatial heterogeneity in habitat quality is known to be a potent source of between-individual differences in fitness

(Fretwell and Lucas 1969; Erikstad 1985; Andren 1990; Calsbeek and Sinervo 2002; Nilsen et al. 2004). The quality of a given habitat is shaped by the combined effects of resource availability (food and shelter) and environmental conditions (abiotic variables such as temperature and biotic variables such as competitors and predators) (Sinclair et al. 2006). Generally, when individuals settle in a given site at moderate to high densities, both 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). Consequently, as density of the focal species increases, density dependence may offset the individual benefits of inhabiting seemingly high quality habitats (Fretwell and Lucas 1969; Morris 2003). However, at low densities, positive interactions among settlers may occur (e.g., Allee effects after Allee 1938) resulting in positive fitness effects with increasing density (Greene and Stamps 2001).

In heterogeneous landscapes individuals select among habitat patches or units of land of varying quality. The fitness rewards of these patches are assumed to play an important role in the distribution of individuals across landscapes (Fretwell and Lucas 1969). To this end, several models have been suggested to explain the distribution of individuals under different conditions (Fretwell and Lucas 1969; Pulliam and Danielson 1991). When applied to breeding-habitat selection, the ideal free distribution model (IFD) predicts that individuals should be distributed in proportion to the amount and quality of the habitat, so that all individuals have equal access to resources causing reproduction to be equal at all sites (Fretwell and Lucas 1969; Milinski 1979). The ideal despotic distribution model (IDD) predicts a hierarchical distribution where 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 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 be similar models despite a major difference in the mechanism (despotism with and preemption without aggressive behavior) (Holmes et al. 1996; Pöysä 2001; Manning and Garton 2013). All three models assume that the individuals are "ideal" in the sense that they are omniscient and select the best option available. Consequently, the spatial arrangement of individuals across the landscape and the spatial distribution of vital rates should be related to the quality of habitat patches throughout the landscape, but the actual relationship is predicted to vary depending on the model that determines the settlement process.

When settling on their breeding grounds, many species use environmental cues to assess the quality of the physical environment (Muller et al. 1997; Campomizzi et al. 2008). If intrinsic habitat quality is important during settlement, then the density of adult individuals and habitat quality should be correlated across the landscape. However, in human-modified landscapes, the ability to recognize site quality or utilize high quality sites may be hampered if the cues used for selecting habitats are corrupted (McClaren et al. 2002; Battin 2004; Bock and Jones 2004). Furthermore, when individuals use environmental cues and the settlement patterns follow IDD or IPD, an ecological trap may occur if high numbers of individuals are forced to aggregate in low quality sites (Van Horne 1983). Many species also rely on social cues during settlement, with settlement patterns being positively affected by the presence or abundance of conspecifics, i.e., conspecific attraction (Stamps 1988; Danchin and Wagner 1997; Pöysä 2001; Ward and Schlossberg 2004; Farrell et al. 2012), or by conspecific reproductive success (Danchin and Wagner 1997; Doligez et al. 2003). The use of either environmental or social cues in settlement decisions can cause aggregated distributions (Stamps 1988; Danchin and Wagner 1997; Doligez et al. 2003) that may have significant impacts on species persistence and conservation (Reed and Dobson 1993; Reed 1999).

The willow ptarmigan (*Lagopus lagopus* Linnaeus, 1758) is a medium-sized tetraonid species distributed in alpine tundra habitats in the northern hemisphere. In Scandinavia, ptarmigan are hunted and bag size, as well as abundance, varies considerably in time and space (Solvang et al. 2007; Kvasnes et al. 2010; Statistics Norway 2013). Within their range, individual birds generally prefer habitats with a high density of food and cover from predators (Erikstad 1985; Bergerud and Gratson 1988; Schieck and Hannon 1993). Males are highly philopatric (Pedersen et al. 1983; Schieck and Hannon 1989; Brøseth et al. 2005) and in spring they defend breeding territories of 2–12 ha (Pedersen 1984). Females are less philopatric but are more likely to re-use a breeding area following a successful breeding attempt in the previous year (Schieck and Hannon 1989). Although some juveniles return to their natal area (Martin and Hannon 1987; Rørvik et al. 1998), most male and female juveniles disperse to other breeding grounds (Martin and Hannon 1987; Brøseth et al. 2005; Hörnell-Willebrand et al. 2014) in the period between brood break up in late September and the following spring (Bergerud and Gratson 1988). Thus birds newly establishing breeding territories in an area are most likely naïve juveniles dispersing from other breeding grounds within a radius of 2–20 km (Brøseth et al. 2005; Hörnell-Willebrand et al. 2014; but see Watson et al. 1994). Steen et al. (1985) were unable to find any vegetative features common to all

territories at breeding grounds in Norway, with broods leaving their territories shortly after hatching. After hatching, brood movements are focused on habitats rich in food, but broods remain within the general area of the natal territory (Andersen et al. 1986). This suggests that breeding territories are not selected on the basis of securing food for chicks after hatching and it has been suggested that the main function of the territory is to signal social status of the males (Steen et al. 1985). As snow usually covers the ground during the settlement period in spring it might be difficult for birds to assess habitat quality, and young birds might use conspecific abundance as a guide when selecting breeding territories (Stamps 1988; Pöysä 2001; Ward and Schlossberg 2004). However, it is not completely clear at what time of the year the actual territory selection occurs in willow ptarmigan, as cocks in southern Norway also display in late autumn before the ground is covered by snow (Pedersen et al. 1983). Old cocks display in their former area (Pedersen et al. 1983), but the role of old females and juvenile birds in autumn displays is not known.

Aggressive behavior during settlement and density dependent territory sizes might suggest some dominance hierarchy among willow ptarmigan males, in accordance with the IDD (Fretwell and Lucas 1969) or IPD (Pulliam and Danielson 1991). However, the relaxation of aggressive behavior after hatching might indicate that individuals are “free” during brood rearing, thus following an IFD (Fretwell and Lucas 1969). If conspecific attraction influences spacing patterns in willow ptarmigan, the resulting distribution would be predicted to be more aggregated than any of the above models predict (Pöysä 2001).

In this paper we used autumn line transect survey data to assess the spatial and temporal variation in density of adult birds (i.e., breeding population) and reproductive success in 42 survey areas distributed across five different mountain regions in south-central and eastern Norway. In particular, we examined the extent to which willow ptarmigan were distributed in agreement with the predictions of the IFD, IDD or IPD. To this end, we used two different approaches. First, we examined the relationship between survey area-specific estimates of adult density and reproductive success. The surveys were conducted in August before autumn dispersal so juvenile birds were assumed to be locally recruited within the survey area (Andersen et al. 1986). If individuals follow an IFD 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). Several studies suggest that when animals form an IDD or IPD, individuals aggregate at higher densities in high quality habitats and achieve higher success rates than individuals settling in low quality habitats at lower densities (Fretwell and Lucas 1969; Holmes et al.

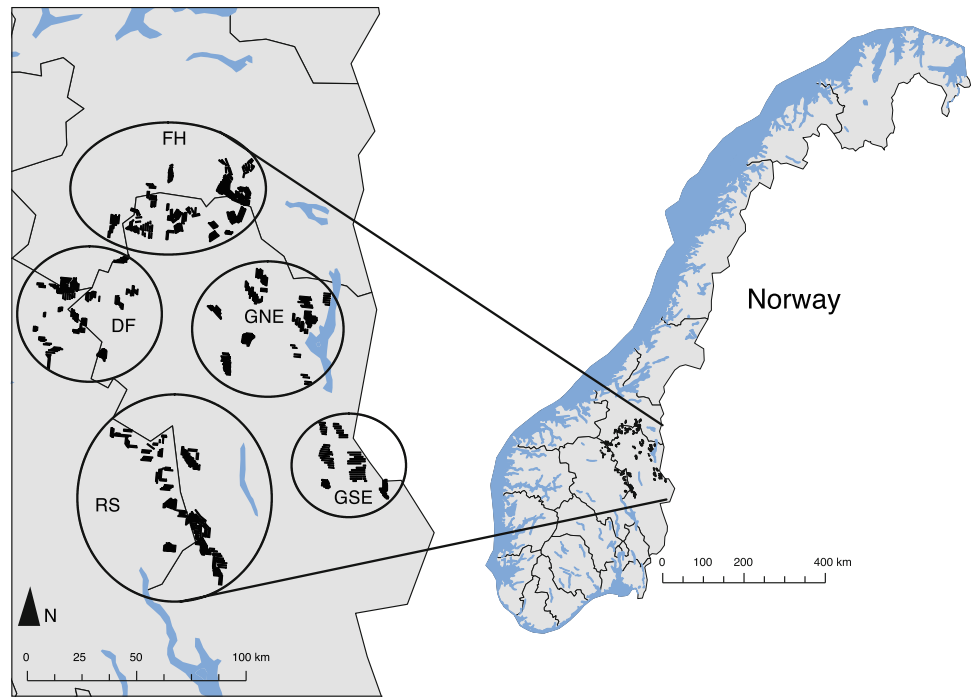
1996; Calsbeek and Sinervo 2002). In these situations one would expect a positive relationship between density of adult birds and reproductive success. In contrast, Skagen and Adams (2011) suggested that an IDD would generally generate a negative relationship between density and per capita fecundity (i.e., reproductive success). This could occur if many individuals were forced to settle in lower quality habitats (Van Horne 1983) either through despotism or preemption (Fretwell and Lucas 1969; Pulliam and Danielson 1991). Most importantly, a critical premise of an IDD or IPD, but not an IFD, is that reproductive success is correlated with density (Fretwell and Lucas 1969; Pulliam and Danielson 1991), either negatively (Skagen and Adams 2011) or positively (Fretwell and Lucas 1969; Holmes et al. 1996; Calsbeek and Sinervo 2002). Second, we used Taylor’s power law (TPL: Taylor 1961) to assess the levels of aggregation within mountain region populations. TPL states that the spatial variance in density increases as a power function of mean density, and that the function reflects the spatial distribution of the population (Taylor 1961). On a logarithmic scale this function becomes linear with the slope (b) considered by several authors to be a useful 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, $b \rightarrow 0$ implies a uniform distribution, $b = 1$ suggests a random distribution and $b \rightarrow \infty$ indicates a higher degree of aggregation. In Taylor’s pioneering work the slope b ranged from 0.7 to 3.1, with most values ranging from 1.0 to 2.0 (Taylor 1961). Gillis et al. (1986) showed theoretically that a slope $b \sim 2.0$ is in agreement with the predictions of an IFD, while a steeper slope ($b > 2.0$) indicates a higher level 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 $b = 2.0$ agrees with the predictions of an IFD, the TPL is not a conclusive test as other mechanisms might also cause $b \sim 2.0$. Following Gillis et al. (1986), $b = 2.0$ might imply that density changes proportionally among areas (i.e., resource matching). Further, $b > 2.0$ might indicate a disproportional change in density among samples, arising either from the attraction of juvenile birds to survey areas of high initial philopatric adult density or as a result of temporal changes in habitat quality.

Methods

Data collection

Line-transect surveys were conducted in August from 1996 to 2011 in up to 54 survey areas across south-

Fig. 1 Study areas (*filled polygons*) within mountain regions in south-central and eastern Norway (*RS* Rondane, *DF* Dovre and Folldal, *FH* Forollhogna, *GNE* Glomma north-east, *GSE* Glomma south-east)



central and eastern Norway (Fig. 1). Four areas were surveyed from 1996 onwards and new areas were subsequently added throughout the study period. Due to logistical constraints, not all areas were surveyed every year. Further, due to the sub-alpine distribution of willow ptarmigan, survey areas were geographically clustered within five mountain regions (Fig. 1). Each survey area was thus assigned to a mountain region based on its geographical location ($n = 5$, Fig. 1). Volunteer dog handlers with pointing dogs walked along predetermined transect lines and the free-ranging dogs searched the area on both sides of the line following the procedure of distance sampling (Pedersen et al. 1999, 2004; Buckland et al. 2001; Warren and Baines 2011). At each encounter, the number of birds (juveniles, adult males, adult females and birds of unknown age/sex) and the perpendicular distance from the line to the observed birds (m) were recorded. Pedersen et al. (2004) provide a detailed description of the sampling protocol, and previous experiments have shown that line transect distance sampling with pointing dogs is a robust method for estimating willow ptarmigan densities (Pedersen et al. 1999, 2004). The number of years in each survey area varied between 3 and 15 (median = 8), the number of areas surveyed each year varied between 4 and 51 (median = 30), the number of observations per year per survey area varied between 5 and 179 (median = 32) and the total transect length per survey area varied between 8 and 107 km (median = 33 km).

Statistical analysis

Density and recruitment assessment

Based on the survey data, we used multiple covariate distance sampling (MCDS) in the program Distance 6.0 (Thomas et al. 2010) to estimate half-normal detection functions and cluster densities (DS) in all survey areas and years (428 survey area–year combinations). Due to few observations in many survey area–year combinations, we opted to pool observations from all years for each survey area and use year as a covariate factor to account for possible variation in detection probability between years (Marques et al. 2007; Pedersen et al. 2012). The data were truncated at distances greater than the 95 % percentile in all analyses (Buckland et al. 2001). Following Buckland et al. (2001), we estimated cluster size (ES) 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 long distances (Pedersen et al. 1999). For the resulting 428 estimates of cluster density and cluster size, the unweighted geometric mean (min–max) coefficients of variation (CV %) were 27.4 % (16.2–49.6) and 16.4 % (9.7–27.8), respectively.

To obtain proper estimates of reproductive success (juveniles/pair) and density of adult birds (adults/km²) we estimated the proportion of juveniles and adults in each survey area and year. Due to missing information about the

age and sex of birds in some encounters, we omitted 23 survey area–year combinations when estimating the proportion of juveniles. Then we used mixed effects models with a binomial link function for each mountain region separately (Crawley 2007) to estimate the proportion of juveniles in the samples. We fitted a variable linking survey areas to years (called survey area–year) as a random intercept. This allowed us to estimate the proportion of juveniles (PJ) from each encounter for each year in all survey areas separately. As large clusters of birds are more likely to be detected at long distances (Pedersen et al. 1999), and larger clusters usually have higher proportions of juveniles than smaller clusters, we fitted distance from the line as a fixed effect (Buckland et al. 2001). To estimate reproductive success (number of juveniles/pair) we first estimated PJ : the proportion of juveniles in the sample estimated at the intercept (i.e., the back-transformed logit-value at the intercept), which corresponded to the proportion of juveniles on the line where detection probability ≈ 1 (Buckland et al. 2001). The number of juveniles/pair was then estimated as $PJ / \left[\frac{1-PJ}{2} \right]$. Finally, the density of adult birds was estimated as $DS \times ES \times [1 - PJ]$, where $DS \times ES$ is the total density.

Prior to further analysis, we excluded estimates from all survey area–year combinations that were lacking information about age and sex (23 survey area–year combinations) and that were based on <10 encounters (1 survey area–year combination). In addition we excluded survey areas with <5 years of data. Our final dataset consisted of 360 estimates of total density, density of adult birds and reproductive success (juveniles/pair) from 42 survey areas between 1996 and 2011. Density of adult birds in August was used as a proxy for the density of breeding birds in spring because mortality in adults is generally low from June to August (Sandercock et al. 2011). Juveniles/pair was used as a measure of per capita reproductive success. In the context of the analysis presented here, successful reproduction at time t in each survey area creates a pool of juvenile birds that will be distributed within the mountain region populations (Brøseth et al. 2005; Hörnell-Willebrand et al. 2014) in the period after our surveys until the next spring and will add into the populations at $t + 1$, i.e., next year's recruits to the breeding population.

Spatial and temporal variation

To investigate the spatial and temporal sources of variation in adult density and reproductive success, we conducted a variance components analysis. This allowed us to quantify the proportion of variation in each that was attributable to differences among mountain regions, survey areas and years (Crawley 2007; Nilsen et al. 2008; Kvasnes et al.

2010). Analyses were performed using mixed effects models, with mountain region (five levels), survey area (42 levels) and year nested within mountain region (16 levels) fitted as random intercepts. By nesting year in mountain region, we assumed year effects to be correlated within mountain regions but not among them.

Evaluation of distribution models

To test the predictions of IFD, IDD and IPD (see “Introduction”), we used a linear mixed effect model to assess the relationship between reproductive success (dependent variable) and adult density (independent variable). We used the same random structure as described above.

Finally, we used Taylor's power law (TPL: Taylor 1961) to assess the level of aggregation. Due to missing data (years) in some survey areas, we opted to create a new data set with no missing records to ensure that variances and means within each mountain region were calculated across the same set of survey areas in all years. Further, to ensure that variances and means were estimated across a sufficient number of survey areas we made a rule to maximize the number of survey areas having at least 5 areas in each mountain region and at least 5 years of data from each mountain region. This rule excluded one mountain region (Glomma south-east). Our final dataset for analyzing the TPL consisted of 4 mountain regions each including 5–10 survey areas covering 5 years (DF: 5 survey areas from 2007 to 2011, FH: 10 survey areas from 2005, 2007 to 2009 and 2011, GNE: 5 survey areas from 2005 to 2007 and 2009 to 2011, RS: 8 survey areas from 2006 to 2009 and 2011, for details see Electronic Supplementary Material). We calculated the spatial variation and the mean density of adult birds among survey areas within each mountain region. First we fitted linear mixed effect models with the log of spatial variance as the dependent variable, the log of mean density as a fixed effect and either mountain region as a random intercept or mountain region as both a random slope and a random intercept. The most parsimonious model describing the relationship was assessed with AIC_c , which is suitable when sample sizes are low as in our case (Burnham and Anderson 2002). Second, since the random effect term only consisted of four levels (i.e., four mountain regions) which is rather low for a random effect, we also fitted an ordinary linear regression model for the Taylor power law with mountain region as a fixed factor. The results from both models were compared and presented.

