Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

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PhD-thesis

Hunting management of a red listed small game species on public land in Norway

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Forord

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Men først har jeg lovet min kone og mine barn at bare jeg blir ferdig med doktorgraden så skal jeg begynne å jakte igjen!

Kulturarven føres videre. Martin og Brede flår elg i Breisjøberget jaktlag.

Jo Inge Breisjøberget

Evenstad, desember 2017

Contents

Sammendrag (Norwegian summary)

Å sikre en bærekraftig høsting av liryper (*Lagopus lagopus*), en populær og nå rødlistet småviltart, er en krevende oppgave. Rypene har potensial for en rask bestandsvekst og bestandsdataene er ofte usikre. Det er vanskelig å evaluere jaktas rolle og effekter av innførte forvaltningstiltak da foreliggende kunnskap om sammenhengen mellom jegerinnsats, jaktuttak og tetthet av ryper er mangelfull. Tidligere evaluering av jegernes holdninger til begrensninger i uttak har i liten grad fokusert på den reelle effekten av de innførte tiltakene på jaktutøvelsen og lirypenes bestandstetthet. Det er også viktig å belyse hvilke andre faktorer som påvirker rypas bestandsendringer, og i denne sammenhengen har en mulig økning i rødrevens (*Vulpes vulpes*) rolle som predator på liryper blitt viet oppmerksomhet. Endringer i predatorfaunaen antas å kunne påvirke lirypas bestandsutvikling negativt, og effekten kan forsterkes av forandringer i smågnagernes sykliske svingninger.

Statskog forvalter rypejakta på statens grunn utenom statsallmenning. Statskogs mål er at flest mulig skal få tilgang til en attraktiv rypejakt, men etter at lirypa kom på rødlista (2015) har mange stilt spørsmål om jakta tilfredsstiller naturmangfoldlovens (2009) krav om bærekraftig høsting. I denne doktoravhandlingen ville jeg derfor (i) estimere jaktuttaket på statens grunn i Nordland og Troms (26 828 km^2) og så evaluere betydningen av ulike faktorer som påvirker uttaket. Analysen var basert på takseringsdata fra 36 jaktfelt og avskytingsdata fra 162 jaktfelt i perioden 2013 – 2016. Videre (ii) brukte jeg en spørreundersøkelse (570 jegere) og jaktstatistikk (8 795 jaktdager) for å studere jegernes holdninger til reguleringer og effekten av ulike jaktrestriksjoner på både ryper og jegere. Til slutt (iii) undersøkte jeg i hvilken grad populasjonsvekst og kyllingproduksjon hos lirype ble påvirket av en interaksjon mellom smågnagere og rødrev. Dette arbeidet var basert på en analyse av snøsporingsdata på rev (621 linjer) og høsttakseringer av lirype og smågnagere (48 takstområder) fra Hedmark (2005-2014).

Tidligere studier har konkludert med at additive effekter av jakt på hønsefugl er merkbare ved uttak over 15-20 % av bestandene. Ved et lavere uttak har jakt vist seg å være delvis kompensert av naturlig dødelighet. Jeg fant et gjennomsnittlig jaktuttak på

mindre enn 10 %, og i bare 21 % av feltene var uttaket over 15%. Dette tyder på at lirypejakta i mitt studieområde i all hovedsak hadde beskjeden effekt. Det viste seg imidlertid at uttaket var tetthetsavhengig. Andelen skutte ryper økte ved lave tettheter, og dette medfører at restriksjoner i jaktuttaket først og fremst bør vurderes når bestandene er små.

Storparten (66 %) av jegerne støttet begrensninger i jaktuttaket, og de fleste (89 %) var villige til å felle færre liryper for potensielt å øke neste års bestand. Det var en tydelig forskjell i holdninger til restriksjoner i jaktutøvelsen mellom lokale- og utenbygdsjegere (besøkende fra andre fylker). Forskjellene reflekterte mer positive holdninger til reguleringer som i minst mulig grad ville ramme egen jaktutøvelse. For eksempel var tilreisende jegere negative til utsatt jaktstart og positive til tidligere sesongavslutning. Disse jegerne besøker jaktområdene hovedsakelig i de første 2-3 ukene av jakta. Det viste seg at de aller fleste jegerne ikke ble berørt av dagens begrensing på 4 ryper pr dag da dette antallet ble oppnådd i bare 6 % av jaktdagene. Basert på de oppgitte fellingstallene måtte den daglige kvoten settes til 1 rype for å oppnå en 50 % reduksjon i uttaket. Jegerne var generelt negative til å innføre en så sterk begrensning i antall skutte fugl.

De studerte lirypebestandene i Sørøst-Norge minket ikke i studieperioden. Populasjonsvekst og hekkesuksess var sterkt korrelert, og begge variablene var påvirket av sammenhengen mellom smågnagere og rødrev. Rødreven påvirket rypene negativt kun i år med sammenbrudd i smågnagerbestandene. Dette støtter den alternative byttedyr-hypotesen (APH), og resultatene bekrefter rødrevens viktige rolle i populasjonsdynamikken til liryper. Resultatene tyder på at dempede topper i smågnagerbestandene kan påvirke rypene negativt gjennom høyere predasjon.

Basert på mine resultater vil jeg anbefale rypeforvaltere å fortsette å taksere sine bestander og måle innsats og uttak, spesielt for å avdekke og sette inn tiltak i dårlige produksjonsår. Om eventuelle restriksjoner i jakta settes inn, må det basere seg på kunnskap om bestandsstørrelse, høstingsrate og en reell effekt av tiltaket. Kvoter bør vurderes i ved lave bestandstettheter og i år med lite smågnagere, og de må settes lave nok til å ha en reell effekt på uttaket. Ved middels- eller høye tettheter av lirype vil ytterlige begrensninger av jakta ikke være nødvendig.

Abstract

Sustainable harvest of willow ptarmigan (*Lagopus lagopus*), a popular and recently red-listed small game species, is a challenging task. The ptarmigan has a potential for rapid population growth, and population abundance estimates are often uncertain. It is crucial for managers to identify correct harvest levels, and to gain knowledge about the relationship between hunters' attitudes towards harvest restrictions and the effect of these restrictions. However, among earlier studies of hunters' attitudes, few have focused on the actual effects on the ptarmigan populations. There is also a need for an improved understanding of what other influential factors affect ptarmigan population changes. Recently, attention has been directed towards an increasing abundance and distribution in red fox (*Vulpes vulpes*) and its potentially negative effect on willow ptarmigan. An increase in generalist predator abundance along with dampened small rodent cycles may contribute to further decline in ptarmigan populations and other alternative prey species.

The Norwegian State-Owned Forest and Land Enterprise (Statskog) manages ptarmigan hunting on public land in Norway. One of Statskogs' main goals is to ensure that harvest levels are sustainable while securing hunting access to the public. Willow ptarmigan and rock ptarmigan (*Lagopus muta*) were defined as near threatened on the Norwegian red list of species in 2015, and there has been a debate whether hunting for ptarmigan is sustainable. In this doctoral thesis I aimed to (i) estimate ptarmigan harvest levels on 26,828 km^2 of state-owned land in Nordland and Troms Counties, and evaluate determinant factors for harvest. In the period 2013-2016, I estimated harvest rates in 162 hunting blocks of which 36 blocks had density estimates. Next, (ii) I studied hunters' attitudes towards imposed harvest restrictions based on a questionnaire (n=570 hunters), and I evaluated their effect by the use of bag statistics (n= 8,795 hunting days). Finally, (iii) I examined to which degree spatiotemporal patterns in willow ptarmigan chick production and population growth were affected by an interaction between small rodents and red fox abundance. I investigated these relationships by analyzing abundance data on red fox, rodents, and ptarmigan from Hedmark County (2005-2014).

Earlier studies of ptarmigan have indicated additive effects of hunting mortality at harvest rates exceeding 15-20 %. At lower harvest rates hunting mortality is probably

partially compensated by natural mortality. I found that the mean harvest rate was below 10 %, and in only 21 % of the hunting blocks did the harvest rate exceed 15 %. This result indicates that hunting for willow ptarmigan had a modest effect on the populations in my study area. However, harvest rates were density dependent, with increasing rates at low ptarmigan densities. Accordingly, hunting restrictions should therefore be considered primarily at low population densities.

Most hunters (66 %) were positive to restrictions in harvest, if needed, and a majority (89 %) was willing to reduce their harvest to increase next year's breeding population. The residency of the hunter was the most influential factor regarding attitudes towards hunting restrictions. The hunters were generally more positive towards the hunting restrictions that had the smallest effect on their own hunting practice. For instance; non-resident hunters were negative towards a delayed opening of the hunting season and positive towards an earlier end of the season. These hunters visit the area mainly in the beginning of the hunting season, within the first two or three weeks. The daily bag limit of 4 birds was reached in <6% of all reported hunting days and had little effect on the hunters and the total harvest. In order to reduce the harvest with 50 %, the daily bag limit would have to be set at one bird per hunter, a restriction the hunters found unacceptable.