All statistical analysis were carried out in the program R (R Core Team 2012) using packages “lme4” for mixed models (Bates et al. 2011), and “AICcmodavg” for model selection (Mazerolle 2013).

Results

The unweighted geometric mean total density in the survey areas was 26.5 birds/km², with the highest survey-area mean density being 91.8 birds/km² and the lowest being 8.2 birds/km². The unweighted geometric mean density of adult birds and reproductive success were 7.8 adults/km² (highest mean: 25.3, lowest mean: 2.2) and 4.8 juveniles/pair (highest mean: 6.4, lowest mean: 3.0), respectively.

Survey areas differed in terms of the density of adult birds. The variance components analysis showed that survey area was the most important component explaining overall variance and accounted for more than three times the variation explained by year or mountain region (Table 1). This result is further supported by the area-specific boxplots in Fig. 2. In contrast, reproductive success varied more between years and less between survey areas and mountain regions (Table 1). This suggests that in a given year reproductive success does not differ much between survey areas or mountain regions but that some years are better than others across all survey areas and regions, i.e., reproductive success is spatially correlated. It is also worth noting that nearly half of the variance in reproductive success was attributable to factors not accounted for in the model (Table 1).

We found no clear relationship between adult density and reproductive success (slope \pm SE: -0.011 ± 0.015 , Fig. 3). When modelling reproductive success, the null model (i.e., with no fixed effects) was better supported, based on AIC_c, than a model with adult density fitted as a fixed effect (AIC_c with adult density: 1213.35 and AIC_c for null model: 1211.84). This is in contrast to the predictions of the IDD and IPD (negative or positive relationship), but supports the predictions of the IFD (no relationship).

Model selection based on AIC_c suggested that a mixed effect model with a random intercept was adequate to describe the relationship between the logs of spatial variance and mean density of adult birds (random intercept model; AIC_c = 46.99, random slope model; AIC_c = 54.49, respectively). As predicted by Taylor's power law, the log of spatial variance in density of adult birds increased with log density of adult birds (slope \pm SE:

2.83 ± 0.27). Similarly, the slope from the linear regression that included mountain region as a fixed factor was highly significant (slope \pm SE: 3.07 ± 0.42 , $F_{4,16} = 22.92$, $P < 0.001$, Fig. 4). The aggregation index b (i.e., the linear slope coefficient) suggested strong aggregation in willow ptarmigan within mountain regions, with the lower 95 % confidence limit above 2 (95 % LCL: mixed effect model 2.3 and linear regression: 2.2).

Discussion

In this paper, we have investigated the spatial distribution of willow ptarmigan in south-central Norway during a period of varying adult densities, and compared the observed distribution to well known models characterizing the distribution of individuals across a landscape (Fretwell and Lucas 1969; Pulliam and Danielson 1991). We found that the density of adult birds (representing density of breeding birds in spring) varied more between survey areas than between years and mountain regions, with some survey areas supporting consistently higher densities of willow ptarmigan than others. In contrast, reproductive success varied more between years and less between survey areas and mountain regions. Moreover, the lack of a clear relationship between area-specific densities of breeding birds and reproductive success supported the IFD (Fretwell and Lucas 1969; Skagen and Adams 2011), whereas the steep scaling coefficient of Taylor's power law suggested that the distribution of breeding birds was even more aggregated than expected under the IFD (Gillis et al. 1986).

Almost half of the variation in density of adult birds was attributable to variation between survey areas. If the local dynamics in the survey areas were mainly driven by local survival and reproductive success, then such patterns might arise because of spatial heterogeneity in survival or reproduction. However, the relatively limited spatial structuring of reproductive success indicates that local variation in reproductive success was not the key factor determining sustained variations in adult densities among survey areas. This is also supported by the fact that we did not find a positive relationship between local densities of adult birds and reproductive success. Survival rates may vary spatially as a consequence of local variation in the risk of harvest mortality (Smith and Willebrand 1999; Sandercock et al. 2011) or spatial variation in predation rates (Marström et al. 1988). Previous studies have also indicated that human activities might facilitate medium sized generalist predators (e.g., Kurki et al. 1998; Støen et al. 2010) which may increase predation on game species and thus affect local demographic rates (Marström et al. 1988) independently of intrinsic quality. Alternatively, spacing

Table 1 Percentage of variation in density of adult birds (adults/km²) and reproductive success (juveniles/pair) explained by the factors survey area, year and mountain region

	Survey area	Year	Mountain region	Residual (%)
Adults/km ²	41.8	12.3	8.6	37.3
Juveniles/pair	19.2	29.5	3.0	48.3

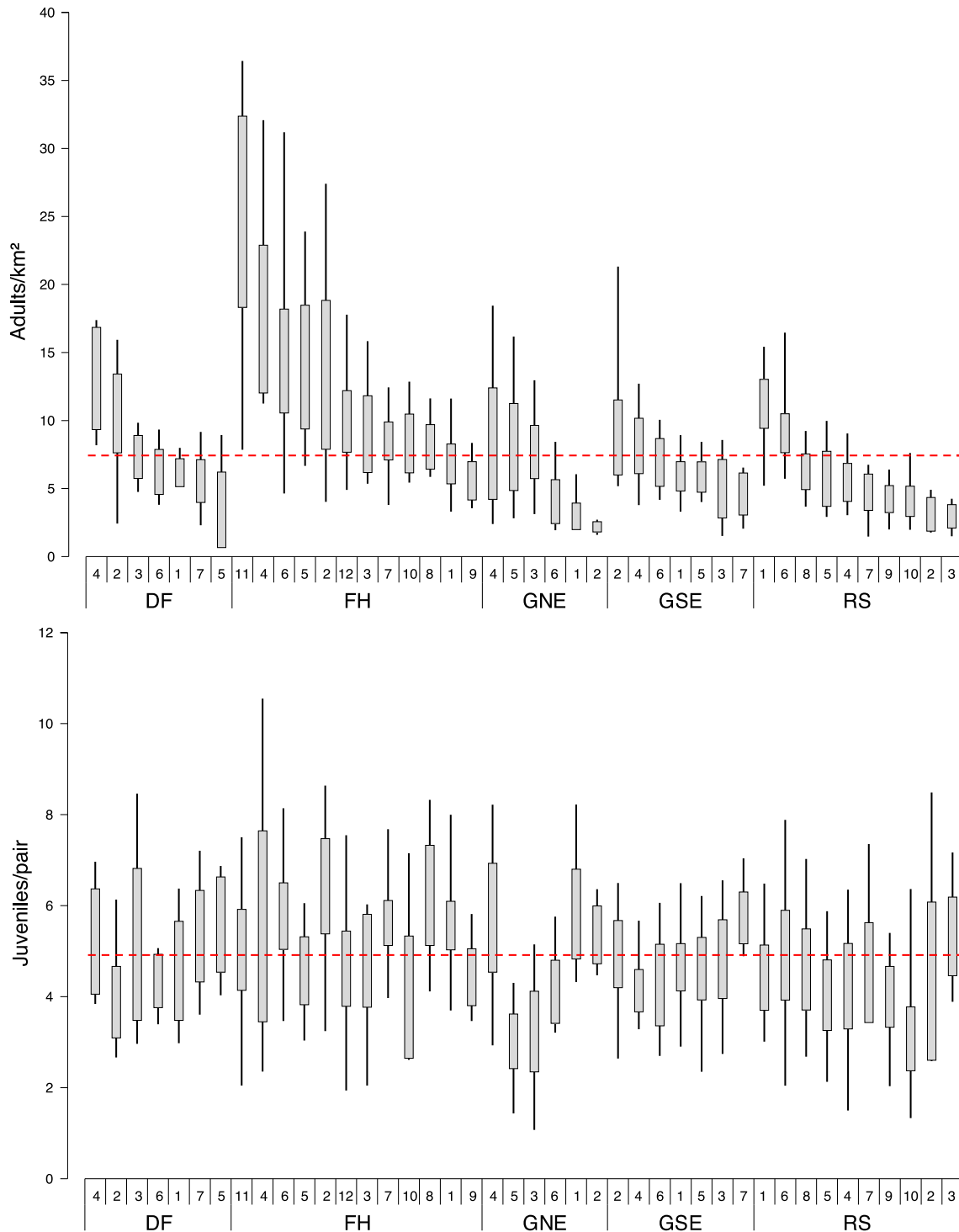


Fig. 2 Boxplots of density of adult birds (*top*) and reproductive success (*bottom*) in the survey areas in south-central and eastern Norway. Survey areas are ranked within mountain regions by density of adult birds from left to right. *Boxes* represent the 95 % confidence intervals ($\pm 2SE$) of the mean with upper and lower ends of the

vertical lines representing maximum and minimum values, respectively. The *horizontal broken lines* represent the overall mean density and reproductive success, respectively. *RS* Rondane, *DF* Dovre and Folldal, *FH* Forollhogna, *GNE* Glomma north-east, *GSE* Glomma south-east

behavior during settlement may cause variation in densities of breeding birds either because young birds select to settle in high quality survey areas using environmental cues (i.e.,

selecting for intrinsic habitat characteristics) or using social indicators (i.e., conspecific attraction) (Stamps 1988; Pöysä 2001; Ward and Schlossberg 2004).

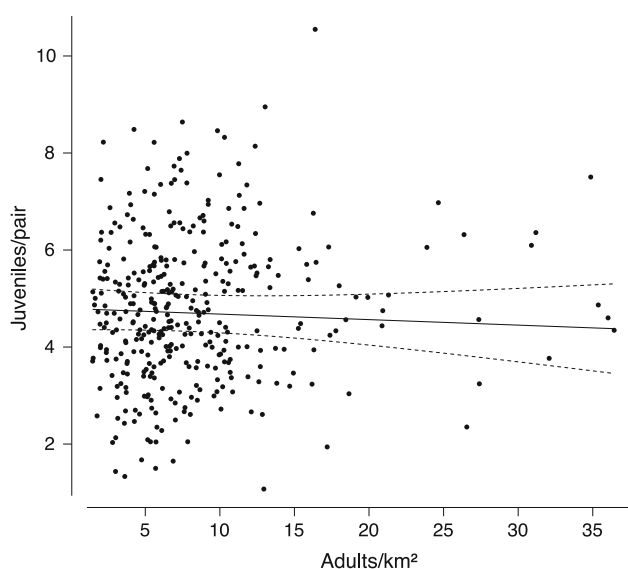


Fig. 3 The relationship between survey area densities of adult birds and reproductive success. The *solid* and *broken lines* represent the estimated slope and 95 % confidence intervals predicted by the mixed effects model, respectively

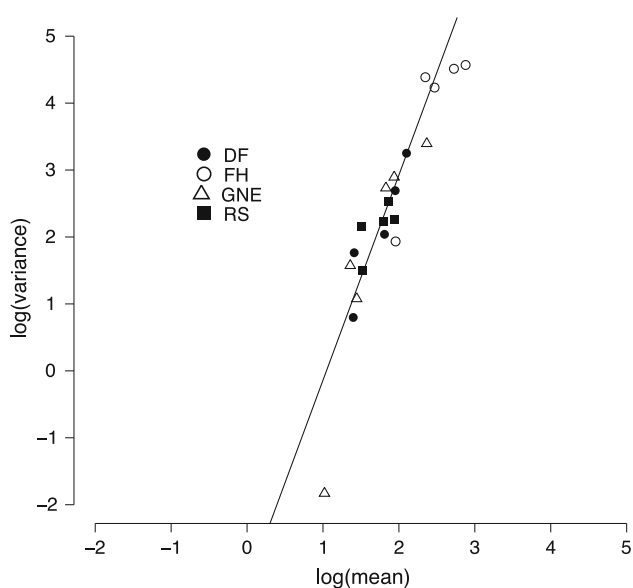


Fig. 4 Logarithm of spatial variance in density of adult birds plotted against logarithm of mean density of adult birds within mountain regions. The *solid line* is fitted from the linear regression model (for details see the “[Methods](#)” section) with slope (*b*)

Although spatial variation in reproductive success was obviously present, it was much smaller than the temporal variation caused by differences between years. Temporal variation in reproductive success of willow ptarmigan is not surprising given that reproduction has previously been shown to be sensitive to environmental variability in factors such as climate and predation (Steen et al. 1988; Martin and Wiebe 2004). These factors might vary between

years and are thus likely explanations for the temporal variation in reproductive success in our survey areas.

The lack of relationship between density of adult birds and reproductive success suggested that willow ptarmigan populations within mountain regions in south-central Norway are distributed in agreement with a resource matching distribution model. This would result in an equal per capita resource availability among survey areas of different quality, i.e., IFD (Skagen and Adams 2011), and an equal proportional increase or reduction in density of adult birds. A precise IFD would thus generate an exponent (*b*) of 2.0 in the relationship between the logs of spatial variance and mean density of adult birds (Gillis et al. 1986). However, with a scaling parameter above 2.0, our results suggest that willow ptarmigan within mountain region populations are more aggregated than would be expected under an IFD. The steep scaling parameter may imply that high density survey areas became increasingly crowded relative to low density areas, when the overall population density increased. Such breeding aggregations could arise by two different mechanisms. (1) Individuals are able to assess intrinsic habitat quality and aggregate in the best areas or (2) individuals settle in breeding areas using the abundance of philopatric adults as a guide. In the first case, breeding aggregations could occur if there were contemporary changes in intrinsic habitat quality causing high quality survey areas to be relatively more suitable compared to low quality survey areas. However, we have no reason to suspect that a disproportional change in habitat quality has occurred during our study. In an example of the second case, Pöysä (2001) found similar breeding aggregations in mallards (*Anas platyrhynchos* Linnaeus, 1758) where high quality areas became increasingly crowded when overall density increased. He suggested that the birds probably used presence of conspecifics as cues when selecting habitats.

Juvenile willow ptarmigan 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. During the period between brood breakup and the next spring, juveniles disperse and most will settle in a breeding area within their natal mountain region (mountain region as defined in this study, cf. the scale of Fig. 1) (Brøseth et al. 2005; Hörnell-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 occurred in spring they would have few opportunities to assess intrinsic habitat quality since the vegetation at that time is usually covered by snow. The majority of new breeders are naïve (1 year old) and may therefore use the abundance of surviving philopatric adults as a cue to assess habitat quality. Due to high levels of philopatry in adults, the spring density of

adults in a survey area may signal high survival probability or good reproductive prospects (Schieck and Hannon 1989). For naïve 1-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).

The aggregated distribution we observed in this study, whether caused by conspecific attraction or not, could be related to the fact that our studies took place during a period of low population densities. Densities of adult birds in our study varied from about 2–25 adults/km², which is much lower than previously reported densities in Norway. Myrberget (1988) reported densities of adult birds ranging from 19 to 172 pairs/km² on an island in northern Norway (1960–1980) while Pedersen (1988) reported densities of territorial cocks of between 12 and 24 cocks/km² in south-central Norway (1979–1986) (same area as DF in Fig. 1). This large difference in abundance also coincides with a significant long-term decline in Fennoscandian willow ptarmigan populations (Lehikoinen et al. 2014) and a marked reduction in national harvest bags in Norway (Statistics Norway 2013). This suggests that most populations in the present study are well below saturation. Greene and Stamps (2001) proposed that settling patterns may change with density, where individuals at low densities have fitness gains rather than reductions with increasing density (Fretwell and Lucas 1969), thus causing positive effects of conspecific interactions at low densities due to Allee effects. Using simulations, Greene and Stamps (2001) showed that Allee effects could generate aggregated distributions even if all habitat patches had the same intrinsic quality.

To our knowledge, social cues have not been considered before when studying willow ptarmigan habitat relationships to predict occurrence and habitat selection across landscapes (Erikstad 1985; Kastdalen et al. 2003; Henden et al. 2011; Ehrich et al. 2012). The role of social cues in habitat selection in general might be more important than previously recognized, and for many species it might be the most influential factor affecting habitat selection (Danchin et al. 2004; Campomizzi et al. 2008), especially for new settlers (Muller et al. 1997). Since little is known about the role of social cues in willow ptarmigan distribution, especially conspecific attraction, they should be considered in future habitat modeling attempts (Campomizzi et al. 2008). The use of conspecifics as cues in the settlement process could also have important implications for the management of harvested populations. If conspecific attraction is operating in willow ptarmigan through the abundance of philopatric adults, management areas with higher adult survival rates (possibly achieved through sustainable harvest rates) may benefit through increased attractiveness, independently of intrinsic habitat quality.

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Paper II

Vegetation Type and Spatial Variation in Demography of Low Density Willow

Ptarmigan Populations

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ABSTRACT: The willow ptarmigan (*Lagopus lagopus*) is an economically important and highly desired game species in Scandinavia. Its abundance varies considerably in time and space, but there has been a long-term decline over recent decades. Earlier studies demonstrated willow ptarmigan strongly select for certain habitat features. We investigated the relationship between area-specific conditions (habitat and harvesting regime) and two variables describing willow ptarmigan demography (adult density and reproductive success). We found no connection between adult density and cover of different six vegetation types. However, willow ptarmigan had lower reproductive success in areas dominated by mountain birch (*Betula pubescens*) forest. The lack of any clear association between willow ptarmigan density and its habitat could be explained by relatively low population densities in our study areas. Thus, relative to years with higher population levels, resources (food and shelter) were plentiful and competition was low. We found strong indications in areas of similar vegetation composition, that adult density was higher in areas managed by private landowners than on state-owned land. The difference in density was 2.56 birds/km², equivalent to 46% of the adult density on state-owned land. This appeared to be due to a consistent difference in hunting pressure. We conclude that habitat management will have little effect on willow ptarmigan populations during periods of relatively low densities.