The willow ptarmigan populations in my study area in Southeastern Norway did not decrease in the study period. I found that the population growth and breeding success of ptarmigan was strongly correlated, and determined by an interaction between red fox- and small rodent abundance. A negative impact of red fox on ptarmigan appeared only when small rodents were in a crash phase. This result is in accordance with the APH hypothesis and confirms the important role of red fox in willow ptarmigan population dynamics. The result also indicates that ptarmigan may experience a higher predation pressure in periods of dampened small rodent cycles.

Based on these results, I recommend managers of ptarmigan to continue population surveys and to record hunting effort and hunting bags in order to be able to implement harvest restrictions when needed. Harvest restrictions should be based on knowledge of population abundance, harvest rates and the actual effect of the restrictions.

List of publications

This thesis is based on the following original publications and submitted manuscripts, listed below. They are referred to in the text by their roman numerals.

Paper I: Breisjøberget, J.I., Odden, M., Storaas, T., Nilsen, E.B. & Kvasnes, M.A.J. Harvesting a red listed species: Determinant factors for Willow Ptarmigan harvest rates, bag sizes and hunting efforts in Norway. Manuscript.

Paper II: Breisjøberget, J.I., Storaas, T & Odden, M. 2017. Ptarmigan hunting restrictions: effects on hunters' opinions and harvest. *Journal of Wildlife Management*, **81**, 1179-1186.

Paper III: Breisjøberget, J.I., Odden, M., Wegge, P., Zimmermann, B. & Andreassen, H.P. The alternative prey hypothesis revisited: still valid for Willow Ptarmigan population dynamics. Submitted manuscript.

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1. Introduction

After decades with population decline all over Fennoscandia, willow ptarmigan is now listed as near threatened in the Norwegian Red List (Henriksen and Hilmo 2015). This marked decline has invigorated a debate whether current management regimes are sustainable and if stricter hunting regulations are required (Kaltenborn et al. 2012, Pedersen and Storaas 2013). The willow ptarmigan is the most popular game bird in Fennoscandia with a high social and economic importance (Bevanger 1995, Brøseth and Pedersen 2010, Pedersen and Karlsen 2007, Steen and Haugvold 2009). In Norway 55,000 - 100,000 citizens (of a population of 5.2 million people) hunt ptarmigan every year, with annual harvests of 120,000 to 365,000 birds during the last decade (Statistics Norway 2017). Population declines have occurred also among non-hunted montane species, which indicate that other factors than hunting are important (Andersen et al. 2014, Lehikoinen et al. 2014). It is crucial for managers to understand which factors affect harvest levels and if hunting restrictions are required. The different management regimes need to be evaluated according to their potential effect on harvest rates and hunting practices in order to optimize ecological, social and economic outcomes of the harvest (Andersen et al. 2014).

1.1 The willow ptarmigan

Willow ptarmigan is a widespread, medium sized grouse, inhabiting alpine tundra habitats (e.g. Hörnell-Willebrand 2005, Johnsgard 1983). The bird produce one clutch per year, with ability to renest if the eggs are depredated, and 8-12 eggs are hatched by the end of June (Erikstad et al. 1985, Martin et al. 1989, Myrberget 1972, Parker 1981). Thus willow ptarmigan has the capacity for rapid population growth with a high proportion of juveniles in the autumn population. Like several other grouse species, the ptarmigan populations fluctuate in cycles with 3-4, 6-7 or 10 years periods depending on geographic region (Moss and Watson 2001, Watson and Moss 1979). These cycles are believed to occur due to a variation in breeding success; with the main demographic factor being recruitment, with higher rates in small rodent peak years (Bergerud and Gratson 1988, Myrberget 1984, Steen and Erikstad 1996). There is a strong correlation between the proportion of young birds in the autumn population and the breeding population of willow ptarmigan the next year (e.g. Lindén 1981, 1989, Myrberget 1988). Ptarmigan nest on the ground and exhibit high predation rates of eggs, chicks and adults by mammals, corvids and raptors (Klaus 1985, Lindström et al. 1987, Myrberget 1988, Parker 1984, Steen and Haugvold 2009, Tornberg and Sulkava 1991). The reproductive success is first and foremost determined by predation on eggs and chicks, but weather conditions and the body condition of the adult birds also play a role (Kvasnes et al. 2014, Martin and Wiebe 2004, Robb et al. 1992).

1.2 Declining populations and influential factors

The underlying causes of the population declines are still unclear, but some theories include poorer survival of eggs and/or chicks, increased adult mortality or a combination of these factors (Pedersen and Storaas 2013). Several studies have investigated this decline and assessed factors influencing temporal and spatial variation in ptarmigan abundance:

(i) *Climate change***.** The strongest impacts of climate change and rising temperatures are expected in higher altitudes and mountainous habitats (Parmesan and Yohe 2003, Post et al. 2009). A niche contraction due to an elevated tree line following climate change together with altered floral and faunal composition is expected to have negative impact on ptarmigan populations (Elmhagen et al. 2015, Lehikoinen et al. 2014). Likewise, dampened small rodent population cycles may lead to negative effects on an alternative prey species like ptarmigan, as the interaction between generalist predators (e.g. red fox) and their main prey (small rodents) may change (Elmhagen et al. 2011, Elmhagen et al. 2015, Henden et al. 2009, Henttonen and Wallgren 2001, Hörnfeldt 2004, Hörnfeldt et al. 2005). Kvasnes et al. (2014) found that recruitment rates of ptarmigan were more affected by the North Atlantic Oscillation (NAO)-index than by rodent dynamics, and explained this result by a weakened link between rodents and ptarmigan following climate change-induced dampening of rodent cycles. Selås et al. (2011) suggested that a negative impact of climate change on grouse could be caused by the elevated plant chemical defense following warmer summers which, in turn, could negatively affect grouse reproduction.

(ii) *Changes in human land use*. There is an increasing development of recreational resorts in mountain regions all over the world (Støen et al. 2010). In Norway, many of these resorts are placed in the highly important birch forest (*Betula* spp.) zone, and research indicate lower breeding success in willow ptarmigan and higher abundance of generalist predators in these areas (Støen et al. 2010, Watson and Moss 2004). Another possible negative effect is development of infrastructure and power lines, resulting in more disturbances, easier access for predators like the red fox and collisions with power lines (Bevanger 1995, Støen et al. 2010). Increase in sheep and/or domestic reindeer husbandry may result in higher grouse mortality due to collisions with fences as reported by Baines and Summers (1997) and Bevanger and Brøseth (2000).

(iii) *Changed predator regime.* The two factors mentioned above (i and ii) favor generalist predators like the red fox, which have increased in density and expanded its range, possibly due to mesopredator release, overabundant cervid populations and altered human hunting pressure and land use (Elmhagen and Rushton 2007, Hersteinsson and Macdonald 1992, Ims et al. 2007, Killengreen et al. 2011).

1.3 Sustainable hunting and game management

Sustainable harvest can be simplified to net population growth rates exceeding annual harvest rates (Boyce et al. 1999, Getz and Haight 1989, Hilborn et al. 1995, Lande et al. 1995). Essential in this conceptually simple principle is reliable population abundance estimates of ptarmigan, which are difficult to obtain in the field (Aanes et al. 2002a, Boyce 1992, Saccheri and Hanski 2006). Moreover, rapid population fluctuations caused by environmental and/or demographic stochasticity further complicate the application of sound harvest strategies (Engen et al. 1997). Another important aspect is to what degree harvest mortality is additive or compensated by increased reproduction or survival (Ellison 1991, Pedersen et al. 2004a, Sandercock et al. 2011). In this context, essential determinant factors are life-history strategies, density-dependence in natural mortality, the species' vulnerability to harvest and the timing that harvest occurs (Burnham and Anderson 1984, Conroy and Krementz 1990, Lebreton 2005, Nichols et al. 1984, Sandercock et al. 2005, Sandercock et al. 2011). To obtain sustainable harvest strategies, it is crucial to understand the thresholds for additive mortality and effects of harvest mortality on annual survival. This can be expressed by the equation: $S_a = S_o (1 - bK)$, where S_o is the survival rate (without harvest), and b is the slope coefficient linking annual survival to harvest rate (Sandercock et al. 2011). When evaluating effects of harvest mortality (K_i) on annual survival (S_i) in exploited populations we normally define three scenarios; (i) additive mortality (b = 1), (ii) partially compensatory mortality ($0 < b < 1$) and (iii) compensatory mortality (b = 0) (Sandercock et al. 2011 and references therein). Sandercock et al. (2011) concluded that a harvest rate of 15% would be sustainable at productivity rates of ≥ 2.5 young per pair. Smith and Willebrand (1999) found mortality additive at a harvest rate of 24%, but populations were sustained by dispersal/immigration. Pedersen et al. (2004a) found a weak compensation in Willow ptarmigan and concluded this was due to long-distance dispersal of juvenile birds unaffected by the harvest.

Different strategies have been recommended to optimize harvest without risk of overexploitation: (i) *A constant harvest* means that a fixed number of individuals are removed annually. An advantage with this simple harvest strategy is that it does not require a density estimate, but caution is needed when populations are decreasing and low to avoid over-harvest (Aanes et al. 2002a, Fryxell et al. 2005, Lande et al. 1997, Sandercock et al. 2011). (ii) *A threshold harvest* or *proportional threshold harvest*, where the first is a strategy of harvesting all individuals above a threshold population size and the latter is harvesting a fraction of the estimated population above the threshold. The latter harvest strategies have been evaluated to maximize cumulative yield, but reliable density estimates are required (Aanes et al. 2002a, Lande et al. 1995, Lande et al. 1997). (iii) *A proportional harvest* is based on the strategy of harvesting a fixed proportion of the population annually. This strategy requires a density estimate if the harvest rate is not proportional to the harvesting effort, and it has proven effective especially with populations with limited demographic stochasticity (Beddington and May 1977, Lande et al. 1995).

Restrictions in harvest can be obtained with bag limits (daily, weekly or annual), by reducing the number of hunters, changing the timing or duration of the hunting season, or by protecting areas from hunting (Angulo and Villafuerte 2004, Peterson 2001, Willebrand and Hörnell-Willebrand 2001, Willebrand et al. 2011). Restrictions can influence hunters' satisfaction and participation in hunting and the effectiveness of restrictions is assumed to depend on both hunters' acceptance and satisfaction (Andersen et al. 2014, Fulton and Manfredo 2004, Wam et al. 2013). It is common for wildlife agencies and managers to face a demand from hunters and the public to be involved in wildlife management (Chase et al. 2000, Decker and Enck 1996, Decker et al. 1996). Perceptions of and skepticism towards new harvest restrictions are common, but they may gain legitimacy over time (Schroeder et al. 2014).

Several studies have investigated hunters' attitudes to different harvest regimes but few studies have looked at the relationship between restrictions and their actual impact on hunters and harvests (Brunke and Hunt 2008, Collier and Krementz 2006, Fulton and Hundertmark 2004, Fulton and Manfredo 2004, Mangun et al. 2007). The hunter's opinions and attitudes need to be evaluated in view of the actual effect on the game populations (Guthery et al. 2004, Peterson 2001). Ptarmigan bag size is believed to be more sensitive to hunter effort than population density, and according to Willebrand et al. (2011), the largest potential for overharvest occurs at low densities due to hunters being more efficient and maybe compensating for low bird encounters by increasing their effort (inverse density-dependent impact of hunting). A somewhat similar pattern was found in northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) where Guthery et al. (2004) and Peterson (2001) found that bag limits were regressive, i.e. restricting harvest only at high bird densities, thus rendering hunting control inefficient when it is most needed.

1.4 Cyclicity and predation dynamics

Cyclicity in rodents and grouse has fascinated researchers for decades. Synchronized cycles in rodents and ptarmigan may be caused by shared predators as suggested by the "alternative-prey-hypothesis" (APH) (Angelstam et al. 1984, Hagen 1952, Lindström et al. 1987, Lindström et al. 1994). The APH predicts a diet shift in generalist predators in rodent crash years, from main prey to alternative prey, and this interaction is a major driver of population dynamics of alternative prey species (Hagen 1952, Hörnfeldt 1978, Kjellander and Nordström 2003, Small et al. 1993). Both increased densities and range expansion of an important generalist predator, the red fox, and dampened small rodent cycles in Fennoscandia, are assumed to arise from climate change and altered human land use (Ims et al. 2008, Kausrud et al. 2008). According to APH, increased abundance of a generalist predator (red fox) together with a change in small rodent dynamics will exert higher predation rates and lower breeding success in an alternative prey such as willow ptarmigan (Angelstam et al. 1984). To my knowledge there are no studies of ptarmigan population dynamics including predator abundance as a predictor variable, and this is an obvious knowledge gap. Investigating the relationship between an important generalist predator like the red fox and an alternative prey; the ptarmigan, is essential for obtaining an improved understanding of how this system works.

2. Objectives

The Norwegian State-Owned Land and Forest Enterprise (Statskog) hold title to 20 % of Norway’s mainland and is a major provider of ptarmigan hunting on state-owned land, with a goal of securing public access while ensuring a sustainable harvest (Statskog 2017). With decreasing ptarmigan densities, securing hunting access may require harvest restrictions that hunters may find unacceptable.

The first objective of this thesis (**Paper I)** was to enhance the knowledge about willow ptarmigan harvest and hunter efficiency on state-owned land in northern Norway. I evaluated if ptarmigan harvest was sustainable and identified determinant factors for hunter effort and hunter efficiency based on detailed hunting records and population estimates.

A second objective (**Paper II)** was to evaluate hunter opinions. First, I evaluated factors associated with hunter opinions about the different management systems and hunting restrictions, and secondly, I analyzed data on hunting practices and performances to investigate to what extent hunters and the ptarmigan are affected by the restrictions.

The third objective (**Paper III)** was to combine census data on willow ptarmigan, rodents and red fox to examine spatiotemporal patterns in ptarmigan population growth and chick production. According to the alternative-prey-hypothesis (APH), predation impact by generalist predators on alternative prey should be high during periods of low availability of main prey. Hence, I investigate if ptarmigan growth is determined by an interaction between rodents and a generalist predator; the red fox.

3. Methods

3.1 Study areas

This study was carried out in the eastern parts of Nordland and Troms counties in the northern boreal birch (*Betula* spp.) forest and alpine tundra in Northern-Norway (Paper I and II, Fig 1 and 2), and in the northern boreal forests in Hedmark County (Moen 1999) in southeastern Norway (paper III, Fig 3). The study area in paper I is divided in 162 hunting blocks (of which 25 also are included in paper II) ranging from 8 – 667 km^2 (mean=167 km^2), where I have collected harvest statistics. In 36 hunting blocks I also estimated population density. Suitable habitat for ptarmigan at and above treeline is characterized by the presence of willows (Salix spp.), dwarf birch (*Betula nana*) and ericaceous shrubs. Main predators on ptarmigan are red fox, stoat (*Mustela erminea*) and large raptors (golden eagle *Aquila chrysaetos* and gyrfalcon *Falco rusticolus*). Prevailing small rodent species are Norwegian lemmings (*Lemmus lemmus*), tundra voles (*Microtus oeconomus*) and bank voles (*Myodes glareolus*). People are mainly living in towns and villages and the study areas have a low population density (6.3 people/km^2 (I and II), and 7.1 people/ km^2 (III)). Ptarmigan hunting is performed by hunters on foot mainly with shotguns, with or without a pointing dog locating and flushing the birds. The hunters have easy access to a majority of the hunting blocks by the use of the many forest- and construction roads or cabins in the areas. The hunting season for ptarmigan was open from 10 September to the end of February (15 March in the northernmost parts).

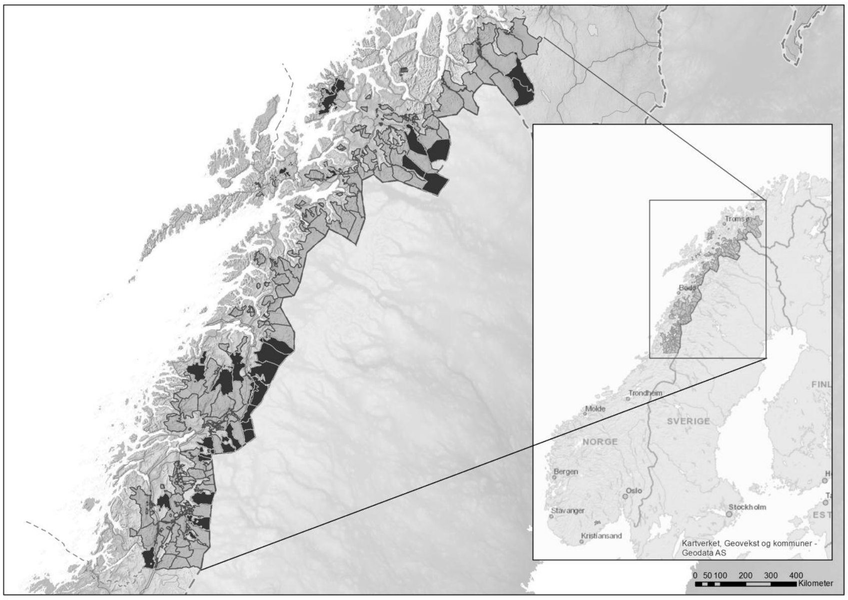

Fig 1. Map of the study area in paper I, showing 162 hunting blocks for small game on state-owned land in Nordland and Troms Counties, Norway. Willow ptarmigan density estimates were obtained from the 36 areas marked in black.