KEY WORDS: habitat selection, hunting pressure, *Lagopus lagopus*, landownership, Scandinavia, willow ptarmigan

Loss and degradation of habitat are currently the greatest threats to the persistence of viable wildlife populations (Groom 2006). Identifying habitat characteristics that improve the distribution and abundance of wildlife species is a central task in wildlife management and conservation. Habitat quality is mainly affected by a suite of environmental conditions such as

temperature, precipitation, competitors, predators, and the availability of resources such as food and cover (*c.f.* Sinclair et al. 2006).

Measures of demography or distribution in relation to habitat attributes, especially vegetation, are frequently used to assess habitat quality for birds (Johnson 2007). Habitat quality assessments may then be based on (1) observations of positions where individuals are found such as habitat selection models (Resource selection functions) (Manly et al. 2002, Kastdalen et al. 2003 [willow ptarmigan], Nelli et al. 2013 [rock ptarmigan, *Lagopus muta*) or (2) relationships between demographic parameters of a species in different areas and the vegetation structure and/or composition (e.g., black grouse [*Tetrao tetrix*], capercaillie [*T. urogallus*], Lande et al. 2013, [roe deer, *Capreolus capreolus*] Nilsen et al. 2004). These approaches assume that individuals settle at higher densities and reproduce better in certain habitats, which may be identified by vegetation structure and/or composition.

The willow ptarmigan is a popular and economically important game species in Scandinavia. Willow ptarmigan population sizes vary considerably in time and space, but over recent decades there has been a long-term decline in abundance (*c.f.* Myrberget 1988, Pedersen 1988, Kvasnes et al. 2014b, Lehikoinen et al. 2014). There are indications that willow ptarmigan at both the population- and individual-scale are highly selective of certain areas or habitats. Densities in some areas consistently fluctuate around a higher mean density than in others (Kvasnes et al. 2014b), and single birds or broods are not randomly encountered with respect to habitat characteristics (Kastdalen et al. 2003, Lande 2011). Consistent difference in abundance between areas over time (Kvasnes et al. 2014b) can be attributed to both active habitat selection and spatial variation in survival rates that are not related to the physical habitat. Harvesting has been shown to reduce yearly survival of willow ptarmigan (i.e., additive to natural mortality; Smith and Willebrand 1999, Pedersen et al. 2004, Sandercock et al. 2011). Thus, consistent variation in harvest rates is a potential source for

variation in density. Landownership might also be a factor causing variation in density among areas as hunting intensity is often considered to be lower on privately- than on state-owned land (e.g., Pedersen and Storaas 2013).

Variation in predation rates can alter the survival of birds independently of vegetation composition and structure (Marcstrom et al. 1988). Habitat selection by individual willow ptarmigan has been evaluated at different spatial scales and it has been suggested that birds aggregate in specific vegetation types or areas (Andersen et al. 1984, Kastdalen et al. 2003, Henden et al. 2011, Lande 2011, Ehrich et al. 2012). Willow (*Salix* spp.), thickets, bogs and dwarf birch (*Betula nana*) have all been identified as important factors affecting willow ptarmigan distribution (Kastdalen et al. 2003, Henden et al. 2011, Ehrich et al. 2012). The level of saturation of a population can potentially affect distribution across the landscape (Greene and Stamps 2001) and the habitat selection process. Kvasnes et al. (2014b) suggested the aggregation in Norwegian willow ptarmigan populations could be affected by conspecific attraction (Stamps 1988). The use of conspecifics as 'guides' during settlement can cause preferred vegetation structures to remain unoccupied reducing the predictability of habitat models (Campomizzi et al. 2008).

Recruitment rates in willow ptarmigan are usually studied as time series and have been related to temporal variation in weather conditions or predation rates (Slagsvold 1975, Steen et al. 1988, Martin and Wiebe 2004, Kvasnes et al. 2014a). However, Erikstad (1985) found evidence of higher brood survival of broods in areas with high larvae densities, and Andersen et al. (1984) found a preference for eutrophic bogs, habitats which also contained more insect food than other habitat types. Moss and Watson (1984) found higher recruitment rates for the Scottish rock ptarmigan, an ecologically similar species, in areas overlying base-rich bedrock, suggesting a habitat effect on recruitment. Kvasnes et al. (2014b) found that recruitment rates

in willow ptarmigan populations varied more between years than between areas, and that area-specific factors had a small but significant role.

We investigated the relationship between habitat, expressed as vegetation types, and two demographic variables; density of adults and reproductive success. Earlier studies in Norway have shown that individual willow ptarmigan and their broods prefer moist sites and those with dense field vegetation (Andersen et al. 1984, Steen et al. 1985, Kastdalen et al. 2003, Henden et al. 2011). This suggests these vegetation types are selected based on food availability and cover (Bergerud and Gratson 1988). We predicted that (1) survey areas vary in terms of vegetation composition and (2) this partly explains the observed spatial variation in adult densities and reproductive success. We predicted that (3) privately-owned areas have higher densities than state-owned land due to differences in harvesting regimes. Reproductive rates generally show less spatial variation and are not correlated with adult density (Kvasnes et al. 2014b), and we also predicted that (4) a possible effect of vegetation composition on recruitment rates different from that affecting adult density.

STUDY AREA

Line-transect surveys were conducted in August 1996 to 2011 in 53 survey areas across south-central and eastern Norway (Fig. 1). The survey methods, including study design, sampling protocols, and the estimation of population parameters are described in detail by Kvasnes et al. (2014b). The survey data initially consisted of 428 survey area–year combinations of adult density (birds/km²) and reproductive success (juveniles/pair), but we excluded 78 survey area–year combinations due to missing data or few observations or few years with data (Kvasnes et al. 2014b). The final data set included 350 estimates of adult density and reproductive success (juveniles/pair) from 40 survey areas in the 1996 to 2011 period. The survey areas were geographically clustered within five mountain regions (Fig. 1). We

assigned survey areas to a mountain region based on geographical location ($n = 5$, Fig. 1) to account for this spatial distribution.

METHODS

Vegetation variables

All surveys were conducted within willow ptarmigan management units (estate boundaries or management boundaries within estates). The transect lines did not perfectly fit the boundaries surveyed and we defined a survey area as within 250 m of each transect line. A buffer of 250 m on either side of the transect gave little overlap between neighboring lines as most lines in a survey area were 500 m apart (one line every 500 m north-south or east-west direction on a 1 x 1 km grid, *cf.* Kvasnes et al. 2014b). We intersected the transect areas of each survey area with a vegetation map (Johansen 2009, Johansen et al. 2009; SatVeg). This map consisted of 25 generalized vegetation types that cover Norway at a spatial resolution of 30 x 30 m. Ten vegetation types are classified as “alpine ” (Johansen et al. 2009) (classification # 12-21), but “forest vegetation types” (classification # 1-8) and “mire and open swamp vegetation” (classification # 9-11) are also present in the survey areas (Table 1). Each cell of 30 x 30 m was classified to the dominant vegetation type (Johansen 2009). The proportional cover of each vegetation type within all survey areas was estimated based on total area surveyed and total area of each vegetation type in the surveyed area.

Earlier studies of willow ptarmigan showed that in general, broods and individual birds select sites on the basis of availability of food and cover (Andersen et al. 1984, Erikstad 1985, Bergerud and Gratson 1988). It is reasonable to assume, at the scale of our survey areas (8–51 km²), that variation in the proportional cover of vegetation types that provide food and cover, would affect demographic rates. We pooled vegetation types into 6 groups with similar attributes to reduce the number of vegetation variables without losing variation in expected density of food and cover (Table 1). The surveys were mainly conducted in sub-alpine areas

and it was reasonable to assume that the forest vegetation types with birch (classification # 6-8, Table 1) were mountain birch (*Betula pubescens czerepanovii*) forests near tree-line. We pooled vegetation classes dominated by birch (MB), and did not consider other forest types (classification #s 1-5, Table 1). Birch forest is traditionally not considered as preferred summer habitat, but the canopy may serve as cover against avian predators, and nutrient-rich versions of these vegetation types, interspersed with mires and swamps, may provide food for both chicks and adults (Andersen et al. 1984, Steen et al. 1985). The three mire- and swamp vegetation types are separated by a moisture gradient where shrubs, willows and heath (*Caluna* spp.) are more abundant in the driest types (# 9-10) and graminoids are dominant in the wettest type (# 11) (Johansen et al. 2009). We pooled the first two into a new variable called bogs with a dense field layer (BDF) and used the latter as a variable representing swamps and bogs with a sparse field layer (BSF). Treeless areas above tree-line (classification #. 12-21) were pooled into three variables: (1) sparsely vegetated areas such as ridges and heathland dominated by lichens (OSF), (2) heathland dominated by shrubs or herbs (ODF), and (3) snow beds dominated by low growth herbs, shrubs or graminoids (SB) (Table 1). The first and third variables were dominated by low growth vegetation which we assumed provide less cover and probably less food than the second variable which was dominated by denser bush and heath vegetation (Johansen et al. 2009). The variables considered as having an effect on reproduction and density were mainly separated by an expected difference in food availability and cover from predators.

Management regime

Previous studies have documented that harvest mortality can be additive to natural mortality (Smith and Willebrand 1999, Pedersen et al. 2004, Sandercock et al. 2011). State-owned land or other public land is often regarded as a *common pool resource* where no individual hunter feels inclined to reduce their catch (i.e., *The tragedy of the Commons* after Hardin 1968).

Managers of state-owned land are also obliged by law to offer open access hunting to local hunters and to sell a certain number of permits to non-resident hunters. Private landowners have more flexibility and may sell exclusive permits to a limited number of hunters (Pedersen and Storaas 2013). It is therefore expected that the management regime would indirectly affect harvest rates of willow ptarmigan. The apparent carrying capacity of an area might be altered if harvest rates are unsustainable. We have information about landownership in all survey areas but not harvest rates, and we used landownership as an index of the harvest rate.

Statistical analysis

We used generalized mixed effect models to analyze the effect of vegetation types on adult density (birds/km²) and reproductive success (juveniles/pair). The models were fitted with survey area and year, nested within mountain region, as random effects. There was a clear negative relationship between adult density and size of the surveyed areas (model with area size as fixed effect; slope \pm SE -0.162 ± 0.065 , AICc 1997.69 and the null model; AICc 2001.32). One potential explanation might be that transect lines in small areas (i.e., total length [m] of the transect-lines within the survey area were shorter) were placed in the best parts of a survey area while in the large survey areas, lines were placed over the entire management area. We restricted the area to the 250 m buffer and included survey area size (km²) as a fixed effect when modeling adult density. We considered a number of candidate models for adult density with different combinations of plausible explanatory variables, but confounded variables were analyzed separately (variables were considered confounded if the correlation coefficient between them was > 0.4). We conducted the same procedure for recruitment rates but did not include terms for hunting pressure or survey area size. This was because harvesting took place from 10 September which was not likely to affect recruitment rates measured in August (recruitment was independent of area size and adult density). We used an information theoretic approach (Burnham and Anderson 2002) to select the most

parsimonious model explaining the variation in adult density and recruitment from the set of candidate models. We used $AICc$ and $\Delta AICc$ as model selection criteria when evaluating the candidate models. $\Delta AICc$ was the difference in $AICc$ from the best candidate model (the model with the lowest $AICc$, cf. Burnham and Anderson (2002)). We calculated $AICc$ weights among the models within 2 $\Delta AICc$ units, as:

$$AICc\ weight = \frac{\exp\{-\frac{1}{2}(\Delta AICc)\}}{\sum_{k=1}^k \exp\{-\frac{1}{2}(\Delta AICc)\}},$$

where the sum of all $AICc$ weights = 1. The $AICc$ weights can be interpreted as a continuous measure of probability that the best candidate model is indeed the best model, given the data and the set of candidate models (Wagenmakers and Farrell 2004).

All statistical analyses were conducted using R (version 3.0.2, <http://www.r-project.org/> accessed 9/25/2013). We used the *lmer* function in the *lme4* package (Bates et al. 2013) for the mixed effect models and the *MuMIn* package (Barton 2013) for the model selection procedure.

RESULTS

The proportional cover of different vegetation types varied considerably among all survey areas (Fig. 2), but there were no significant differences in the cover of different vegetation types between privately- and state-owned lands (Fig. 3).

The highest ranked model explaining adult density included the effect of landownership in addition to area size (Table 2a). Privately-owned survey areas generally had higher adult densities than state-owned survey areas with a mean of 8.54 birds/km² (6.07–11.01, 95% CI) compared with 5.86 birds/km² (3.23–8.46, 95% CI), respectively. Four other models were within 2 $AICc$ units ($\Delta AICc < 2$) of this model; (1) the null model (i.e., only area size), (2) a model with a significant negative effect of snowbed cover, (3) a model with a positive effect of cover of open areas with dense field layer, and (4) a model with a negative effect of mountain birch cover. The $\Delta AICc < 2$ suggests that all models were equally

supported by the data and, based on parsimony, we should select the second ranked model which was the null model with no explanatory power as it was the simplest model. There were, however, strong indications of an actual effect of landownership. First, the model accounted for 37% of the AIC_c model weights compared to only 18% for the second and third ranked models (Table 2a). Second, the bootstrapped confidence intervals for effect of state-owned land in the model with landownership did not overlap zero (-5.61 and -0.09, 2.5 and 97.5% percentiles). Third, the difference in effect size was substantial, 2.56 birds/km², which corresponded to 46% of the average density on state-owned land.

There were five models within 2 AIC_c units (table 2b) for reproductive success and all were equally supported by the data. The model with the lowest AIC_c included a negative effect of bogs with sparse field layer and a negative effect of mountain birch forest cover. The second ranked model ($\Delta\text{AIC}_c = 0.09$) included mountain birch cover, was the only univariate model within $\Delta\text{AIC}_c < 2$ and parsimony would suggest this was the preferred model. The difference in AIC_c weights between the two highest ranked models was only 1% suggesting that little was gained by including bogs with scarce field layer cover as a term in the model. The negative effect of mountain birch cover was the only term that occurred in all models within 2 ΔAIC_c . The effect size of mountain birch on reproductive success in the simplest model was -4.85 (Fig. 4) with bootstrapped confidence intervals not overlapping zero (-7.87 and -1.71, 2.5 and 97.5% percentiles). This suggested the negative effect of mountain birch cover on reproductive success was significant.

DISCUSSION

We found large differences in vegetation composition among survey areas and the survey areas differed considerably in adult density (Prediction 1). We were not able to link adult density to habitat attributes (Prediction 2), but privately-owned survey areas supported higher densities than state-owned survey areas (Prediction 3). There were only weak

indications that densities were higher in survey areas rich in open areas with dense field layer and lower densities in areas rich in snow-beds and mountain birch (Table 2a). We found indications of poorer recruitment in survey areas where a high proportion of the area was covered by mountain birch forests (Prediction 4).

Our results appear to differ from previous studies, where individual ptarmigan selected specific vegetation types (Andersen et al. 1984, Kastdalen et al. 2003, Henden et al. 2011, Ehrich et al. 2012). Selection at the individual scale did not, however, affect the density at the population scale in the surveyed hunting units.

One possible explanation for the lack of a clear relationship between vegetation composition and either adult density or recruitment rates in our study was that willow ptarmigan populations in most survey areas were well below carrying capacity (*c.f.* Myrberget 1988, Pedersen 1988, Kvasnes et al. 2014b, Lehikoinen et al. 2014). Thus, relative to years with higher population levels, resources (food and shelter) were plentiful and competition was low. A small proportion of an important habitat component (unidentified) might be sufficient to support relatively high densities. Kastdalen et al. (2003) found that willow ptarmigan selected willow thickets at relatively high bird densities. However, Henden et al. (2011) reported the same at very low ptarmigan densities indicating that we should also expect evidence for habitat selection. Overbrowsing by large ungulates was a problem in Henden et al.'s study area in northern Norway, but not in our study area in southern Norway. Ungulates might reduce the quality of tundra habitats to a level where the resources are no longer plentiful even for low density ptarmigan populations, which could affect habitat selection. Earlier studies (e.g., Andersen et al. 1984 and Steen et al. 1985) have also shown that vegetation types with willow are important habitat components for willow ptarmigan. Willows in our study occur in vegetation types #s 6 (bilberry- low fern birch forest within the MB category), 10 (tall-grown lawn vegetation within the BDF category), and 17 (fresh

heather and dwarf-shrub communities within the ODF category), (*cf.* Table 1) (Johansen et al. 2009). However, when this habitat was available in great excess due to low ptarmigan density, as in our study, we were not able to find any selection for specific vegetation types.

Five models regarding recruitment rates were within 2 $\Delta AICc$ with a negative effect of mountain birch cover included in all models. The simplest model of reproductive success was the univariate model with a negative effect of mountain birch cover and a non-zero effect size based on the bootstrapped confidence intervals. This implied that survey areas with high proportions of mountain birch had lower reproductive success. This effect was weak, but coincided with the data of Andersen et al. (1984) which demonstrated that willow ptarmigan broods avoided mountain birch during the first three weeks after hatching. Andersen et al. (1984) also found selection for rich bogs in central Norway, contrary to our study. A possible explanation for the weak relationship between recruitment and vegetation cover was the low ptarmigan density and subsequent low competition for brood rearing habitats. An effect of vegetation composition may be clearer, in theory, at higher densities because of increased competition for optimal habitats (Fretwell and Lucas 1969).

The lack of a clear connection between vegetation and adult density or recruitment seemed surprising based on our initial predictions. Our predictions were reasonable based on earlier findings and experience, yet our analyses suggested no or only weak associations between the two demographic variables and habitat composition within our study areas. The vegetation variables explained little of the variation in adult density, but the direction of the effects was as expected and all effects from the most parsimonious models ($\Delta AICc < 2$) followed our predictions.