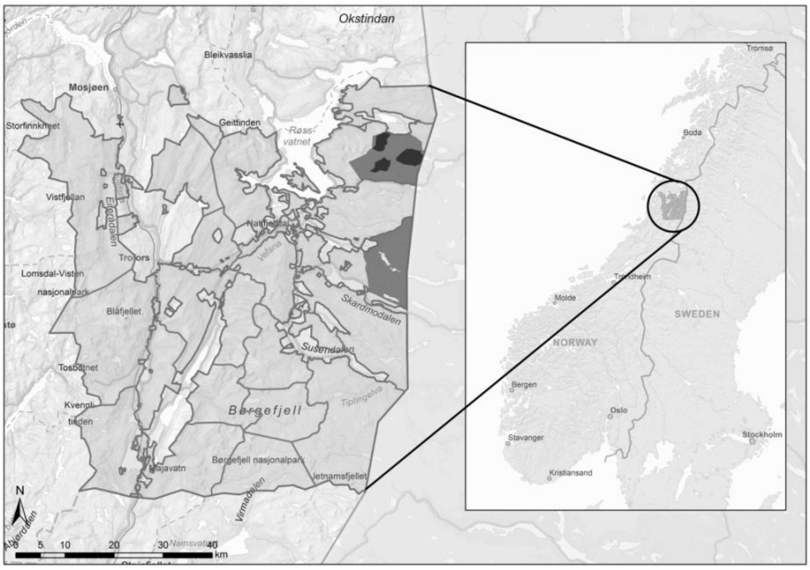

Fig 2. Twenty-five hunting blocks for ptarmigan on state-owned land in 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway used in paper II. The 2 dark grey polygons are experiment area (north) and control area (south) for a source-sink experiment. The 3 black areas are refuges with no hunting.

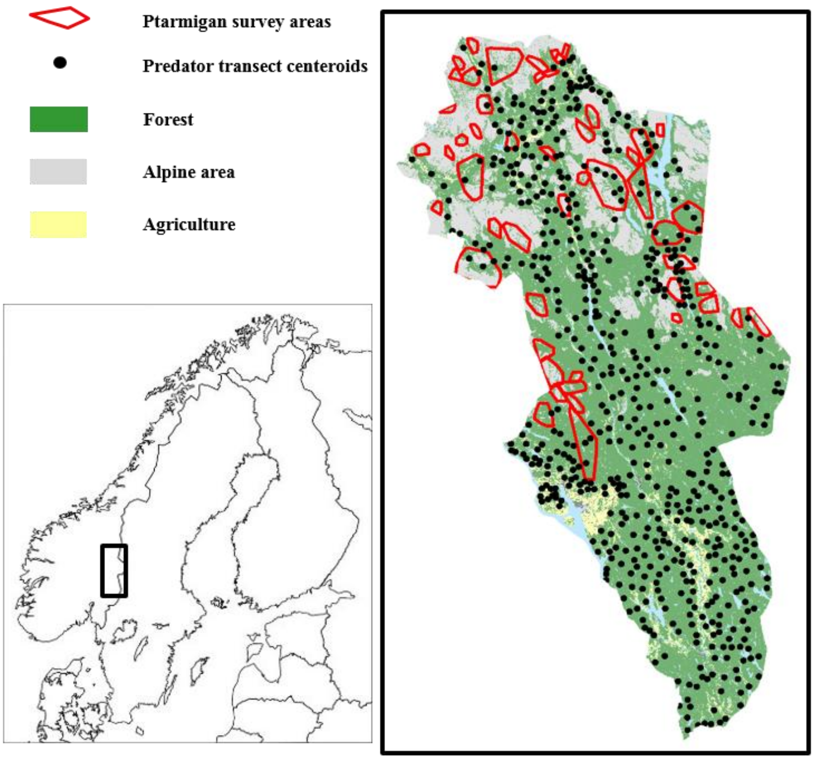

Fig 3. Overview of locations of ptarmigan survey areas and predator snow tracking transect centroids within the county of Hedmark, southeast Norway, used in paper III.

3.2 Hunter efficiency and influential factors (Paper I)

I based my analyses on an extensive line transect survey of willow ptarmigan. The counts were conducted in early August 2013-2016 in Nordland and Troms by volunteer dog handlers following the procedure of distance sampling (Buckland 2004) with a detailed sampling protocol described by Pedersen et al. (1999) and Solvang et al. (2007). The dog handlers noted all observations of willow ptarmigan (i.e. sex, young and adult birds, birds of unknown age and sex, location and distance to the line), and presence of small rodents along predetermined transect lines placed approximately 500 m apart. The estimation procedure is described in detail by (Buckland et al. 2001) and I followed this to estimate cluster size (average number of birds per encounter), breeding success (juveniles/pair) and density of birds (young and adult birds/km^2) for all survey areas and years. The total transect length in each survey area varied between 17 and 167 km (median=53.5, mean=58.0, SD=34.2), with estimated densities (sum of young and adult birds) between 2.1 and 132.5 birds/km^2.

I used Statskog's web-based system to obtain bag records. Records were received from 91 to 97 % of small game hunters in all areas, thus giving detailed information about the hunters' harvest and effort. I did not extrapolate the missing data due to the small proportion that had not reported their bag. I assumed that most of the hunters in this group had not bagged any game as shown by Asferg (1996). I defined harvest rate as the proportion harvested willow ptarmigan/hunting block, hunting effort as total number of hunter-days/km^2, and catch-per-unit-effort (CPUE) as the sum of willow ptarmigan harvested divided by accumulated hunting days per hunting block. Hunting effort, bag size and CPUE were estimated based on the amount of suitable willow ptarmigan habitat/hunting block (in km^2).

I used a resource selection map developed for willow ptarmigan in August (Kvasnes and Nilsen 2017) to estimate suitable and unsuitable areas for willow ptarmigan. As proxies for hunter's accessibility to willow ptarmigan hunting blocks, I calculated the mean distances to roads, cabins and other buildings, which I considered as potential starting points for willow ptarmigan hunting trips. Then, I estimated possible constraints on hunting performance as the mean slope of the terrain in degrees, a mean vector ruggedness measure (VRM) and the proportion of forest in suitable willow ptarmigan habitat in each hunting block. Slope and VRM were estimated with a 30 meter resolution digital elevation model (DEM) from Statens kartverk (The Norwegian Mapping Authority 2017a). To extract cover of forest in the hunting blocks I used a digital vegetation map, NORUT (Johansen 2009).

I used program R for handling all data and analyses in all three papers (R Version 3.3.3, www.r-project.org, 2017). All environmental variables were assessed by the use of ArcGIS. I used mixed effects logistic regression models (GLMER) to analyze hunting effort and CPUE. The three global models were estimated with similar sets of explanatory variables (year, density, mean distance to roads, mean distance to cabins, ruggedness (VRM), mean slope in degrees and proportion of forest), with hunting block as a random effect. Overdispersion was corrected using a negative binomial family distribution. I performed an automated model selection with subsets of the supplied global model using the *dredge* function with a limit of five terms in a single model. To incorporate model selection uncertainty I used model averaging for the top models returning a conditional and a full model according to (Burnham and Anderson 2003). I used the full model since our aim was to determine which factors have the strongest effect on the response variable following Nakagawa and Freckleton (2011). In the full model the parameter estimates were weighted using their corresponding model weight and summed for each candidate model. I used the 95 % confidence level (summed weight) as a cut-off criterion to delineate the top model set, according to Burnham and Anderson (2003).

3.3 Harvest regulation and hunter opinions (Paper II)

In this paper I evaluated a management system termed accumulated hunter days (AHD) where 25 hunting blocks were closed to ptarmigan hunting when the hunting effort exceeded 3 accumulated days of hunting/km^2. There was a daily bag limit of 4 ptarmigan and no annual quota.

In addition; an experimental area of 110 km^2 was set aside to test a source-sink system, where dispersal of ptarmigan from high quality habitats with no hunting (sources) was intended to counteract higher mortality in areas with unrestricted hunting (sinks). In this area, hunting was unrestricted in terms of hunting bags and access within 72% of the area, whereas hunting was banned in the remaining 28%. Three refuges (30.5 km^2) were placed within the experimental area of 110 km^2. Near the experimental area, a control area of 118 km^2 had no refuges and no bag limit.

I used Statskog's web-based system to obtain bag records (described in paper I, section 3.2), and in this study the hunters had to complete a hunting report every 10 days of hunting to continue their hunt. In the source-sink experimental areas, the hunters had to report their bag 3 times during the hunting season. Bag records were received from in average 92 % of small game hunters in all areas and years.

To evaluate the hunters' opinions, I used a structured digital online questionnaire distributed to all small game permit holders (n=943) after the hunting season ended. Among 53 primary questions with 33 sub-questions, I selected 9 questions relevant for the study. These were questions regarding the necessity and opinions of different alternatives to regulate hunting pressure, including the AHD system, the source-sink system, bag reduction, periodic ban of hunting at low ptarmigan densities, and shortening the hunting season.

Factors affecting hunters’ opinions towards different harvest regulations and scenarios were examined with logistic regression models (GLM). Response variables were the binary answers (i.e., agree vs. disagree and neutral) to 9 different questions, with the same set of explanatory variables in all full models. I used backwards selection to identify the most parsimonious model (i.e., a model with only significant terms at $P < 0.05$). Generalized linear models (GLM) were used to identify factors associated with bag sizes. I used a quasi-poisson error structure in the models of annual bags because of data overdispersion, and a normal error structure in the models of daily bag size. In the latter, I normalized the response variable using ln-transformation.

3.4 Predator-prey dynamics (Paper III)

Willow ptarmigan were censused with line transect surveys conducted in early August 2005-2014 by the use of pointing dogs. During this period (2005-2014), an average of six annual counts (SD = 2.6) were conducted in each of 48 different survey areas. The size of the survey areas averaged 56.0 km^2 (SD = 61.1), and in each area, an average of 15.4 (SD=10.9) transect lines (mean=3.2 km ± 1.1 SD) with an average total length of 47.1 km (SD=34.5) per survey area were monitored. The dog handlers noted all observations of willow ptarmigan (i.e. group size and location), and whether or not small rodents had been observed along the transect lines.

I estimated red fox track frequencies along 2.95 km (SD=0.5) snow tracking transect lines in January in the period 2006 to 2014 (Fig 3). The transect line density was 3-4 lines per 100 km^2 as described by Tovmo and Brøseth (2011). Of a total of 621 unique lines, 281 to 484 lines were surveyed annually during favorable snow conditions, i.e. 2-5 days after snowfall (Tovmo and Brøseth 2011).

I calculated a density index for willow ptarmigan by dividing the total number of flushed birds by the total length of the surveyed transect lines (i.e. birds per km of survey), for each survey area and year. Willow ptarmigan population growth rates (r) were estimated as the logarithm of the density index in year t divided by density index in year t-1 ($r = \ln(N_t/N_{t-1})$). As indices of breeding success, I used the proportion of juvenile ptarmigan among all counted birds per survey area. The number of juveniles per brood was estimated by subtracting two adults from each group of birds. For each survey area and year, I also calculated small rodent density indices by dividing the number of transect lines where rodents had been observed with the total number of surveyed transect lines. Track frequency indices for red fox were calculated by dividing the number of tracks per km with the number of days since last snowfall. Because the predator sampling took place some distance from the ptarmigan areas, I used the inverse-distance weighting (IDW) method for spatial interpolation of predator tracks, giving predicted index values for red fox per survey area and year.

I analyzed the data using generalized linear mixed effects models (GLME) following (Bates et al. 2014). Willow ptarmigan growth rate and breeding success were used as dependent variables and track indices of red fox and small rodent indices as explanatory variables. All independent variables were from year t, i.e. from January for red fox and August in the same year for rodents. Willow ptarmigan survey area was set in the models as a random term. I used the same sets of models to analyze variation in breeding success and growth rates.

4. Results and discussion

4.1 Hunting effort, CPUE and harvest rates (Paper I)

The mean hunting effort in the 36 hunting blocks with density estimates in our study was 1.56 (median=1.24, SD=1.20) days/km^2. However, hunting effort varied markedly in all hunting blocks among years; see Table 1. The hunting effort decreased with distance to roads and cabins, which is in accordance with previous studies by (Bergerud and Huxter 1969, Brøseth and Pedersen 2000, Gullion 1983, McGowan 1975, Weeden 1963, Willebrand and Hörnell-Willebrand 2001). I found a relationship between harvest rate and hunting effort, but with a large variation, see Fig 4. Hence, restricting access to the hunting blocks with a high proportion of roads and cabins may therefore be a useful intervention to reduce harvest in our study area.

Table 1. Summary showing total number of hunters, effort (total number of hunting days), bag (total harvested willow ptarmigan), density (mean population density estimates ptarmigan/km^2 from the 36 hunting blocks with density estimates) and CPUE (mean ptarmigan shot per hunter/day in every hunting block), the two latter with median values in parentheses, from 162 hunting blocks on state-owned land in North-Norway during September 10-30, 2013-2016.

Year	Hunters	Effort	Bag	Density	CPUE
2013	2548	9485	4012	17.60 (12.60)	0.35 (0.26)
2014	4426	15271	11647	16.58 (16.90)	0.59 (0.44)
2015	4058	12878	8355	27.59 (14.40)	0.47 (0.31)
2016	2761	7241	5735	15.97 (9.35)	0.65 (0.67)

During 2013-2016 the average harvest rate was 7.6% (SD=4.0%) in the 36 hunting blocks with density estimates, and interestingly, this is at the same level as estimated by Hagen (1952) more than 50 years ago. A harvest rate of < 10 % in a highly productive and small-bodied species like willow ptarmigan is relatively low and probably partially compensated for, as additive mortality from hunting has not been observed below harvest rates of 20% (Braun and Rogers 1971, Sandercock et al. 2011, Smith and Willebrand 1999). Mean CPUE in the hunting blocks with density estimates was 0.77 (median=0.71, SD=0.48), and it increased with increasing ptarmigan densities. However, the increase in harvest was not proportional with increase in density and a possible consequence may be that hunters become more efficient at low densities, as described by Willebrand et al. (2011). This may explain why the highest harvest rates were recorded in areas and/or periods with relatively low ptarmigan densities. Based on our models, the predicted daily removal of ptarmigan increased markedly when densities became lower than ca 10/km^2 (Fig 4). Accordingly, although harvest rates were generally low and probably partially compensatory, it is important to take into account the elevated impact of hunting during periods of population decline.

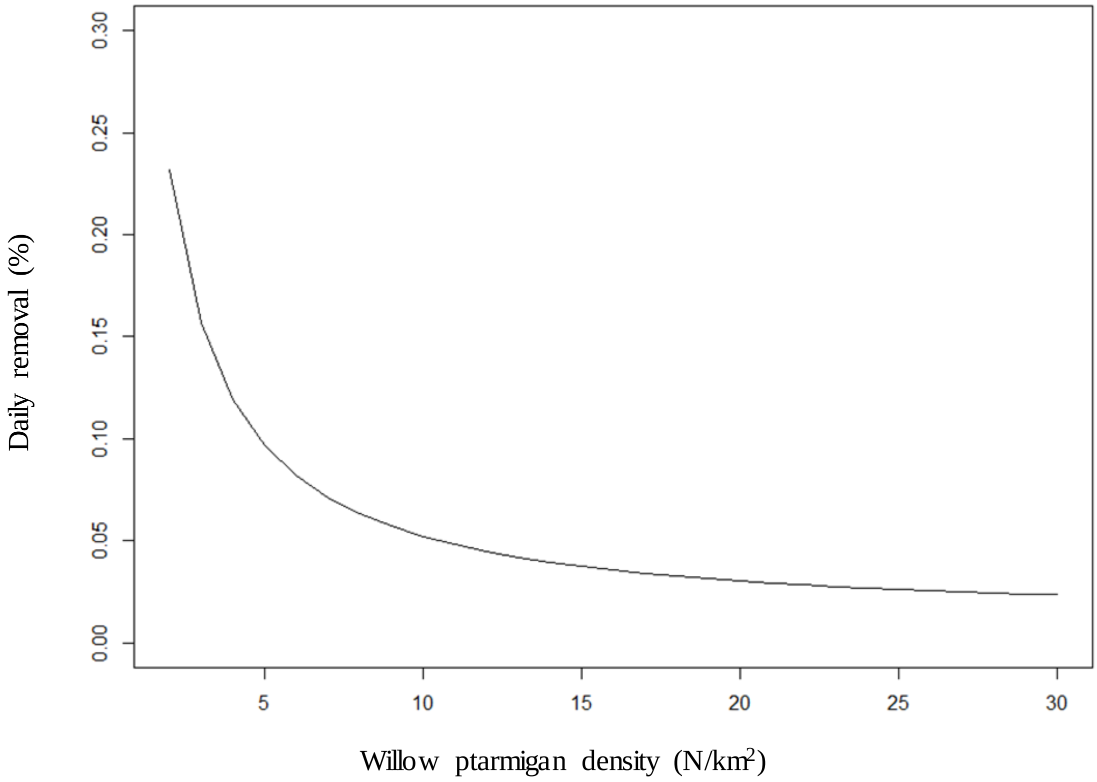

Fig 3. Predicted proportions of the ptarmigan population shot per day on 36 hunting blocks in North-Norway, 2013-2016. Daily removal rates are estimated by dividing predicted CPUE values with estimated densities.