The minimal adequate model for adult density was the null model containing only an effect of survey area size. The model with landownership had a lower $AICc$ and twice the $AICc$ weight of the null model and had bootstrapped confidence intervals that did not overlap

zero. Further, the effect size was 2.56 birds/km², amounting to 46% of the average density on state-owned land. The total number of birds on privately-owned areas was clearly greater considering this was only the adult proportion of the population. However, confidence intervals were wide for both regimes, implying there was high variation in hunting pressure, within both state- and private-owned areas. 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 rates might cause spatial variation in densities (Smith and Willebrand 1999, Pedersen et al. 2004, Sandercock et al. 2011). It is worth noting that landownership is only a simple index of hunting pressure. Actual harvest records must be used to estimate harvest rates precisely, but since private- and state-owned areas have similar vegetation composition, we believe that the most plausible explanation is that hunting pressures differ. Kvasnes et al. (2014a) suggested that dispersing juvenile ptarmigan were attracted by established adult conspecifics before choosing where to breed. Single adult males often remain in their former territories and display autumn territoriality when ptarmigan flock in October (Pedersen et al. 1983, Pedersen 1988), and may sit tight for pointing dogs (personal observations). More dispersing ptarmigan should be attracted to private land if hunting pressure is higher on state-owned hunting units, especially later in the autumn..

MANAGEMENT IMPLICATIONS

Willow ptarmigan select habitat at the individual level, but differences in habitat composition do not explain consistent density differences between areas. It is unlikely that habitat management will have any effect on the densities of willow ptarmigan populations in Norway during periods of relatively low densities. We suggest possible higher survival of adults on private hunting units may attract dispersing young ptarmigan from neighboring hunting units with a higher adult harvest pressure.

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Figure captions

Figure 1. Survey areas (filled areas) within mountain regions (open circles) in south-central Norway. RS = Rondane, DF = Dovre and Folldal, FH = Forollhogna, GNE = Glomma northeast, GSE = Glomma southeast.

Figure 2. Boxplots showing the proportional cover of different vegetation types (definitions in Table 1) across all survey areas. Different scales on y-axis.

Figure 3. Boxplots with the proportions of different vegetation types (definitions in Table 1) by private (priv) or state (stat) landownership. There was no significant difference with ownership (All $P > 0.05$).

Figure 4. Number of juveniles/pair plotted against the proportional cover of mountain birch forest.

Tables

Table 1. Vegetation classes within the survey areas. The first column (left) shows the original classes and classification numbers defined in Johansen et al. (2009). The third column from left is the pooled vegetation types defined in this paper. We 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). Lowland forest vegetation types are not included. Mean and median values are proportional cover calculated across all survey areas. There are no cities or built-up areas present in the

study areas. The *Original vegetation types* is the original vegetation types from the vegetation map (Johansen 2009) described in (Johansen et al. 2009) and *Pooled vegetation types* is the simplification of the *Original vegetation classes* into 6 broader vegetation types.

<i>Original vegetation type(classification no)</i>	<i>Mean (median)</i>	<i>Pooled vegetation types</i>	<i>Mean (min-max)</i>
Bilberry- low fern birch forest (6)	0.026 (0.021)		
Crowberry birch forest (7)	0.013 (0.003)	Mountain Birch forests (MB)	0.062 (0.000-0.289)
Lichen-rich birch forest (8)	0.023 (0.003)		
Wet mires, sedge swamps and reed beds (11)	0.008 (0.004)	Swamps and bogs with sparse field layer (BSF)	0.008 (0.000-0.041)
Ombrotrophic bog and low-grown lawn vegetation (9)	0.116 (0.110)		
Tall-grown lawn vegetation (10)	0.044 (0.032)	Bogs with dense field layer (BDF)	0.161 (0.000-0.465)
Exposed alpine ridges, scree and rock complex (12)	0.004 (0.000)		
Graminoid alpine ridge vegetation (13)	0.026 (0.006)		
Heather-rich alpine ridge vegetation (14)	0.233 (0.247)	Open areas with sparse field layer (OSF)	0.319 (0.001-0.754)
Lichen-rich heathland (15)	0.057 (0.043)		
Heather- and grass-rich early snow patch community (16)	0.050 (0.025)		
Fresh heather and dwarf-shrub communities (17)	0.293 (0.252)	Open areas with dense field layer (ODF)	0.384 (0.127-0.811)
Herb-rich meadows (18)	0.041 (0.031)		
Grass and dwarf willow snow-patch vegetation (19)	0.009 (0.003)		
Bryophyte late snow patch vegetation (20)	0.008 (0.003)	Snowbeds (SB)	0.017 (0.000-0.112)
<i>Coniferous Forest – dense canopy layer (1)</i>			
<i>Coniferous forest and mixed forest - open canopy (2)</i>			
<i>Lichen rich pine forest (3)</i>	-	<i>Lowland forest</i>	<i>0.043 (0.000-0.190)</i>
<i>Low herb forest and broad leaved deciduous forest (4)</i>			
<i>Tall herb - tall fern deciduous forest (5)</i>			

Glacier, snow and wet snow-patch vegetation (21)

Water (22)

- Other

0.005 (0.000-0.056)

Agricultural areas (23)

Unclassified and shadow affected areas (25)

Table 2. Model selection tables based on AICc selection criteria for adult density (a) and recruitment (juveniles/pair) (b). Only models within 2 $\Delta AICc$ units considered. (+), (-) and (Private +) shows the direction of the effects. Definitions of vegetation variables (BSF, MB, ODF, SB) are in Table 1.

a) *Adult density*

<i>Variables</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>		
			<i>AICc</i>	$\Delta AICc$	<i>weight</i>
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*

<i>Variables</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>		
			<i>AICc</i>	$\Delta AICc$	<i>weight</i>
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

Paper III

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Spatial dynamics of Norwegian tetraonid populations

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Abstract Different species in a given site or population of a given species in different sites may fluctuate in synchrony if they are affected similarly by factors such as spatially autocorrelated climate, predation, or by dispersal between populations of one species. We used county wise time series of hunting bag records of four Norwegian tetraonid species covering 24 years to examine patterns of interspecific and intraspecific synchrony. We estimated synchrony at three spatial scales; national, regional (consisting of counties with similar climate), and county level. Ecologically related species with overlapping distributions exhibited strong synchrony across Norway, but there was much variation between the different regions and counties. Regions with a long coastline to both the North Sea and the Norwegian Ocean exhibited an overall stronger synchrony than those consisting of more continental areas. Intraspecific synchrony was generally low across all counties, but stronger synchrony between counties within regions defined by climatic conditions. Synchrony was negatively related to distance between populations in three of four species. Only the synchrony in willow ptarmigan showed a clear negative relationship with distance, while the other species had both strong positive and negative correlations at short distances. Strong interspecific synchrony between some species pairs within regions and weak intraspecific synchrony across counties within regions suggest a stronger synchronizing effect from environmental factors such as weather or predation and less effect from dispersal. Our results suggest that the complete tetraonid community is structured by environmental factors

affecting the different species similarly and causes widespread interspecific synchrony. Local factors affecting the population dynamics nevertheless frequently forces neighbouring populations out of phase.

Keywords Synchrony · Growth rates · Hunting statistics · Willow ptarmigan · Rock ptarmigan · Capercaillie · Black grouse

Introduction

Population dynamics are driven by abiotic and biotic environmental factors through their effects on demographic rates, potentially resulting in synchronous dynamics in populations influenced by the same forces (Moran 1953; Ranta et al. 2006). When these environmental forces are spatially autocorrelated, segregated populations of one species might fluctuate in synchrony (i.e. intraspecific synchrony; Lindstrom et al. 1996; Hornell-Willebrand et al. 2006; Kerlin et al. 2007). Further, sympatric populations of different species may also be synchronised when the same environmental forces affect them similarly (i.e. interspecific synchrony; Ranta et al. 1995, 2006). In general, three principal factors have been identified as possible causes of synchrony: (1) predation (Ims and Andreassen 2000), (2) shared climate (i.e. Moran effect; Moran 1953) and (3) dispersal (Lindstrom et al. 1996; Paradis et al. 1999). While both shared predators and climate might cause synchrony both within and across sympatric species, dispersal is limited to cause intraspecific synchrony. Importantly, environmental factors like predation (Smedshaug et al. 1999; Ims and Andreassen 2000), climate (Moran 1953; Grenfell et al. 1998; Grotan et al. 2005) and food availability (Erikstad 1985) may all work alone or simultaneously to affect population dynamics through changes in reproduction, mortality or dispersal.

In Norway, Capercaillie (*Tetrao urogallus*), black grouse (*T. tetrix*), willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. muta*) are widely distributed

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tetraonid species. Although they share many ecological characteristics, there is a clear ecological gradient through the species assemblage in life histories and habitat use (for spatial distribution, see Fig. 1a). The largest species, capercaillie, and the second largest, black grouse, are sympatric, forest dwelling, promiscuous, lekking birds. Their distributions overlap largely over the boreal forest zone in Scandinavia, although capercaillie prefer old forest patches and black grouse prefer younger successional stages (Seiskari 1962; Swenson and Angelstam 1993). Willow and rock ptarmigan are smaller, sympatric, alpine-dwelling monogamous species. Willow ptarmigan is slightly larger than rock ptarmigan and their distributions usually overlap in the alpine zones in Norway, with the rock ptarmigan being restricted to the mid- and high alpine zones. In many mountain forest areas, the willow ptarmigan distributions overlap with both black grouse and capercaillie (Pedersen 1991; Pedersen and Karlsen 2007). The Norwegian tetraonid community is subject to predation from a number of avian and mammalian predators, and variation in egg and chick predation as well as adult survival might vary largely between years and cause autumn densities to vary accordingly (Bergerud and Gratson 1988; Myrberget 1988; Steen et al. 1988; Wegge and Storaas 1990; Steen and Erikstad 1996; Munkebye et al. 2003; Wegge and Kastdalen 2007). Little is known about the spatial autocorrelation of these processes, and to which extent they affect the complete tetraonid community in a way that causes strong interspecific synchrony.

Here we used hunting-bag statistics to examine the patterns of synchrony in Norwegian tetraonid popula-

tions, to ask the following broad questions: (1) Do ecologically related tetraonid species show interspecific synchronous population fluctuations? (2) Does the intraspecific synchrony decrease with distance between the populations? Neighbouring or overlapping populations are likely to be affected by the same weather regime, have a relatively high exchange probability (i.e. dispersal) and share a similar predator-guild. On the basis of this, we expect ecologically related species with substantial overlap in distribution to show temporal match in their fluctuations. In addition, we expect populations of single species to be synchronised across counties and that synchrony will level off as distance between the populations increases.

Methods

Hunting statistics

The time series analyses based on annual, county-level hunting bags between 1982 and 2006 were obtained from Statistics Norway (<http://www.ssb.no>). The statistics from 1982 to 1992 were based on interviews with a random sample of hunters registered in the The Norwegian Register of Hunters and the bags were statistically estimated (Statistics Norway). From 1992 to 2000, all hunters were instructed to report their bags. However, due to low response, this was supplemented with statistical estimations. The change in sampling method happened synchronously for all species and counties, and should thus not affect the interpretation of our re-

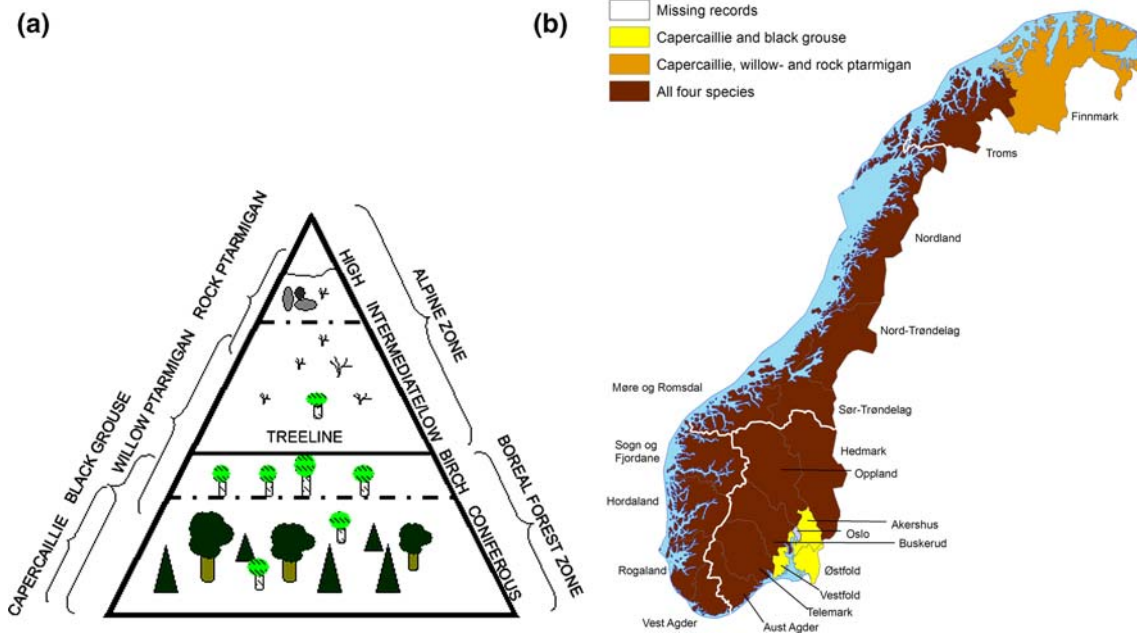


Fig. 1 a Illustration of the four species position in the landscape and the overlap between them. b Map of the study area with colours indicating species in the hunting records included in the analysis. White lines depict borders between regions (region east at the right,

region west at the left, centre region in the middle and region north at the top). Regions are defined on the basis of similarity in precipitation rates between counties

sults. After 2000, 90% of the hunters reported their bags, and no additional estimation has been conducted (<http://www.ssb.no>).

Due to differences in county sizes and amount of preferred habitat, there were large variations in numbers of birds shot in the different counties. In general, the relative variability (i.e. coefficient of variation) was negatively correlated with the mean number of birds shot, indicating that the time series from counties with few birds harvested were less reliable. Time series of shot birds from a county with five or more missing or outlying values in the raw data were excluded from further analysis (see “Statistical analysis of the time series” further down). Time series of willow and rock ptarmigan from four counties (Vestfold, Oslo, Akershus and Østfold) were not included due to only sporadic or no occurrence of the species in the bag records. In the analysis, we used capercaillie, black grouse, willow and rock ptarmigan time series data from 18, 17, 15 and 15 counties, respectively (Fig. 1b).

Hunting bag records are widely used as population size indexes in analysis of spatial and temporal patterns in population dynamics, and it is assumed that such indexes reflect the actual fluctuations in population size (Cattadori et al. 2000; Slåttå et al. 2002; Kerlin et al. 2007). Although there are known problems related to the use of hunting statistics as population indexes (Linden 1981; Hornell-Willebrand et al. 2006), a recent comparison of census data and hunting bag statistics in Finland suggested largely similar conclusions for both line transect and hunting bag data (Ranta et al. 2008), with details of the models varying. As no time series based on transect line census is available that covers all of Norway, we assumed that long-term hunting statistics provide an acceptable index of fluctuations in abundance in tetraonid populations (Cattadori et al. 2000, 2003; Kerlin et al. 2007).

Weather data

We obtained monthly means of precipitation in millimetres (mm) from The Norwegian Meteorological Institute (<http://www.met.no>). In total, 1044 (average 62 in each county) weather stations were operational between 1980 and 2007. Some stations covered the whole period and a few only partly, but all were included in the calculation of county-level mean values. Some stations were manually monitored and thus located close to human settlement, whereas others registered precipitation automatically and were distributed to give a representative value at the county level. We estimated mean summer (May–August) precipitation in the 18 counties from where we had time series of hunting statistics.

To define regions with similar precipitation in summer months, we clustered the time series using a cluster analysis. Mean summer precipitation was rescaled to Euclidean distances between precipitation rates among counties and applied as a dissimilarity matrix (PROC

DISTANCE in SAS statistical software). In the agglomerative hierarchical clustering (PROC CLUSTER in SAS statistical software), each time series first formed a cluster itself. Then, the two closest clusters were merged to form a new cluster that replaced the old ones. The procedure was repeated until only one cluster was left. The distance between two clusters was computed by the Ward’s minimum variance method (Ward 1963). To validate the clusters, we calculated mean cross-correlation within regions and compared it to the national mean correlation coefficient. The cluster analysis revealed four regions consistent with the spatial arrangement (Fig. 1b), and in general the precipitation was well correlated within these clusters (mean within-cluster correlations; North $r = 0.57$, Centre $r = 0.62$, West $r = 0.43$, and East $r = 0.66$).

Species habitat overlap

To obtain an index of distribution overlap between pairs of species, we used data from the Norwegian bird atlas database (<http://www.fugleatlas.no>). This database contains UTM-positions with an accuracy of 1×1 km for reported observations of all four tetraonid species from 1970 to 2007. The data collection was based on voluntarily work by ornithologists, who observed grouse, noted the UTM-position and registered this in a database. In total, 4505 observations of all grouse species (willow ptarmigan 1565, rock ptarmigan 791, capercaillie 875 and black grouse 1274) were used. To calculate an index of habitat overlap at the county level between pairs of species, buffers with a radius of 1 km (approximate summer home range) were placed around all positions. This buffer area represents an approximate summer range for the species, and it is assumed that individual tetraonids living in this area share similar extrinsic factors such as weather and predator regime. Then, the number of buffers of a species that overlapped with the other species was counted. A small number of buffers that crossed a county border were counted as one observation in both counties. All calculations on overlap data were executed in ArcGIS 9.2 (<http://www.esri.com>). To calculate an overlap index for each pair of species within a county, we divided the number of overlapping buffers with the total number of buffers for both species in the comparison, and obtained a proportion of overlap between the species. Although this method is likely to underestimate the true distribution overlap, the pattern obtained when comparing pairs of species largely followed the expected pattern.