4.2 Harvest regulations and hunter opinions (Paper II)

I found a strong willingness to shoot fewer birds among hunters, but I found no factors influencing this opinion. Only 16% of the hunters were willing to accept a daily bag limit of 1 bird or a seasonal quota of 4 birds, which would have reduced harvest by approximately 50 %. Hence, this reflected a tendency to approve restrictions with the smallest impact on their own hunting practice. For instance; hunters that bagged few birds were more likely to agree to a prohibition of hunting at low densities. Furthermore, non-resident hunters were more likely to agree to this restriction than local hunters. Probably, non-resident hunters had a lower site fidelity, as revealed by Cornicelli et al. (2011), and were willing to move to other areas if hunting was restricted. Those that had hunted in the areas of the source-sink experiments were more positive to this system compared to those that had not, and I suspect that this is an effect of being familiar with this type of management. Managers may face a general skepticism from hunters towards introduced management systems, but Schroeder et al. (2014) revealed that introduced hunting regulations may gain legitimacy over time.

The most influential factor regarding hunter opinions was the residency of the hunter. Non-resident hunters were more positive than local hunters to the AHD-management system, towards closing the season 3 months earlier, and to a ban of hunting at low population densities, while local hunters were more positive than non-resident hunters to a 2-week delay in the opening of the hunting season. Again, this reflects a tendency to approve restrictions with the smallest impact on their own hunting practice in combination with site fidelity and fear of losing hunting opportunities. The majority of non-resident hunters visit these areas in the beginning of the hunting season. When the blocks are closed due to the imposed limit of 3 hunter-days km^{-2}, it may mainly affect local hunters, since few non-resident hunters are present at this time. For the same reason, closing the hunting season 3 months earlier will probably have a greater effect on local hunters. A 2-week delay in the opening of the hunting season would probably reduce hunting access for non-resident hunters more than for local hunters and the difference in attitudes towards a ban of hunting at low densities may be explained by higher site fidelity among local hunters. Cornicelli et al. (2011) found a somewhat similar result in a study of hunter opinions about management of white-tailed deer

(*Odocoileus virginianus*) in Minnesota, USA. They revealed strong site fidelity among the hunters, with an approval of management strategies that first and foremost secured access to their hunting areas, even if quotas were limited (Cornicelli et al. 2011).

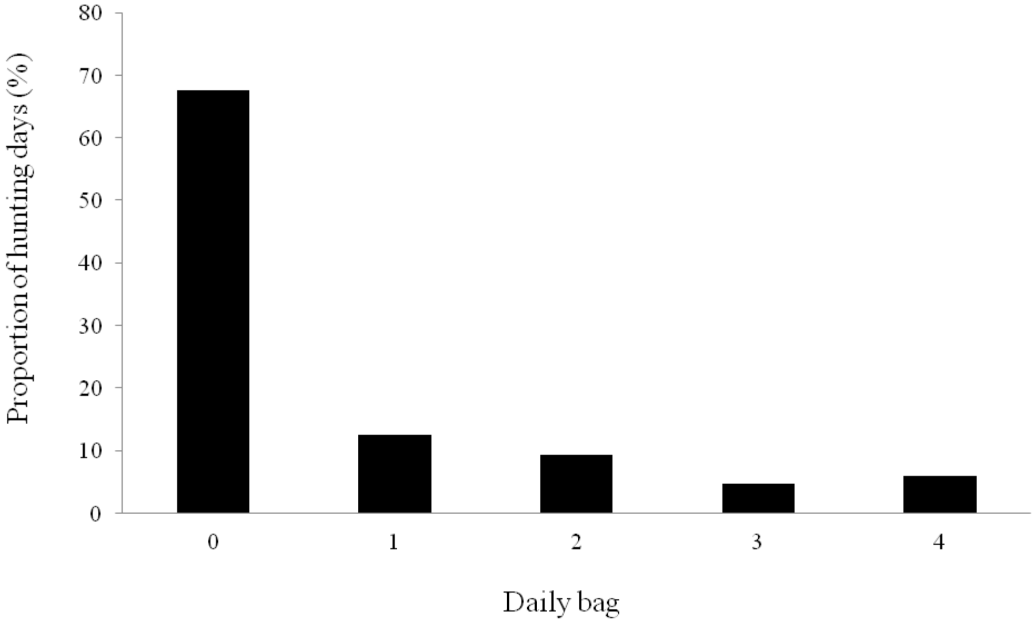

Figure 5. Proportions of hunting days with daily bags of 0–4 ptarmigan within areas with an accumulated hunter days management system and daily bag limit of 4 birds. Data are based on reported bags from 8,795 hunting days on state-owned land in the 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway, during hunting seasons in 2009–2010, 2010–2011, and 2011–2012.

Hunters with dogs harvested more ptarmigan per day and season than hunters without dogs. My results seem to contradict earlier studies of the recreational specialization concept where more specialized hunters are assumed not to be bag oriented, but motivated by the quality of the experience (Bryan 1977, Kuentzel and Heberlein 1992). Assuming that the use of dogs indicates a higher degree of specialization, I would have expected smaller bags among this group of hunters. One simple explanation is that almost any hunting dog will be able to find a dead and/or wounded bird and therefore these hunters will bring more birds home. Another possible explanation is that a small and dedicated elite of experienced hunters with dogs bag more birds due to their skills and dedication. Asmyhr et al. (2012) found a similar pattern in Sweden and showed that harvest rates were regulated through grouse encounters which varied by experience rather than local knowledge. Hörnell-Willebrand (2005) and Lindberget (2009) found that < 2 % of the hunters reached the daily bag limit of 8 ptarmigan on state-owned land in Sweden. In my study the daily bag limit of 4 birds was reached during < 6 % of hunting days and a small proportion (5%) shot ≥15 birds during the whole season (Fig 5 and 6).

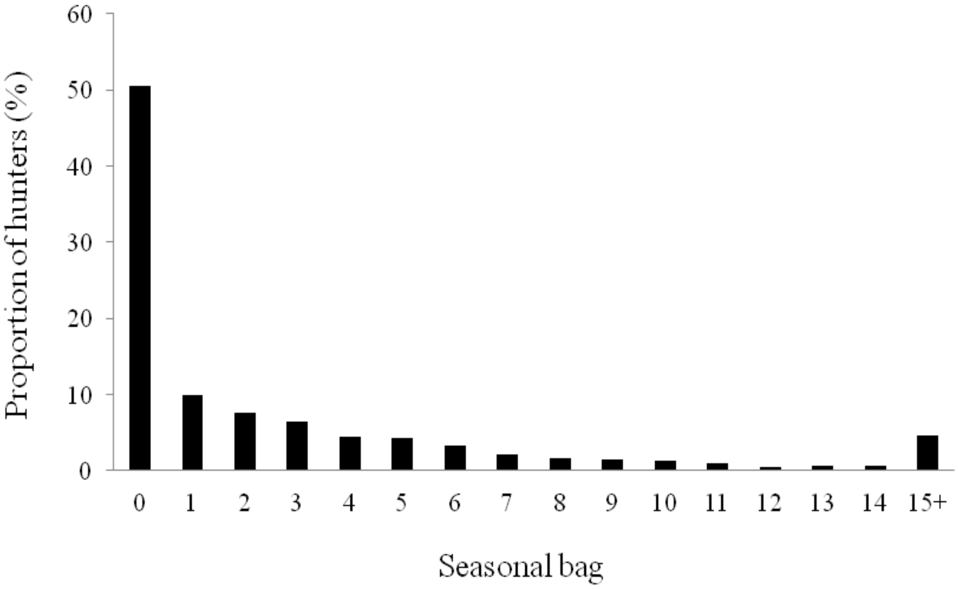

Figure 6. The proportion of hunters obtaining bags of 0 to >15 ptarmigan during the hunting season within areas with an accumulated hunter days management system and daily bag limits of 4 birds. Data are based on reported bags from 8,795 hunting days on state-owned land in 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway, during hunting seasons in 2009–2010, 2010–2011, and 2011–2012.

I found that no birds had been shot in 67 % of all hunting days and more than half of the hunters (51 %) did not bag a bird at all during the whole season. Hence, it is apparent that the opportunity and access to hunt is more important to hunters than bagging many birds. A possible consequence of the low hunter efficiency is a regressive effect of bag limits, i.e., reducing harvest when it is least needed, as indicated by Peterson (2001) and (Guthery et al. 2004).