Statistical analysis of the time series

Population growth rates were calculated as: $r_t = \ln(N_{t+1}/N_t)$. To avoid unnecessary high influence from single extreme rates of change, values that were located outside a 5% threshold set by the 2.5 and 97.5% per-

centiles in county-wise distributions was characterised as outliers and removed from the time series.

We analysed patterns of synchrony in population growth at three spatial scales. First, we pooled all the time series from each species, and investigated the national-level interspecific synchrony by constructing a matrix of pairwise Pearson cross-correlations between each pair of species (Ranta et al. 1995; Cattadori et al. 2000). Second, we performed the same procedure on region scale (based on cluster analysis described above) (Fig. 1b) and county scale.

To examine the relationship between habitat overlap index and interspecific synchrony at national scale, we estimated the correlation between the interspecies correlations and overlap index. Further, at regional and county level, we fitted linear mixed-effect models, implemented by the *lmer* function in the library *lme4* (Bates 2005) in the software R (R Development Core Team 2006). This function allowed for crossed random effects (Bates 2005), which were appropriate here since there was no nested structure in the data. The models were fitted with county or region, respectively, and species pairs as random effects, and the amount of variation attributable to each factor was assessed by variance decomposition analysis (Borger et al. 2006; Nilsen et al. 2008). To investigate the effect of habitat overlap index on interspecific synchrony, we fitted the models with and without habitat overlap index as fixed effect, and compared the total residual variance to obtain a measure of this effect.

Spatial intraspecific synchrony was also initially assessed by constructing matrices of pairwise Pearson cross-correlations between all pairs of time series (within species), both between all counties and between counties within each region. A corresponding inter-county, distance matrix was also constructed, containing distances between centroid-points in each county. Then at the county level, a two-step approach was used to assess the spatial scaling of the synchrony. First, we estimated the

correlation between bootstrapped (see next paragraph) intraspecific correlations and the distance between counties to achieve a robust estimate on the relationship between synchrony and distance. Thereafter, to describe the relationship visually, we analysed the relationship between synchrony and distance with a generalized additive model (GAM) using the software R (R Development Core Team 2006). The GAM is based on a non-parametric regression and smoothing techniques. Non-parametric regressions reveal structures in the relationship between the predictor and response variable that might otherwise be missed, which is useful in assessing the spatial scaling of synchrony.

Due to a lack of statistical independence of intraspecific pairwise cross-correlations, we calculated median cross-correlation coefficients and confidence limits with a bootstrap procedure (Ranta et al. 1995; Cattadori et al. 2000; Kerlin et al. 2007) in R (R Development Core Team 2006). Pairwise cross-correlation coefficients were sampled with replacement to generate 10000 matrices of sampled coefficients. This histogram was then used to estimate the median together with 2.5 and 97.5% percentiles of the original matrix of pairwise cross-correlation coefficients.

All cross-correlation coefficients used in this study were estimated using the PROC CORR procedure in SAS statistical software.

Results

Interspecific synchrony

Capercaillie and black grouse ($r = 0.768$, $P < 0.01$), willow ptarmigan and rock ptarmigan ($r = 0.668$, $P < 0.01$) and black grouse and willow ptarmigan ($r = 0.515$, $P = 0.01$) fluctuated in synchrony at the national scale (Fig. 2). Willow ptarmigan and caper-

Fig. 2 Fluctuations in rate of change in hunting bags of Norwegian tetraonids in the period 1982/1983–2005/2006

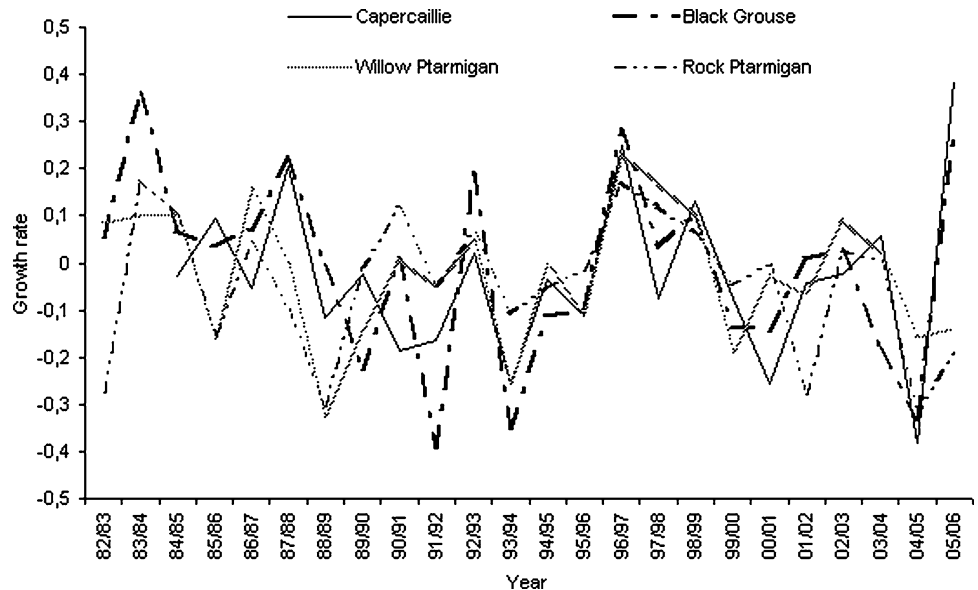
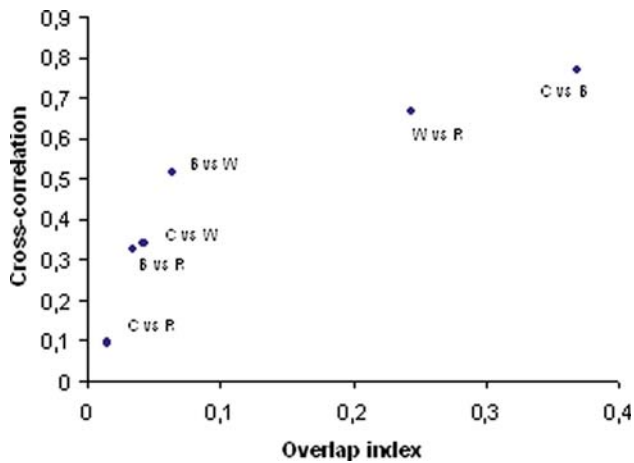


Table 1 Pairwise interspecific correlation coefficients at national scale and mean correlation with max and min values for regional and county scale

	Norway	Region			County		
	<i>r</i>	Mean <i>r</i>	Max	Min	Mean <i>r</i>	Max	Min
Capercaillie versus black grouse	0.768	0.595	0.852	0.079	0.478	0.919	0.190
Capercaillie versus willow ptarmigan	0.341	0.282	0.607	-0.028	0.241	0.769	-0.290
Capercaillie versus rock ptarmigan	0.095	0.154	0.341	-0.049	0.216	0.665	-0.361
Black grouse versus willow ptarmigan	0.515	0.360	0.730	0.019	0.338	0.705	-0.077
Black grouse versus rock ptarmigan	0.325	0.386	0.658	0.203	0.313	0.702	-0.272
Willow ptarmigan versus rock ptarmigan	0.668	0.731	0.827	0.586	0.581	0.779	0.278

**Fig. 3** Synchrony plotted against overlap index between tetraonid species in Norway. *C* Capercaillie, *BG* black grouse, *WP* willow ptarmigan, *RP* rock ptarmigan

caillie ($r = 0.341$, $P = 0.10$), and rock ptarmigan and black grouse showed weak synchrony ($r = 0.325$, $P = 0.12$), and the two most different species, rock ptarmigan and capercaillie, showed no synchrony at all on the national level ($r = 0.095$, $P = 0.67$) (Table 1). Also at the region and county scale, ecologically related pairs of species (capercaillie and black grouse, and willow ptarmigan and rock ptarmigan) fluctuated in rather close synchrony, while black grouse showed weak and capercaillie no synchrony with neither willow nor rock ptarmigan (Table 1). When comparing correlations at the different scales, there was a tendency, however, but not a significant one. The mean synchrony was stronger at the national level than at the county level (Table 1; sign test; $P = 0.22$).

There was a strong, positive relationship between the synchrony and the overlap index at the national scale ($r = 0.888$, $P = 0.02$, Fig 3). At the region and county scale, a mixed-effect model fitted with habitat overlap index as fixed effect revealed a similar pattern, i.e. species pairs with high overlap index tended to fluctuate in stronger synchrony than those with low overlap index (region; $b = 1.567$, $t = 3.671$, $P < 0.01$, county; $b = 0.923$, $t = 4.896$, $P < 0.01$). The variance decomposition analysis further revealed that on both scales,

Table 2 Amount of variation in interspecific synchrony attributed to area (county and region) and species pairs at county and region scale

Variance components (%)	A (%)	B (%)
County scale		
County	27	30
Species pair	21	5
Residual	52	65
Region scale		
Region	27	26
Species pair	33	5
Residual	40	69

Model A is fitted with only random effects whereas model B is fitted with overlap index as a fixed effect. At both spatial scales there is a significant effect of species overlap fitted as fixed effect

area (i.e. region or county) and species attributed almost equally to the variation in synchrony when the model was fitted without any fixed effects, whereas area attributed much more to the total variation than species pairs (region: nine times, county: five times) when species overlap index was fitted as fixed effect (Table 2). The relative difference in total residual variance between models with and without overlap index as fixed effect, showed that the overlap index is attributable to ~27 and ~52% of the variation in synchrony at county and region scales, respectively. Best linear unbiased predictions (BLUP) from the region scale mixed model indicates an overall stronger interspecific synchrony in west and centre than in east and north (in ranking order) when spatial overlap is fitted as fixed effect (Fig. 4).

Intraspecific synchrony

Different spatial patterns were observed within the species. Bootstrapped cross-correlation between counties indicated overall weak synchrony in capercaillie (median correlation, [2.5, 97.5% percentiles]: 0.09 [0.05, 0.13]) and rock ptarmigan (0.12 [0.07, 0.16]), stronger, but still low in black grouse (0.19 [0.15, 0.24]) and willow ptarmigan (0.21 [0.16, 0.27]).

Synchrony in willow ptarmigan, rock ptarmigan and capercaillie are negatively correlated with distance (bootstrapped correlation [2.5, 97.5% percentiles]:

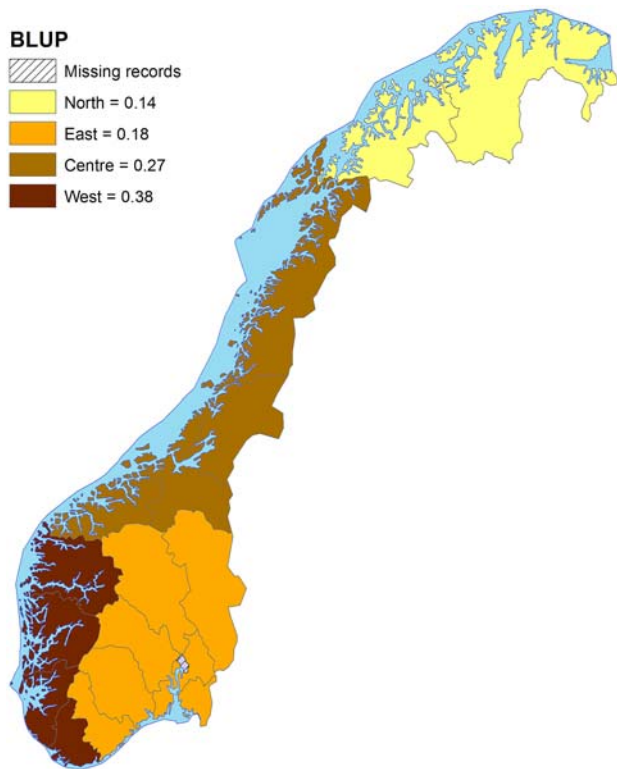


Fig. 4 Best linear unbiased predictions (*BLUP*)—predicted (random) intercepts at the region level. Based on the mixed-effects model. The value indicates the strength of the synchrony between all species pairs in the region

$-0.69 \pm [-0.74, -0.64]$, $-0.34 \pm [-0.44, -0.24]$, $-0.14 \pm [-0.23, -0.05]$, respectively) while synchrony in black grouse is unrelated to distance ($-0.09 \pm [-0.18, 0.02]$). Similarly, the GAMs indicate a negative relationship between distance and synchrony in all species except black grouse (Fig. 5). Willow ptarmigan populations were mainly positively correlated at distances less than 750 km, beyond that the populations were mainly negatively correlated before a positive trend began around 1200 km. Both capercaillie and rock ptarmigan showed a weak, negative linear relationship with distance. In capercaillie, black grouse and rock ptarmigan there was much variation in the cross correlations also at smaller spatial scales, indicating that also neighbouring populations often were out of phase (Fig. 5).

Mean interspecific correlation between counties within precipitation-defined regions was stronger than between all counties (mean r , [max, min]; capercaillie 0.17 [0.72, -0.54], black grouse 0.31 [0.81, -0.37], willow ptarmigan 0.43 [0.74, 0.13] and rock ptarmigan 0.16 [0.61, -0.22]) (Table 1; sign test: $P = 0.03$).

Discussion

Using long-term, large-scale hunting bag data, we have examined interspecific and intraspecific synchrony in

four Norwegian tetraonids. As in other studies (North America: Butler 1953; Sweden: Small et al. 1993; Finland: Ranta et al. 1995; Italy: Cattadori et al. 2000), ecologically related species were highly synchronous across Norway, and the synchrony was closely correlated with the habitat overlap index. Also, within weather regions and within counties, we found strong mean synchrony between ecologically related species with a high habitat overlap index. There was, however, much variation between regions and counties. The synchrony observed at county level corresponded to what Ranta et al. (1995) found in capercaillie, black grouse and hazel grouse (*Bonasa bonasia*), at the county level in Finland.

Species with overlapping distributions were strongly synchronous in their population dynamics. When accounting for distribution overlap in the linear mixed-effects models, more of the remaining variation was attributed to differences between areas than to differences between pairs of species. Thus, species living in close proximity often shared common dynamics, and this spatial proximity appears to be more important than differences between species in life histories and body size. This pattern corresponds to what should be expected if the different species in the tetraonid community are affected by the same environmental factors. The interspecific synchrony varied, however, between regions, and the two regions that showed an overall stronger interspecific synchrony (Centre and West) have long coastlines and short distances between shore and inland, whereas the two regions with least interspecific synchrony (North and East) have shorter coastlines and include more continental/inland areas. This might suggest that local and regional environmental factors are important and that they work differently among regions or counties, and have strong local influence on the dynamics in tetraonid populations.

Low intraspecific synchrony at the national scale and a weak relationship with distance in most species (except willow ptarmigan) suggest that although the synchronizing force(s) are correlated in space, large variation even at short distances indicates that local factors may be predominant (Tavecchia et al. 2008). If dispersal was the main synchronizing factor, it could be expected that species with the greatest dispersal distances should have the highest mean synchrony (Paradis et al. 1999); this was, however, not a clear pattern. Further, modelling studies predict that dispersal-induced synchrony causes a stronger negative relationship between synchrony and distance than synchrony caused by stochastic events (Lindstrom et al. 1996). However, in our study, there was a strong decline in synchrony with distance only in willow ptarmigan. The strong interspecific synchrony contra weaker intraspecific synchrony in our results, suggest that extrinsic factors are more important than dispersal in causing synchrony at the spatial scales studied here.

The strong synchrony between species inhabiting areas in close proximity indicates that the same envi-

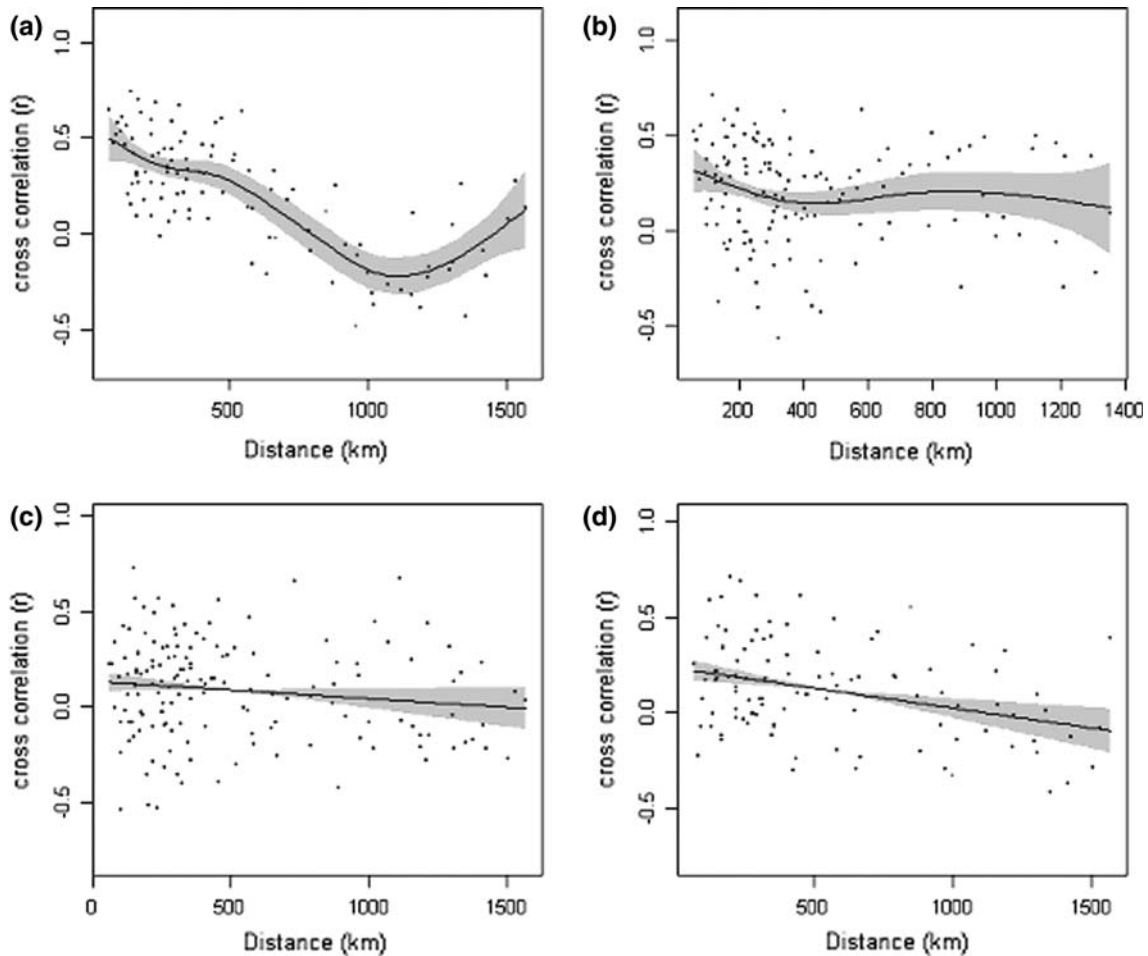


Fig. 5 The relationship between distance and cross-correlation for willow ptarmigan (a), black grouse (b), capercaillie (c) and rock ptarmigan (d), based on GAM non-parametric regression. *Black points* are cross-correlations plotted against distance. *Shaded area* is

the 95% point-wise confidence limit. Estimated degrees of freedom (i.e. edf) for the different slopes: willow ptarmigan (edf = 3.489), black grouse (edf = 3.199), capercaillie (edf = 1) and rock ptarmigan (edf = 1)

ronmental forces affect the tetraonids similarly. Few studies document direct effects of weather on tetraonids, most likely because the birds are well adapted to small deviations from the mean weather conditions (Myrberget 1988; Steen et al. 1988). However, extreme climatic events might affect chick survival either directly or by predisposing the chicks to predation (Erikstad and Andersen 1983; Wegge and Kastdalen 2007). As temporal variation in chick mortality is expected to contribute substantially to variation in population growth rates in tetraonids (Myrberget 1988; Steen and Erikstad 1996; Wegge and Kastdalen 2007), such extreme weather events could be capable of synchronizing tetraonid populations (Cattadori et al. 2000). Another potential effect of climate is mediated through its effects on the community dynamics. For instance, if densities of alternative prey or predator species are affected by climatic conditions, this will also affect the predation pressure on the tetraonid community (Kausrud et al. 2008). The strong synchrony between species with high overlap index also indicates that a shared predator-guild

affecting all species might play a key role in shaping the dynamics.

In this study, we have found answers to the questions stated in the introduction. Ecologically related species fluctuated in synchrony at national, region and county levels, but the strength of the correlations varied strongly between regions/counties. Furthermore, the intraspecific synchrony was generally weak in all species (willow ptarmigan the strongest) and only willow ptarmigan showed a clear decrease in the correlations with distance. Our results suggest that environmental conditions are affecting the tetraonid species similarly and cause the observed patterns of synchrony, and that local conditions are very important and cause the intraspecific synchrony to be variable also for populations in relative close proximity.

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Paper IV

Large-scale climate variability and rodent abundance modulates recruitment rates in Willow Ptarmigan (*Lagopus lagopus*)

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Abstract Recruitment of juveniles is important for the size of the next year's breeding population in many bird species. Climate variability and predation may affect recruitment rates, and when these factors are spatially correlated, recruitment rates in spatially separated populations of a species may be synchronized. We used production data from an extensive survey of Willow Ptarmigan from 2000 to 2011 to investigate spatial synchrony in recruitment of juveniles within and among mountain region populations. In addition, we assessed the effects of predation and large—as well as local—scale climate on recruitment of juveniles. Recruitment was synchronized both within and among mountain regions, but the mean spatial correlation was strongest among mountain regions. This may be caused by small-scale factors such as predation or habitat structure, or be a result of sampling variation, which may be large at small spatial scales. The strong synchrony suggests that populations are subject to similar environmental forces. We used mixed effect models at the survey area and mountain region scales to assess the effect of rodent abundance (a proxy for predation rates) and local and regional climate during the breeding season on the recruitment of juvenile birds. Model selection based on AICc revealed that the most parsimonious models at both spatial scales included positive effects of rodent abundance

and the North Atlantic oscillation during May, June and July (NAO_{MJJ}). The NAO_{MJJ} index was positively related to temperature and precipitation during the pre-incubation period; temperature during the incubation period and positive NAO_{MJJ} values accelerate plant growth. A comparison of the relative effects of NAO_{MJJ} and rodent abundance showed that variation in NAO_{MJJ} had greatest impact on the recruitment of juveniles. This suggests that the climate effect was stronger than the effect of rodent abundance in our study populations. This is in contrast to previous studies on Willow Ptarmigan, but may 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.

Keywords Spatial synchrony · NAO · Recruitment of juveniles · Ptarmigan · Temperature · Precipitation · Breeding season · Alternative prey hypothesis · Local weather · Breeding success · Onset of plant growth

Zusammenfassung

Großräumige klimatische Schwankungen und Abundanz von Nagetieren bestimmen die Rekrutierungsraten von Moorschneehühnern *Lagopus lagopus*

Die Rekrutierung von Juvenilen ist von großer Bedeutung für die Größe der Brutpopulation vieler Vogelarten im folgenden Jahr. Klimaschwankungen und Prädation können Rekrutierungsraten beeinflussen. Wenn solche Faktoren räumlich korreliert sind, können Rekrutierungsraten in räumlich getrennten Populationen synchronisiert sein. Wir

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nutzten Brutdaten einer umfangreichen Bestandsaufnahme von Moorschneehühnern aus den Jahren 2000–2011 zur Untersuchung räumlicher Synchronie in der Rekrutierung von Juvenilen innerhalb und zwischen Populationen in Bergregionen. Darüber hinaus schätzten wir die Effekte von Prädation und groß- wie kleinräumigem Klima auf die Rekrutierung von Juvenilen ein. Die Rekrutierung war sowohl innerhalb als auch zwischen Bergregionen synchronisiert, wobei die durchschnittliche räumliche Korrelation am stärksten zwischen den Bergregionen war. Die könnte durch kleinskalige Faktoren wie Prädation oder Habitatstruktur begründet sein oder aber durch unterschiedliche Stichproben, die größer sein können bei kleinen Maßstäben. Die starke Synchronie deutet darauf hin, dass die Populationen ähnlichen Umwelteinflüssen ausgesetzt sind. Wir wendeten Gemischte Modelle auf Untersuchungsgebiet und Bergregion an, um den Einfluss der Nagerabundanz (Parameter für Prädationsraten) sowie lokales und regionales Klima während der Brutsaison auf die Rekrutierung juveniler Vögel zu berechnen. Die Modellauswahl basierend auf AICs zeigte, dass die minimalsten Modelle auf beiden räumlichen Skalen positive Effekte auf die Nagerdichte und die nordatlantische Oszillation im Mai, Juni und Juli (NAO_{MJJ}) beinhalten. Der NAO_{MJJ} Index war positiv verbunden mit der Temperatur und Niederschlag in der Vorbrutzeit. Temperatur während der Bebrütungsphase und positive NAO_{MJJ} Werte überstiegen das Pflanzenwachstum. Ein Vergleich der relativen Effekte von NAO_{MJJ} und Nagerdichte zeigten, dass Schwankungen des NAO_{MJJ} den größten Einfluss auf die Rekrutierung von Juvenilen haben. Das deutet darauf hin, dass klimatische Effekte stärker wirkten auf die untersuchten Populationen als die Nagerabundanz. Dies steht im Gegensatz zu vorherigen Untersuchungen an Moorschneehühnern, könnte aber erklärt werden durch den Zusammenbruch der Nagerzyklen seit den 1990er Jahren. Wenn die Dynamik von Moorschneehuhn Populationen in der Vergangenheit gekoppelt war mit den Nagerzyklen durch ein gemeinsames Prädatorenregime, dann kann diese Beziehung geschwächt worden sein, als die Nagerzyklen unregelmäßiger wurden. Dies resultiert in einem stärker ausgeprägten Einfluss von störenden Umwelteinflüssen auf die Dynamik von Moorschneehühnern.

Introduction

For many bird species, changes in abundance are closely related to recruitment of juveniles in the preceding breeding season (Newton 1998), although density-dependent effects during the winter might weaken this link (Reed et al. 2013). Recruitment of juveniles in birds is strongly

dependent on biotic factors such as predation on eggs and chicks (Newton 1998) and abiotic factors like weather conditions before and during the breeding season (Saether et al. 2004; Newton 1998). Spatial autocorrelation in predation (Ims and Andreassen 2000) or weather (Moran 1953; Grenfell et al. 1998; Kvasnes et al. 2010) across large areas can potentially force demographic rates of spatially structured populations into synchrony. Although adjacent populations may experience similar weather events, their dynamics can, nonetheless, be out of phase due to differences in local factors such as predator density or habitat (Tavecchia et al. 2008), or as an effect of sampling variation or demographic stochasticity, which may be larger on smaller scales due to reduced sample sizes (Tedesco et al. 2004; Lande et al. 2003).

Species with short generation times and high per-capita reproductive capacities are suitable targets for examining the effects of environmental conditions as their dynamics suggest sensitivity to variation in environmental conditions (Morris et al. 2008). The Willow Ptarmigan (*Lagopus lagopus*) is a medium-sized grouse distributed in alpine tundra habitats in the northern hemisphere (Johnsgard 1983). They have a short generation time ($T = 1.8$, Sandercock et al. 2005 and annual mortality $>46\%$, Sandercock et al. 2011; Smith and Willebrand 1999) and each female may produce up to 12 chicks annually, although recruitment of juveniles as well as densities of breeding birds vary both in time and space (Johnsgard 1983; Kvasnes et al. 2013). Several studies have documented that weather conditions during the breeding season can influence recruitment rates in ptarmigan (Hannon and Martin 2006; Novoa et al. 2008; Slagsvold 1975; Martin and Wiebe 2004; Steen et al. 1988a, b). A general finding is a positive effect of early onset of spring, i.e. warm weather and rainfall before laying and during incubation causing early snowmelt and early onset of the plant growth season (Rock Ptarmigan [*Lagopus muta*]; Novoa et al. 2008 and Willow Ptarmigan; Slagsvold 1975; Steen et al. 1988a, b). It has further been proposed that an early onset of plant growth (OPG) positively affects maternal nutrition during the pre-laying period, which in turn enhances the viability of newly hatched chicks (Moss and Watson 1984; Steen et al. 1988a). Timing of plant growth may also affect viability of young chicks through its effect on availability of important insect prey species (Erikstad 1985b; Erikstad and Spidso 1982) that live on and off the vegetation (Erikstad and Spidso 1982). Young chicks need to be brooded by the hen, and the brooding frequency increases when the weather is cold and wet (Pedersen and Steen 1979; Erikstad and Spidso 1982). Thus, cold and wet weather during the brood rearing period may also reduce the viability of chicks since the time available for foraging is reduced (Erikstad and Spidso 1982; Erikstad and Andersen 1983). Studying

causes of chick mortality in another tetraonid species, the Capercaillie (*Tetrao urogallus*), Wegge and Kastdalen (2007) observed high predation rates during and shortly after heavy rainfall, and the authors suggested that adverse weather predisposed chicks to predation. In general, ptarmigan are well adapted to variability within the normal range of their extreme environment (Martin and Wiebe 2004), but severe conditions, e.g. late snowmelt (Novoa et al. 2008; Martin and Wiebe 2004), delayed plant growth (Steen et al. 1988a), or heavy rainfall (Steen and Haugvold 2009) may negatively affect recruitment rates. Most studies investigating climate effects on ptarmigan populations have used local climate data (Martin and Wiebe 2004; Novoa et al. 2008; Steen et al. 1988b; Slagsvold 1975). However, Hornell-Willebrand et al. (2006) and Kvasnes et al. (2010) found large-scale synchrony in the recruitment of juvenile Willow Ptarmigan and rate of change in bag records, respectively, suggesting that driving factors may work across large areas. In fact, the rate of change in Willow Ptarmigan bag records were more synchronous within large regions of similar precipitation than between regions, suggesting that weather effects may affect population dynamics across large areas (Kvasnes et al. 2010). Similar large-scale effects have been found in Black Grouse (*Tetrao tetrix*) (Barnagaud et al. 2011).

Predation rates on eggs and chicks are generally high and can potentially have a great impact on annual recruitment in Willow Ptarmigan populations (Myrberget 1988; Steen and Haugvold 2009; Smith and Willebrand 1999). Recruitment rates of ptarmigan are often synchronized with the abundance of small rodents (Steen et al. 1988b; Myrberget 1988; Kausrud et al. 2008) and it has been suggested that the link between rodents and Willow Ptarmigan is a shared predator regime. The “alternative prey hypothesis” predicts that a shift occurs in the diet of generalist predators (i.e. Red Fox [*Vulpes vulpes*], Pine Marten [*Martes martes*] and Stoat [*Mustela erminea*]), from main prey (rodents [*Microtus* spp.]) to alternative prey (Ptarmigan and hares [*Lepus* spp.]), during rodent crashes and vice versa (Hagen 1952; Kjellander and Nordstrom 2003). Predation rates on eggs and chicks of Willow Ptarmigan may, therefore, increase as rodent populations decline. Steen et al. (1988b) and Myrberget (1988) found that rodent population cycles were regular with a 4-year periodicity and that this was coherent with the recruitment of juvenile Willow Ptarmigan. Fluctuations in rodent populations have, however, become more irregular during the last two decades (Kausrud et al. 2008; Ims et al. 2008) than before 1983 (Myrberget 1988; Steen et al. 1988a, b). This apparent collapse in regular periodicity of rodent dynamics has been ascribed to changes in climatic conditions during winter (Ims et al. 2008; Cornulier et al. 2013; Kausrud et al. 2008). It is likely that this also affects

alternative prey species in mountain areas (Kausrud et al. 2008). In addition, the timing of a rodent crash can be important for recruitment of juvenile birds. If the rodent population crashes before fledging, the effects on alternative prey may be more severe than if the crash occurs after most chicks have fledged, as fledged chicks are capable of escaping mammalian predators (Erikstad 1985a).

We used Willow Ptarmigan survey data from 60 survey areas in south-central Norway from 2000 to 2011 (3–12 years per area) to investigate: (1) the degree of synchrony in the recruitment of juveniles within and among mountain region populations, and (2) the effect of predation and large—as well as local—scale climate on local and regional recruitment rates in Willow Ptarmigan. To our knowledge, no other studies have used such an extensive survey to investigate how extrinsic environmental factors shape the temporal variation in the recruitment of juvenile Willow Ptarmigan.

Methods

Data collection and study areas

Line-transect surveys were conducted in August from 1996 to 2011 in up to 60 survey areas across south-central and eastern Norway (Fig. 1). Four areas were surveyed from 1996, and new areas were subsequently added to the study design throughout the period. For practical reasons (weather, illness, shortage of voluntary field workers etc.), surveys were not conducted in all survey areas in all years and not all transects were sampled in a survey area every year. Because of the sub-alpine distribution of Willow Ptarmigan, survey areas were geographically clustered within five mountain regions (Fig. 1). Volunteer dog handlers with pointing dogs walked along predetermined transect lines and the free-running dogs searched the area on both sides of the line following the procedure of distance sampling (Buckland et al. 2001; Pedersen et al. 1999, 2004; Warren and Baines 2011). At each encounter, the number of birds (chicks, adult males, adult females and birds of unknown age/sex) and perpendicular distance from the transect line to the observed birds (m) were recorded. Pedersen et al. (2004) provide a detailed description of the sampling protocol. The number of years with data in each survey area varied between three and 15 (median = 7); the number of transects per survey area varied between two and 39 (median = 11), giving total transect lengths varying between 7.6 and 107 km (median = 33 km); and the number of encounters per year per survey area varied between four and 179 (median = 30). The lowest total transect length, number of transects and number of encounters were independent of each other (not from the

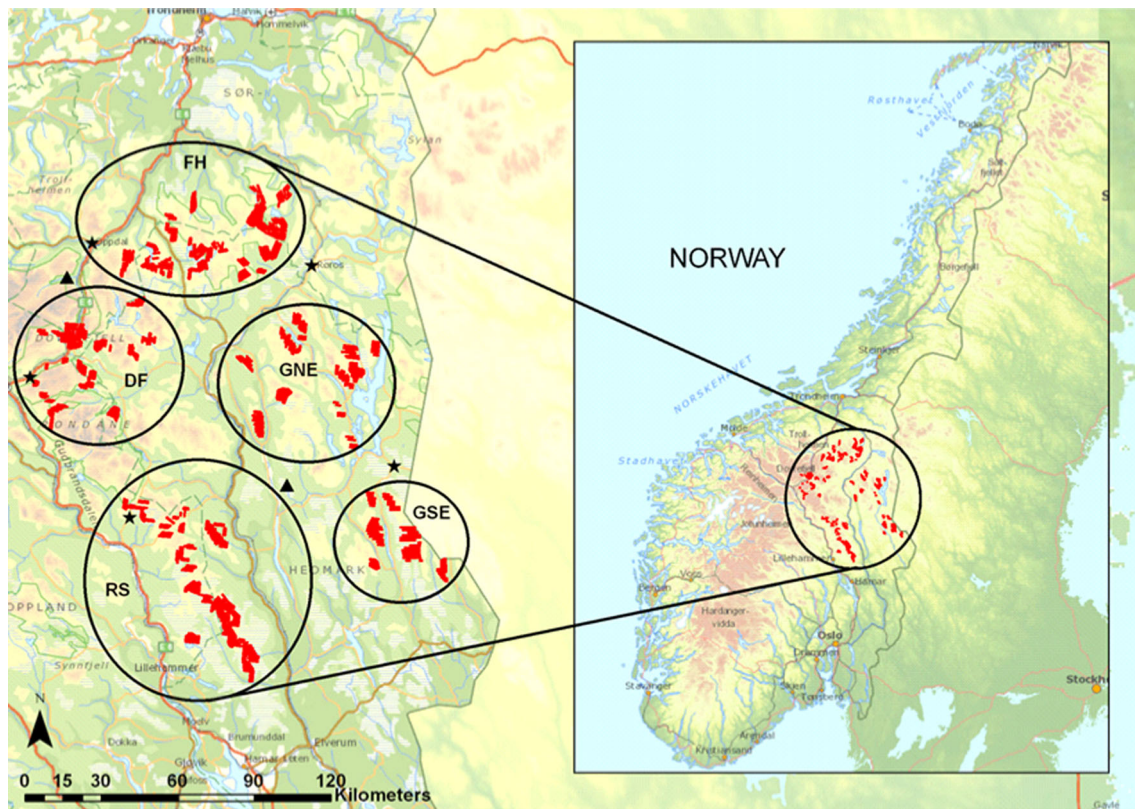


Fig. 1 Study areas (filled polygons) within mountain regions (open circles) in south-central Norway. RS Rondane, DF Dovre and Follidal, FH Forollhogna, GNE Glomma northeast, GSE Glomma southeast).