4.3 The APH – and willow ptarmigan population dynamics (Paper III)

The ptarmigan populations showed no declining trend during the study period, and annual variations corresponded with marked periodic small rodent peaks and declines, see Fig 7. The rodent abundance indices exhibited high amplitudes that corresponded with ptarmigan density, while the red fox index varied less among years (Fig 7). Population growth rate and breeding success of willow ptarmigan were strongly and positively correlated ($R^2 = 0.42$), The close relationship between recruitment rates and population growth is a typical attribute of r-selected species such as ptarmigan; where low annual survival, early maturity and high fecundity produce pronounced population fluctuations and large variation in recruitment (Sæther et al. 1996). The best models of population growth and breeding success included the interaction between rodent- and red fox abundance. The negative impact of red fox on ptarmigan appeared when small rodent densities were low, whereas breeding success and population growth were high when small rodents were abundant (Fig 7). As predicted by APH, this effect may be caused by red foxes foraging mainly on primary prey (small rodents) during rodent peaks, and prey switching to alternative prey (e.g. ptarmigan) during rodent population declines (Angelstam et al. 1984, Hagen 1952, Kjellander and Nordström 2003, Lack 1954).

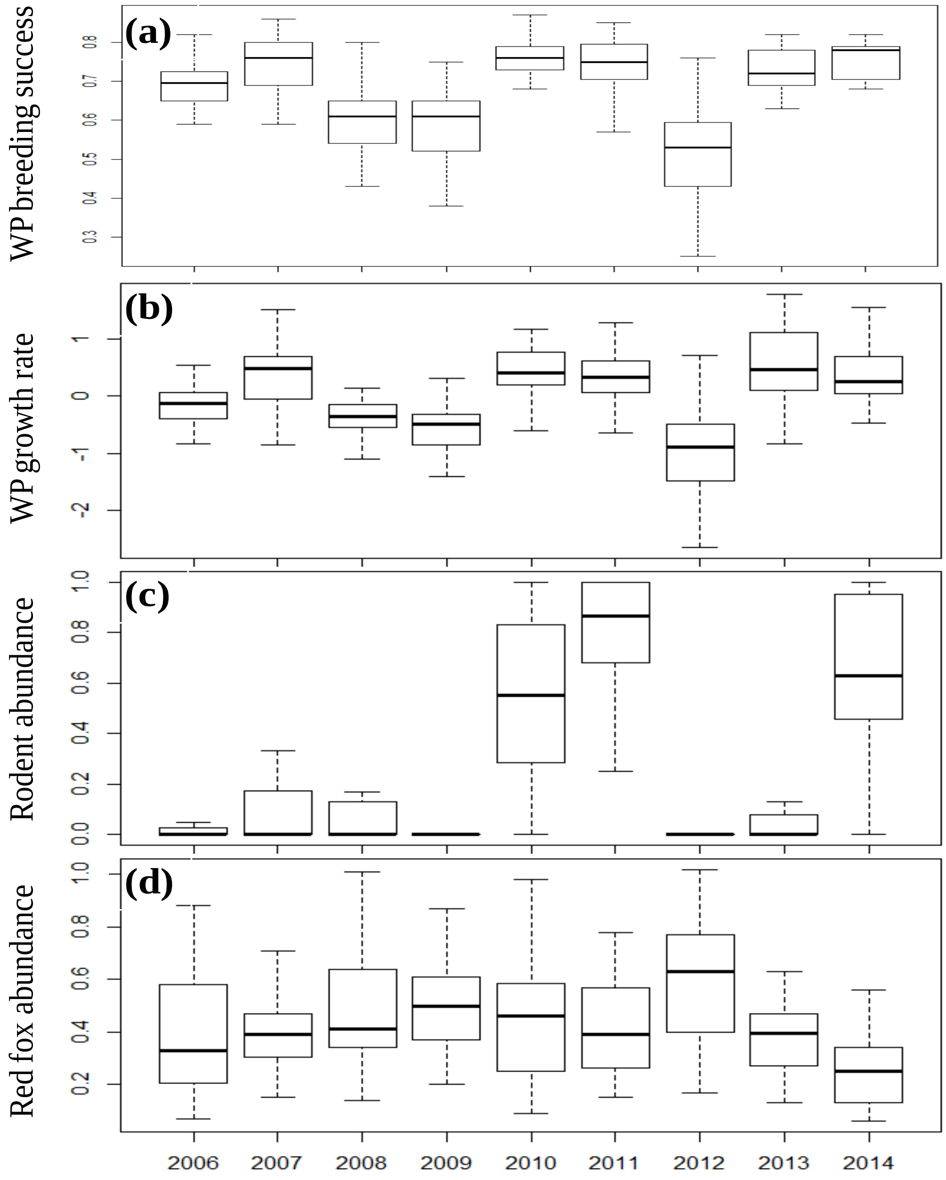

Fig 7 a, b, c and d. Temporal patterns of willow ptarmigan (WP) breeding success, population growth (r = ln (λ)), rodent abundance and red fox abundance indices obtained from 48 survey areas in Hedmark county, SE Norway 2005-2014. Outliers are exluded from the box plot.

Several studies have predicted an increased influence of mammalian predators in the Scandinavian mountains, due to climate change and dampened small rodent dynamics (Aars and Ims 2002, Elmhagen et al. 2015, Kausrud et al. 2008). There is a rising concern about the negative impact on mountain wildlife communities of increased densities and range expansion of the red fox (Hersteinsson and Macdonald 1992, Linnell et al. 1999, Tannerfeldt et al. 2002). The Scandinavian red fox population density was substantially reduced by an outbreak of sarcoptic mange (*Sarcoptes scabiei vulpes*) during the late 1970s and 1980ies, and this revealed the particular importance of red fox predation by a marked population increase in several small game species (Danell and Hörnfeldt 1987, Lindström et al. 1994, Smedshaug et al. 1999).

My study has established a clear link between ptarmigan, red fox and small rodent dynamics, and according to APH, this interaction is potentially a major driver of population dynamics of ptarmigan and other alternative prey species (Angelstam et al. 1984, Hagen 1952, Kjellander and Nordström 2003).

5. Conclusions and management implications

I propose that no further restrictions are needed with the current management system for ptarmigan on state-owned land in northern Norway due to harvest rates being low and probably partially compensatory. The imposed daily bag-limits are most likely regressive (i.e., only affecting harvest at high population densities when they are least needed), and restrain the hunting practice instead of limiting the actual harvest. The bag limit had to be reduced to 1 bird/day or 4 bird/season to obtain a 50 % reduction in harvest, which the hunters found unacceptable. Lastly, I found the breeding success and growth rate of willow ptarmigan depend on the interaction between small rodents and the red fox. My results suggest that dampened small rodents cycles together with an increase in predator abundance may contribute to further decline in ptarmigan and other alternative prey species.

Sustainable management of a red listed small game species while securing hunter access is a demanding task. Hunters may fear losing hunting opportunities and conservationists tend to blame declining populations on overharvest by hunters. It is therefore crucial for managers to identify correct harvest levels and evaluate other influential factors before implementing stricter harvest regulations. There is a need for reliable census data on population abundance and breeding success together with bag records and data on hunter effort. With such data on hand, managers are capable of implementing further restrictions at low densities and/or poor breeding success, but also loosen up strict harvest regulations and even allowing more hunting opportunities at high population levels. I have shown that most hunters are positive to hunting restrictions but more diffuse in which restrictions they prefer among those that actually have an effect on the game populations. Managers have to bear this in mind before introducing restrictions proposed by hunters. There is an obvious need for more knowledge of management alternatives, especially at low densities, and this information needs to be communicated thoroughly to the hunters to gain acceptance and legitimacy. I have also established a link between a generalist predator (the red fox) and its main (rodents) and alternative prey (ptarmigan), but still more research is needed to understand the impact of predation, human influence and climate change on the dynamics of this mountain ecosystem.

6. Acknowledgments

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The work with paper I and II had not been possible without the help from all the small game hunters reporting their bags and effort, and kindly answering the questionnaire survey. Thank you so much for your contribution.

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Paper I

Harvesting a red listed species: Determinant factors for Willow Ptarmigan harvest rates, bag sizes and hunting efforts in Norway

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Abstract

A main objective of game management on public lands in Norway is to ensure that harvest levels are sustainable while securing hunting access to the public. The willow ptarmigan is a popular but red-listed small game species, and it is challenging for managers to optimize harvest levels based on uncertain population estimates and limited knowledge of the factors influencing hunting impact. We studied how willow ptarmigan hunting effort, catch per unit effort and harvest rates were influenced by ptarmigan density, topography, vegetation and infrastructure. Data were collected during 2013 – 2016 from 162 hunting blocks covering 26,828 km^2 state-owned land in the Counties Nordland and Troms, northern Norway. Hunting effort averaged 1.27 days/km^2 (SD = 2.08), and it was highest in areas close to roads and cabins. We found an opposite effect on the catch per unit effort (CPUE, mean = 0.77 ptarmigan/day, SD = 0.48), which was lower close to roads. There was a marked positive effect of density on CPUE, whereas terrain steepness (slope) had a negative effect. On average, harvest removed < 10 % of the autumn population in the hunting areas during the study period. This indicates a relatively low and partially compensatory hunting mortality in most years and areas. Although this study shows a low harvest rate, we recommend managers to survey ptarmigan populations, hunting effort and harvest, especially in easily accessible areas close to infrastructure and in periods of low population density.