Filled stars and filled triangles are the positions of meteorological stations and rodent trap sites, respectively

same area and year). Data from different transects were pooled per site and year.

We defined recruitment as the number of juveniles per pair in a given survey area a given year, based on the encounters described above. To obtain estimates of recruitment, we estimated the proportion of juveniles (PJ) from the raw data. We used data from all survey areas and years, but included only transect lines with recorded encounters, and only encounters where the sex and age class (i.e. no observations with unknown sex or age, c.f. above) were noted, including pairs without broods. The total number of observations was 16,468 (per mountain region: DF = 2,321, FH = 6,672, GNE = 1,735, GSE = 2,192 and RS = 3,548, c.f. Fig. 1). To estimate the proportion of juveniles in each survey area each year, we used generalized mixed effect models with a logit link function for each mountain region separately (Crawley 2007), with number of juveniles/adult in each encounter as the dependent variable and a variable linking survey areas to year (called survey area-year) fitted as a random intercept. Then, we estimated the proportion of juveniles for each mountain region in each year by fitting a random intercept linking mountain region to year (called mountain region-year). This allowed us to estimate the proportion of

juveniles from each encounter for each year in all survey areas and mountain regions separately. Large clusters are easier to detect than small clusters, and dogs spend more time searching close to the transect line than farther away (Pedersen et al. 2004). This might result in a size bias where average cluster size becomes larger at long distances compared to distances close to the transect line, and consequently, estimates of cluster size might be overestimated. As there is a positive correlation between cluster size and recruitment, we included distance from the transect line to the observation as a covariate in the models (Buckland et al. 2001). Consequently, we assumed that the effect of detection distance on cluster size was linear on the logit scale. While other relationships are also possible, low sample sizes in some areas/years would preclude more complex modelling of the relationship.

To estimate the recruitment of juveniles (number of juveniles/pair) we first estimated PJ, the proportion of juveniles in the sample estimated at the intercept (i.e. the back-transformed logit-value at the intercept). This corresponded to the proportion of juveniles at zero distance from the transect line, where detection probability is assumed to be one (Buckland et al. 2001). The number of juveniles/pair was then estimated as: $PJ / \left[\frac{1-PJ}{2} \right]$. The total number of

estimates was 464 and 60 for the survey area and mountain region scales, respectively.

Weather and rodent data

The breeding season was divided into three time periods: Pre-incubation (PRE-INC), Incubation (INC) and Brood (BROOD). Based on an average hatch date of 24 June (Erikstad et al. 1985), we backdated 21 days of incubation (Westerskov 1956) and defined this period (3–24 June) as the incubation period (INC). The period prior to incubation was defined as the pre-incubation period (PRE-INC), and included laying and pre-laying days (1 May–2 June), and we defined the period after hatching (25 June–15 July) as the brood rearing period (BROOD). At the end of this period, most chicks are fledged and mortality is reduced compared to the preceding periods (Erikstad 1985a).

Local weather data

We obtained data on mean daily temperature (°C) and daily precipitation (mm) from local meteorological stations located >600 m above sea level. Not all stations recorded both temperature and precipitation, and many stations were opened or closed during our study period. Thus, we selected the five stations close to our survey areas with the most complete time series that included both temperature and precipitation data (Fig. 1). We measured distance between meteorological stations and the centre points of the survey areas and mountain regions. Ptarmigan data were then linked to data from the nearest meteorological station at both spatial scales. As a measure of temperature, we estimated the mean of all daily mean-temperatures (T) in all periods ($T_{\text{PRE-INC}}$, T_{INC} , and T_{BROOD}). Further we summed all daily precipitation in millimetres (RR) to obtain a measure of total precipitation in each period ($\text{RR}_{\text{PRE-INC}}$, RR_{INC} , and RR_{BROOD}). All local meteorological data were obtained from the open access database of the Norwegian Meteorological Institute at: <http://www.eklima.met.no/>.

Onset of plant growth

The OPG in spring is related to weather conditions such as snow-cover and temperature (Wielgolaski et al. 2011; Odland 2011). Variation in the timing of plant growth can possibly affect recruitment of juveniles through its effect on maternal nutrition and prey availability (Steen et al. 1988a; Moss and Watson 1984; Erikstad and Spidso 1982). To obtain estimates of OPG, we first used *Geospatial Modelling Environment* (Beyer 2012) to create minimum convex polygons (MCPs) for each mountain region, based on the centre points of survey areas within each region.

Then, we extracted OPG from MODIS satellite data from 2000 to 2011 separately for each mountain region. The time-series of MODIS data have been atmospheric corrected and the measurement of OPG is well correlated with field observations of the onset of leafing (Karlsen et al. 2009, 2012). Because of data deficiencies, the OPG estimates for Rondane and Glomma southeast were only based on parts of the mountain regions. Nonetheless, we believe the data were adequate since the general year to year variation was present, and the focus of this study is the temporal, rather than spatial variability in driving factors. The mean start of the growing season across all years and regions was 3 June, while the earliest mean start of the growing season was 28 May in 2011, and the latest mean start was 10 June in 2005.

Large-scale climate variation

Large-scale climatic variability, such as the North Atlantic oscillation (NAO), is known to impact on population dynamics and ecological processes in birds (Forchhammer and Post 2000; Stenseth et al. 2002; Barnagaud et al. 2011). The NAO gives an index of the difference in atmospheric pressure over the North Atlantic and, during winter, it strongly influences temperature and precipitation in Northern Europe (Hurrell 1995). The focus in this paper is climatic variability during the breeding season (cf. 1 May–15 July, above), thus we choose to use a seasonal station-based NAO-index for the period May, June and July (NAO_{MJJ}) (Hurrell 2013) obtained from an open-access database at: <https://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-station-based>.

Rodent abundance data

Steen et al. (1988b) demonstrated that recruitment of juveniles 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. We obtained long term rodent trap data from two sites in our study area; Åmotsdalen from 1991 to 2011 (Framstad 2012; Selas et al. 2011) and Fuggdalen from 1974 to 2009 (Selas et al. 2011) (see Fig. 1). Rodents were caught in snap-traps in September and abundances were indexed as number of rodents caught per 100 trap nights. The dynamics of rodent populations is complex, but one important determinant is the winter climate (Cornulier et al. 2013; Ims et al. 2008; Kausrud et al. 2008), where favourable conditions during winter can result in high densities in early spring and vice versa. There is often a close relationship between spring and autumn densities of rodents (Kausrud et al. 2008); hence, data collected in

September are likely to provide a good index of rodent abundance throughout the Willow Ptarmigan breeding season. We linked Willow Ptarmigan data from survey areas and mountain regions to the nearest rodent trapping site.

Since the OPG data were restricted to the period 2000–2011, we used this period as the time-frame for further analyses. Then we omitted 36 estimates from the survey areas including two survey areas that were lacking data after 2000. For the mountain region scale we omitted six estimates. Hence, when assessing spatial synchrony in the period 2000–2011, the data consisted of 428 (57 survey areas) and 54 (five mountain regions) estimates of juveniles/pair at the survey area and mountain region scale, respectively. Further, as there were missing records in the meteorological and rodent data series as well (c.f. above), the dataset used for investigating climatic and predation effects was additionally reduced to 330 (57 survey areas) and 40 (five mountain regions) estimates of juveniles/pair with corresponding predictor variables at the survey area and mountain region scale, respectively.

Statistical analysis

We assessed spatial synchrony in recruitment rates by constructing matrices of pair-wise Pearson cross-correlations, both between survey areas and between mountain regions. Because of a lack of statistical independence of pair-wise cross-correlations, we calculated mean cross-correlation coefficients and confidence limits with a bootstrap procedure (Kvasnes et al. 2010). Pair-wise cross-correlation coefficients were then sampled with replacement to generate 100,000 matrices of randomly drawn correlation coefficients (Crawley 2007). This distribution was then used to estimate the mean, together with 2.5 and 97.5 % percentiles from the original matrix of pair-wise cross-correlation coefficients. We estimated bootstrapped means and percentiles across all survey areas, across survey areas within mountain regions and across mountain regions. We also assessed the level of synchrony in the rodent trap data by calculating a Pearson cross-correlation between the two trap sites.

The effect of climatic conditions and predation (indexed by rodent abundance) on recruitment of juveniles was modelled with linear mixed effect models at the survey area and mountain region scale (c.f. Fig. 1). We only considered additive effects and did not combine confounded variables. The local and regional climatic variables were modelled separately. At the survey area scale we included survey area, mountain region and year nested within mountain region as random effects, and at the mountain region scale we included mountain region and year as random effects. From the set of candidate models we used an information

theoretic approach (Burnham and Anderson 2002) to select the most parsimonious model explaining the variation in recruitment of juveniles at survey area and mountain region scales, respectively. Because of the low sample size (~ 12 years), we used AICc as the selection criteria. ΔAICc values of <2 suggest that the models are equally parsimonious, but in such cases we selected the simplest model. As the amount of variance explained (R^2) by the explanatory variables can be of biological interest (Nakagawa and Schielzeth 2013), we estimated R^2 of the fixed effects from the most parsimonious models following the guides in Nakagawa and Schielzeth (2013).

To investigate how local conditions (weather variables and OPG) were related to the NAO index, we fitted linear mixed effects models with local variables as dependent variables and NAO_{MJJ} as fixed effect. Since local weather variables and OPG data were derived from different locations (five meteorological stations and five mountain regions, respectively), we considered two models for each variable: one with additive effects of location and NAO_{MJJ} , and one with the interaction between the two terms. All models were fitted with year as random effect. We used an information theoretic approach (as described above) to select the most parsimonious model (Burnham and Anderson 2002), and we calculated bootstrapped confidence intervals and used these to evaluate if the slopes relating NAO_{MJJ} to the climate variable of interest from the selected models were different from zero.

All statistical analyses were carried out using R (R-Core-Team 2012). For the mixed effect models we used the *lmer* function in the *lme4* package (Bates et al. 2011), and for the model selection procedure we used the *MuMIn* package (Barton 2013).

Results

Mean recruitment of juveniles across all survey areas varied from 3.52 juveniles/pair in 2009 to 5.84 juveniles/pair in 2007, and the overall mean (2.5 and 97.5 % percentiles) was estimated to be 4.76 juveniles/pair (4.62 and 4.90). At the mountain region scale, the mean (2.5 and 97.5 % percentiles) recruitment of juveniles was 4.65 juveniles/pair (4.36 and 4.91) (Fig. 2).

Correlation in recruitment of juveniles between mountain regions in south-central Norway was generally high and significant (Table 1). The mean correlation between the five mountain regions was higher than between survey areas located within mountain regions (Table 2). Even though correlation coefficients between some pairs of mountain regions and some pairs of survey areas were not significant, the overall bootstrapped mean correlations were significantly positive (Table 1). The rodent trap data

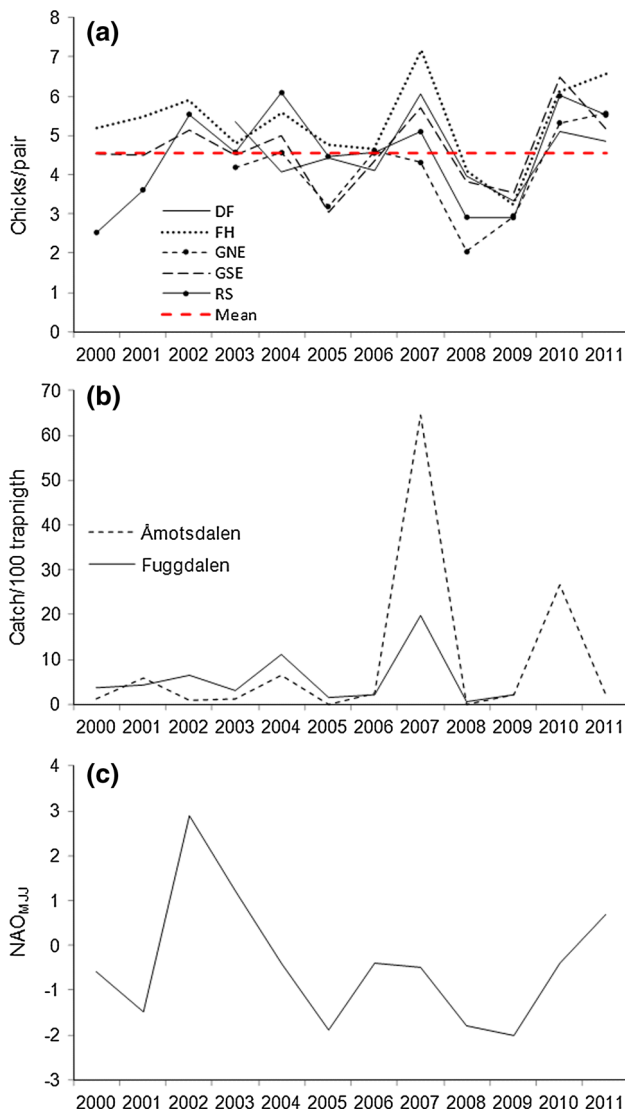


Fig. 2 **a** Recruitment of juveniles (juveniles/pair) in mountain regions, **b** standardized rodent abundance indices and **c** the seasonal NAO index for May, June and July between 2000 and 2011. In **(a)** Dotted horizontal line indicates the overall mean number of juveniles per pair and RS Rondane, DF Dovre and Folldal, FH Forollhogna, GNE Glomma north-east, GSE Glomma south-east. In **(b)** cross-correlation coefficient between rodent trap sites was 0.89 ($n = 10$ years)

were also highly synchronous with a correlation coefficient (95 % CI) of 0.89 (0.60–0.97).

Modelling recruitment as a function of environmental covariates, model selection suggested that models including additive effects of rodent abundance and NAO_{MJJ} performed much better than all other candidate models (Table 3). Both variables had a positive effect on recruitment of juveniles (Slope \pm SE; mountain region scale: $NAO_{MJJ} = 0.53 \pm 0.10$, Rodent = 0.03 ± 0.01 and survey area scale: $NAO_{MJJ} = 0.54 \pm 0.08$, Rodent = 0.03 ± 0.01 , Fig. 3). This implies that Willow Ptarmigan

Table 1 Pair-wise cross-correlation coefficients between mountain region recruitment rates (juveniles/pair)

	DF	FH	GNE	GSE	RS	Number of years
DF	█					9
FH	0.81*	█				12
GNE	0.50	0.73*	█			9
GSE	0.64**	0.79*	0.77*	█		12
RS	0.53	0.67*	0.87*	0.66*	█	12

RS Rondane, DF Dovre and Folldal, FH Forollhogna, GNE Glomma northeast, GSE Glomma southeast

* p value <0.05

** p value <0.1

Table 2 Mean cross-correlation coefficients for recruitment of juveniles during the period 2000–2011 with confidence intervals (2.5 and 97.5 % percentiles, respectively) based on bootstrap

	Mean r	2.5 %	97.5 %
FH	0.39	0.31	0.45
DF	0.52	0.42	0.62
GNE	0.61	0.51	0.71
GSE	0.63	0.55	0.71
RS	0.48	0.42	0.55
Among all areas	0.44	0.42	0.46
Among mountain regions	0.70	0.63	0.77

Correlations are between areas within mountain regions (FH, DF, GNS, GSE and RS), among all areas and among mountain regions (for the latter, c.f. Table 1)

RS Rondane, DF Dovre and Folldal, FH Forollhogna, GNE Glomma northeast, GSE Glomma southeast

recruitment was high in years with a high abundance of rodents and positive NAO_{MJJ} values. The $\Delta AICc$ values for the second best supported models were 18.33 and 5.86 at the survey area and mountain region scales, respectively (Table 3). The fixed effects from the most parsimonious models explained 27 and 51 % of the variation in recruitment, while the second ranked models explained 16 and 34 %, at the survey area and mountain region scales, respectively. Models with the single effects of either rodent abundance or NAO_{MJJ} were not sufficient to explain the observed variation in recruitment of juveniles (Table 3). However, when comparing these two variables, NAO_{MJJ} models explained more of the variation in recruitment than rodent abundance models at both scales (Table 3). A sensitivity analysis based on the most preferred model at both scales (Table 3) confirmed the greater influence of NAO_{MJJ} than rodent abundance. When holding NAO_{MJJ} constant at its mean value and varying the rodent abundance across the observed values, predicted recruitment of juveniles changed from 4.25 to 6.03 juveniles/pair (survey area) and from 4.11 to 6.27 juveniles/pair (mountain region). Similarly, when holding rodent abundance constant and letting

Table 3 Model selection tables (10 best supported models) based on AICc selection criteria for the survey area scale (a) and mountain region scale (b)

Model	df	AICc	Δ AICc	logLik	AICc weight
(a)					
NAO _{MJJ} , Rodent	7	1,055.80	0.00	-520.73	1.00
NAO _{MJJ}	6	1,074.10	18.33	-530.94	0.00
Rodent, T_{BROOD} , RR _{INC}	8	1,077.10	21.28	-530.32	0.00
Rodent, T_{BROOD} , RR _{INC} , RR _{PRE-INC}	9	1,077.90	22.13	-529.69	0.00
Rodent, T_{BROOD} , T_{INC}	8	1,079.50	23.68	-531.52	0.00
Rodent, RR _{INC}	7	1,080.30	24.44	-532.96	0.00
Rodent, OPG, RR _{INC}	8	1,080.70	24.85	-532.11	0.00
Rodent, T_{BROOD}	7	1,080.80	25.02	-533.24	0.00
Rodent, OPG, T_{INC}	8	1,081.20	25.35	-532.36	0.00
Rodent, T_{INC}	7	1,081.40	25.61	-533.54	0.00
(b)					
NAO _{MJJ} , Rodent	6	98.40	0.00	-41.87	0.91
NAO _{MJJ}	5	104.20	5.86	-46.21	0.05
Rodent, RR _{INC}	6	108.20	9.78	-46.76	0.01
Rodent	5	109.90	11.52	-49.04	0.00
Rodent, T_{INC}	6	109.90	11.57	-47.66	0.00
Rodent, T_{BROOD} , RR _{INC}	7	110.40	12.02	-46.39	0.00
Rodent, RR _{BROOD} , RR _{INC}	7	110.80	12.38	-46.57	0.00
Rodent, RR _{INC} , RR _{PRE-INC}	7	110.80	12.42	-46.59	0.00
Rodent, OPG, RR _{INC}	7	110.90	12.53	-46.64	0.00
Rodent, $T_{PRE-INC}$, RR _{INC}	7	111.10	12.77	-46.76	0.00

T_x and RR_x are mean temperature and sum of precipitation (mm.) in period x , respectively. *PRE-INC* period before incubation, *INC* incubation period and *BROOD* is the period after hatching (for exact dates of the periods, see section “Local weather data” in the methods). OPG is the average day for onset of plant growth within a mountain region (for details, see section “Onset of plant growth” in the methods). NAO_{MJJ} is the station-based seasonal NAO index for May, June and July (for details, see section “Large-scale climate variation” in the methods). Rodent is the standardized rodent abundance index (catch/100 trap nights) (for details, see “Rodent abundance data” in the methods)

NAO_{MJJ} vary across the observed range of values, recruitment of juveniles was predicted to display a larger change; 3.94–6.59 juveniles/pair (survey area) and 3.79–6.41 juveniles/pair (mountain region).

In general, models including meteorological data or plant growth indices rather than NAO_{MJJ} received little support. The best models including such variables consisted of a positive effect of rodents and precipitation during incubation and a negative effect of temperature

during the brood period at the survey area scale, and a positive effect of rodents and a positive effect of precipitation during the incubation period at the mountain region scale (Table 3).

The relationship between local climate variables and NAO_{MJJ} was generally consistent across the meteorological stations and mountain regions, as the models with an interaction between station or mountain region and NAO_{MJJ} generally performed poorer than the additive models (Table 4). For temperature during the incubation period (T_{INC}) and precipitation during the pre-incubation period (RR_{PRE-INC}) Δ AICc was <2 (Table 4) suggesting that the models were equally supported by the data. Parsimony suggests, however, that the interaction term was not needed to model the relationship, and that effect of NAO_{MJJ} on local conditions was similar among the meteorological stations and mountain regions in the study area. Examining parameter estimates from the additive models, confidence intervals for the slope parameter (i.e. the NAO_{MJJ}-effect) did not overlap zero for temperature during the incubation and pre-incubation periods, precipitation during the pre-incubation period and for the OPG (Table 5). The signs of the coefficients suggested a positive effect of NAO_{MJJ} on local temperature during pre-incubation and incubation and on precipitation during pre-incubation, and that high NAO_{MJJ} values are related to an early onset of spring.

Discussion

In this paper we have investigated synchrony in the recruitment of juveniles within and among mountain region populations, and the effect of predation and large—as well as local—scale climate on local and regional recruitment rates in Willow Ptarmigan. First, we found that recruitment of juveniles was synchronous among and within mountain regions in southeastern and central Norway (mean distance between mountain region centrepoints: 96.5 km, c.f. Fig. 1). Second, variation in recruitment of juveniles at both mountain region scale and survey area scale were related to variability in rodent abundance and the NAO during the breeding season (NAO_{MJJ}). Although there were only two rodent trap sites, they were highly synchronous at a distance of 118 km, suggesting that rodent populations elsewhere in the study area also follow a similar pattern.

The relatively strong correlation in recruitment of juveniles among mountain regions, and the strong correlation in abundance indices between rodent trap sites, suggest that spatially separated populations are subject to similar extrinsic environmental forces. The spatial scale of this correlation further suggests that these environmental forces work similarly across large regions. Within mountain regions, correlations in recruitment were more variable

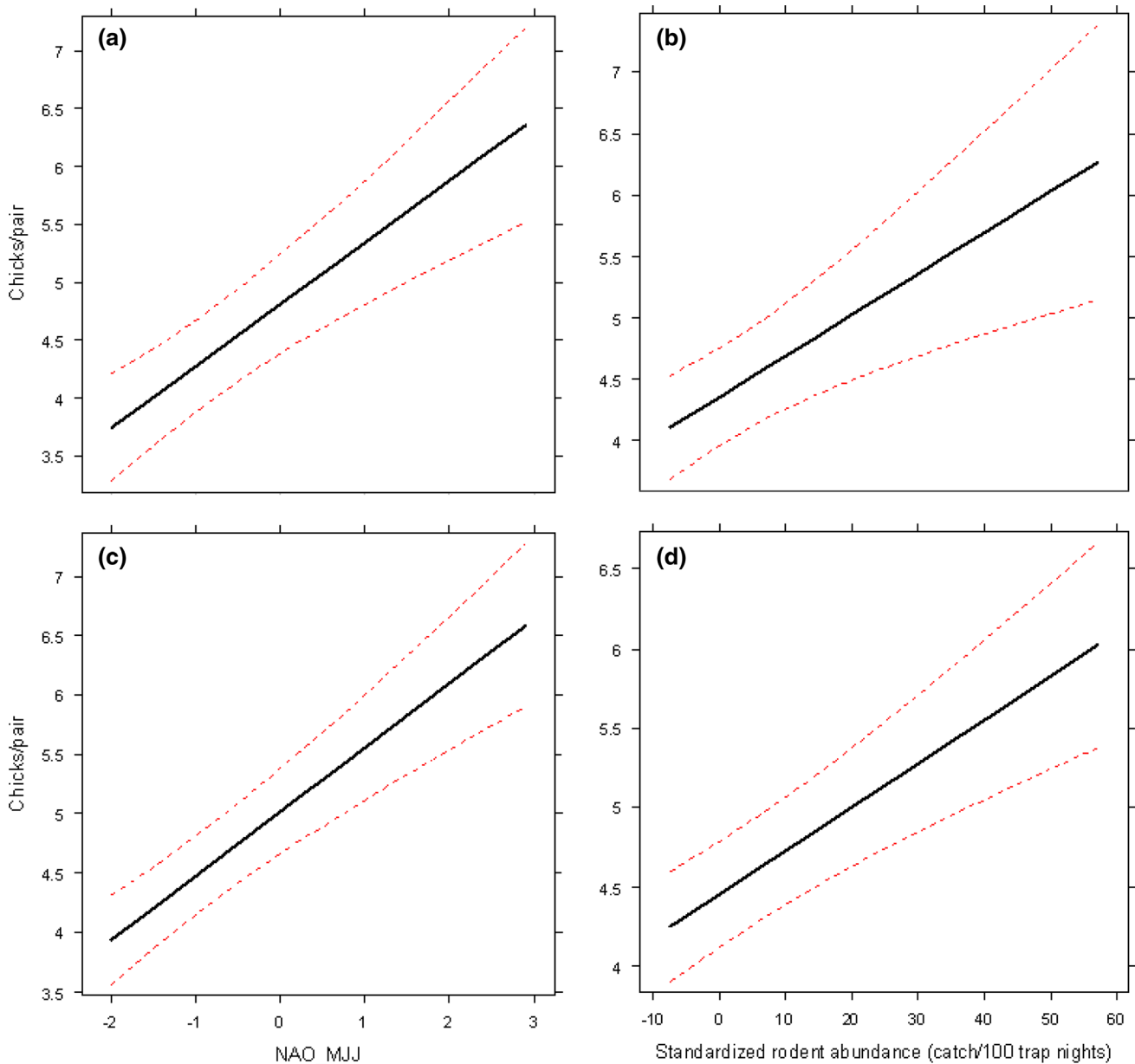


Fig. 3 Number of juveniles/pair plotted against NAO (a, c) and standardized rodent index (b, d). Top (a, b) is mountain region scale and below (c, d) is survey area scale. Slope \pm SE from generalized

mixed effect models; mountain region scale: NAO = 0.53 ± 0.10 , Rodent = 0.03 ± 0.01 and survey area scale: NAO = 0.54 ± 0.08 , Rodent = 0.03 ± 0.01

and the average correlation was lower within than between regions. This local variation could arise from variation in local factors such as habitat and predation rates (Tavecchia et al. 2008), but the pattern may also be due to the small size of local populations and low sample sizes making them more vulnerable to demographic stochasticity and sampling variation (Tedesco et al. 2004).

When examining the effects of extrinsic environmental factors on Willow Ptarmigan recruitment, the models gaining the strongest statistical support included both a positive effect of rodent abundance and NAO during May,

June and July. This suggests that a high abundance of rodents in the breeding season and high values of NAO_{MJJ} increase recruitment rates in Willow Ptarmigan. The positive effect of rodent abundance on recruitment of juveniles is most likely related to lower predation rates at rodent peaks (Steen et al. 1988b), as predicted by the alternative prey hypothesis (Kjellander and Nordstrom 2003; Hagen 1952). A high abundance of rodents in autumn generally follows high numbers in the preceding spring (Kausrud et al. 2008). High densities of rodents during laying, incubation and early brood rearing periods

Table 4 Model selection table for models investigating the relationship between NAO_{MJJ} and local climate variables (i.e. column *Variable*)

Response variable	Model	df	AICc	$\Delta AICc$	logLik	AICc weight
T_{Brood}	Additive	8	127.72	0.00	-54.36	0.99
	Interaction	12	136.41	8.68	-52.66	0.01
T_{Inc}	Additive	8	160.44	0.00	-70.72	0.7
	Interaction	12	162.14	1.7	-65.52	0.3
$T_{Pre-inc}$	Additive	8	126.53	0.00	-53.77	0.98
	Interaction	12	134.46	7.93	-51.68	0.02
RR_{Brood}	Additive	8	474.87	0.00	-227.72	0.99
	Interaction	12	485.45	10.58	-226.62	0.01
RR_{Inc}	Additive	8	473.76	0.00	-227.16	0.99
	Interaction	12	483.85	10.09	-225.82	0.01
$RR_{Pre-inc}$	Interaction	12	462.69	0.00	-215.24	0.55
	Additive	8	463.11	0.43	-221.84	0.45
OPG	Additive	8	314.54	0.00	-147.86	0.99
	Interaction	12	323.44	8.90	-146.4	0.01

For each local variable, we considered two models, one with interaction between NAO_{MJJ} and spatial location (interaction), and one without interaction (additive)

Table 5 Parameter estimates with confidence intervals (2.5 and 97.5 % percentiles, respectively) based on bootstrap for the effect of NAO_{MJJ} on local conditions, from the additive models in Table 4

Variable	Estimate	2.50 %	97.50 %
T_{Brood}	-0.41	-0.02	0.23
T_{Inc}	0.94*	0.34	1.62
$T_{Pre-inc}$	0.4*	0.002	0.81
RR_{Brood}	4.8	-5.82	14.69
RR_{Inc}	0.51	-7.05	7.99
$RR_{Pre-inc}$	6.3*	1.25	11.54
OPG	-1.58*	-3.1	-0.17

* Confidence limits not overlapping zero

may thus indirectly reduce predation on ptarmigan eggs and chicks if generalist predators prefer easily caught rodent prey. Interestingly, our models explained a similar amount of variation in recruitment as the models of Steen et al. (1988b). However, contrary to Steen et al. (1988b), more of the variation in our models was explained by weather conditions (NAO_{MJJ}) than rodent abundance.

None of the models that included local meteorological variables received as much support as those including the NAO_{MJJ} index. One possible reason for this is that local meteorological data can contain noise which may reduce the predictability of such data. Further, local data such as temperature and precipitation can be interpreted in many ways and it might be difficult to identify important

variables (Hallett et al. 2004). The NAO index, however, might be more useful as it integrates the effects of several local weather variables simultaneously. Our finding that recruitment of juveniles is more related to large-scale climate than local climate is in agreement with other studies (Hallett et al. 2004; Stenseth et al. 2003).

The effect of NAO_{MJJ} provides limited information about the underlying mechanisms unless it can be related to some local climatic condition. It is already known that positive values of winter NAO are related to warm and moist conditions in Western Europe (Hurrell 1995). We found that NAO_{MJJ} had a similar effect on local conditions in our study area. In general, there was a significant positive relationship between NAO_{MJJ} and temperatures during the incubation and pre-incubation periods and between NAO_{MJJ} and precipitation in the pre-incubation period. High temperatures together with precipitation during this period (May to late June) will probably accelerate snow melt in mountain areas, and might thus be one of the reasons for the positive effect of NAO_{MJJ} on recruitment of juveniles (Slagsvold 1975; Steen et al. 1988a, b). This is further supported by the fact that OPG was negatively related to NAO_{MJJ} , i.e. that positive NAO_{MJJ} values accelerate plant growth. Potential mechanisms behind the climate effect detected here might thus be a positive effect of early plant growth on maternal nutrition (Moss and Watson 1984), food availability for chicks (Erikstad and Spidso 1982; Erikstad 1985a; Erikstad and Andersen 1983) and the timing of laying (Erikstad et al. 1985), which are all known to affect recruitment of juveniles positively.

In North American Willow Ptarmigan, the probability of reneesting was higher in a year with normal weather than during a year with harsh weather (Martin and Wiebe 2004), and reneesting can potentially increase yearly recruitment (Martin et al. 1989; Parker 1985). Sandercock and Pedersen (1994) found that females that reneested had larger eggs in their first clutch than females that did not, suggesting that reneesting probability could be related to female nutrition. Similarly, in Capercaillie, reneesting increased recruitment (Storaas et al. 2000) and the reneesting probability was highest for heavy females. Favourable conditions in spring may thus buffer some of the effect of egg predation through increased reneesting frequency.

It is interesting to observe that recruitment of juveniles in all mountain regions was above average in 2011 when rodent populations in Åmotsdalen collapsed (c.f. Figs. 2, 3). Since rodent populations were highly synchronized across the study area, it is likely that a collapse also occurred in Fuggdalen and other areas within the study region that year. This may be a result of a mismatch between rodent abundance in spring and autumn because of a collapse in the rodent population during summer (c.f. Kausrud et al. 2008; Wegge and Storaas 1990). Alternatively, the strong positive

NAO_{MJJ} that year may have reduced the otherwise negative effect of predation that would be expected (e.g. through increased reneating frequency). In connection to this and in contrast to Steen et al. (1988b), it is also interesting to see that at both spatial scales, the relative effects of large-scale climate were stronger than the effect of local rodent abundance (predation). There might be several reasons for this: First, this might be related to the scale at which the rodent and NAO_{MJJ} are collected. As for the local climate data, the rodent data were measured at a finer scale than the NAO index, and might then be more vulnerable to demographic stochasticity and sampling variation (Tedesco et al. 2004). Strong correlation between rodent trap sites, however, suggests that this is not the case for this data. Second, the rodent abundance might be a good index for predation rates, but not a perfect one. Rodent dynamics are complex with regard to the timing of a collapse, and the Willow Ptarmigan is subject to predation from other non-rodent-eating specialist predators, as well as rodent-eating generalist predators (Munkebye et al. 2003), and this might induce unexplained variability. Third, climatic forcing on population dynamics of ptarmigans might potentially have become more pronounced in recent years, due to the collapse in small rodent population cycles (Kausrud et al. 2008; Steen et al. 1988b; Ims et al. 2008). It is likely that other species, such as ptarmigan, were entrained in the rodent cycle by shared predators when regular population fluctuations existed (Hagen 1952; Kjellander and Nordstrom 2003). This link may have weakened since the late 1980s and mid 1990s as small rodent fluctuations became more irregular (Kausrud et al. 2008; Ims et al. 2008) and the effects of environmental perturbations and climatic variation became more pronounced in the dynamics of ptarmigan.

In this study we demonstrate that recruitment of juvenile Willow Ptarmigan is synchronized across south-central Norway. The seasonal NAO during May, June and July and rodent abundance positively affect recruitment of juveniles, and are, therefore, possible drivers of the observed spatial synchrony. We suggest that global climate change may indirectly affect Willow Ptarmigan recruitment through its effects on the rodent cycle (Ims et al. 2008; Kausrud et al. 2008), but also directly by affecting plant growth and snow conditions during spring.

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