KEY WORDS: Small game, Lagopus lagopus, CPUE, harvest effort, over-harvest, sustainability

Introduction

For a harvest regime to be sustainable, annual harvest rates should not exceed net population growth rates over a long time span (Boyce et al. 1999, Getz and Haight 1989, Hilborn et al. 1995, Lande et al. 1995). Although conceptually simple, a range of factors complicate the application of this principle. Firstly, estimates of population sizes and demographic rates are challenging to obtain in the field and are therefore ridden with large uncertainties (Aanes et al. 2002b, Boyce 1992, Eriksen et al. 2017, Saccheri and Hanski 2006). In addition, environmental and/or demographic stochasticity may lead to rapid population fluctuations that further complicate the adoption of a sound level of harvest (Engen et al. 1997). Moreover, there is often not a clear and simple link between harvest regulations and harvest off-take in these game management systems (Johnson and Williams 1999). An example of this is the willow ptarmigan (*Lagopus lagopus*), hereafter ptarmigan, whose high intrinsic rate of increase and highly variable breeding success produce marked annual variation in abundance (Henden et al. 2011a, Hörnell-Willebrand 2005, Kvasnes et al. 2010, Moss and Watson 2001, Myrberget 1988).

Historically, hunting of small game has been considered as compensatory mortality and thus having little effect on the populations (Pedersen et al. 2004b, and references therein). However, these assumptions were based on weak quantitative studies assuming density dependent growth (Ellison 1991). In Norway, small game hunting is a privilege of the landowner, who has the right to hunt and trap without restrictions in harvest within a wide hunting season. The largest landowner in Norway, the Norwegian State-Owned Land and Forest Enterprise (hereafter Statskog), aims to secure wide public access to hunting (Statskog 2017). In recent years, there has been a rising concern among hunters, managers, ornithologists and the general public about decreasing ptarmigan populations (Kaltenborn et al. 2012, Pedersen and Storaas 2013). In Norway, willow ptarmigan was classified as near threatened in 2015 (Henriksen and Hilmo 2015), following a country-wide population decline during the last decades. For example, in the northern counties of Nordland and Troms, the number of bagged ptarmigan declined from 107,300 during the hunting season of 2000/2001 to 37,750 during 2015/2016 (Statistics Norway, 2017). This has invigorated a debate on the role of sport hunting and the need for improved management strategies. In many areas, intensive monitoring and hunting restrictions have been introduced (Pedersen and Storaas 2013). However, there is still limited information on the actual impact of hunting and the efficiency of regulations (Hörnell-Willebrand 2005, Sandercock et al. 2011, Willebrand and Hörnell-Willebrand 2001, Willebrand et al. 2011). Several papers have shown a strong relationship between hunting effort and harvest rates, indicating that bag size is determined more by effort than by density of birds (Hörnell-Willebrand 2005, Tomeček et al. 2015, Willebrand et al. 2011). Factors influencing the harvest effort are thus important, and may include topography, vegetation and infrastructure (Brøseth and Pedersen 2000, Lyon and Burcham 1998, Tanner et al. 2016).

Whether harvest is mainly additive or compensatory is influenced by the species' life-history strategy, i.e. compensatory mortality is expected predominantly in small bodied, short lived species with high fecundity (Sandercock et al. 2011 and references therein). Sandercock et al. (2011) demonstrated partial compensatory hunting mortality in willow ptarmigan below a harvest rate of 15 %, while hunting mortality was additive above 20%. Smith and Willebrand (1999) showed that hunting mortality was additive at a harvest rate of 24 %, while Braun and Rogers (1971) suggested that harvesting 30 % of the autumn population of White-tailed ptarmigan (*Lagopus leucurus*) had no effect on the breeding density the following spring.

Different harvest strategies have been theoretically evaluated and recommended for willow ptarmigan; constant harvest (a fixed number of individuals are removed annually), threshold harvest (harvesting all individuals above a given threshold) and proportional harvest (harvesting a fixed proportion of individuals) (Aanes et al. (2002b), Andersen and Kvasnes (2013), Engen et al. (1997), Fryxell et al. (2005), Lande et al. (1997). However, actual thresholds are commonly unknown due to uncertainty in population estimates and fluctuating population sizes. Few studies have investigated this issue (but see Engen et al. (1997) and Aanes et al. (2002b))

In Norway, common restrictions in ptarmigan hunting include daily or seasonal bag limits, prohibiting the use of dogs, geographic zoning and shortening or delaying hunting seasons (Aanes et al. 2002b, Andersen et al. 2014, Willebrand and Hörnell-Willebrand 2001). Access to hunting, rather than bagging many birds, seems to be most important for hunters, and management that aims to reduce access tends to be very unpopular (Breisjøberget et al. 2017, Wam et al. 2013). Daily bag limits are widely used, but in many cases, harvest is only affected during periods of high population densities, i.e. when restrictions are less important, (Breisjøberget et al. 2017, Guthery et al. 2004, Peterson 2001). Willebrand et al. (2011) found that hunters are more efficient at low population densities, probably because they spent longer days in the field to compensate for few bird encounters. The largest potential effect of harvest will thus occur at low densities, making small game management at low population density difficult.

Harvest rate is the ratio of the number of harvested birds and population abundance. The numbers harvested, in turn, is determined by the cumulative number of hunters per unit area and their catch-per unit effort. These components may be influenced by several interacting factors. For instance, variation in hunter density may be influenced by factors related to the accessibility of the hunting areas, e.g. infrastructure, topography and distances to cabins (Gratson and Whitman 2000, Thomas et al. 1976). Catch per unit effort may be influenced by both bird density, vegetation and topography (Brøseth and Pedersen 2010, Willebrand et al. 2011). Hence, in order to disentangle the relative importance of different factors affecting ptarmigan harvest, we focused on three aspects; (1) hunting effort, (2) hunter efficiency i.e. catch per unit effort, and (3) ptarmigan harvest rate. We expected hunting effort to be mainly determined by factors associated with the accessibility to the hunting areas, i.e. infrastructure, and that catch per unit effort was determined by population abundance, topography and vegetation structure. We expected harvest rates to vary spatially and annually according to ptarmigan density, and that stricter hunting regulations is needed in hunting blocks with markedly high hunting pressure.

Study area

This study was carried out during 2013-2016 on Statskog's land in the eastern parts of Nordland and Troms counties in northern Norway, covering 26,828 km^2 (Fig 1). We collected annual harvest statistics from 162 hunting blocks ranging from 8 – 667 km^2 (mean = 167 km^2, SD = 139). In addition, we obtained population density estimates from 36 of these blocks. Per 1 January 2017, the two counties had a human population density of 6.3 inhabitants per km^2, mainly residing in small towns and villages

(Statistics Norway 2017). Below the tree line, the vegetation is dominated by mountain birch (*Betula pubescens*) with some coniferous forests consisting of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Above the tree line, alpine heath, shrubs and patches of dwarf birch (*B. nana*) dominate. The climate is continental with low annual precipitation, cold winters (-5 to -10 °C in January) and moderately warm summers (14-15 °C in July), (Norwegian Meteorological Institute 2017). The mountainous landscape is naturally fragmented with valleys surrounded by mountain tops up to 1,900 m asl in Nordland. Main predators on ptarmigan are large raptors (golden eagle *Aquila chrysaetos* and gyrfalcon *Falco rusticolus*) in addition to red fox (*Vulpes vulpes*) and stoat (*Mustela erminea*). Hunting is performed by hunters on foot with shotguns, with or without a pointing dog for locating and flushing the birds. Accessibility to the areas vary mainly by the distribution of forest roads or cabins. We limited the period of this study from the opening of the hunting season 10 September until 30 September, before brood-break up and natal dispersal (Brøseth et al. 2005, Smith 1997). This is the most intensive hunting period as studies have shown that 2/3 of all harvest takes place during the first 10 days in both Sweden and Norway (Kastdalen 1992, Willebrand 1996). Daily bag limits varied between 1-6 birds among years.

Methods

Willow ptarmigan population surveys

We surveyed ptarmigan populations in 36 hunting blocks each year in early August 2013-2016. We followed a distance sampling line transect protocol where straight lines were placed 500 meters apart (Buckland et al. 2001, Pedersen et al. 1999, Pedersen et al. 2004b, Solvang et al. 2007). The counts were performed by volunteers from the

Nordland and Troms Chapters of the Norwegian Association of Hunters and Anglers using dogs searching both sides of the transect lines. The dog handlers recorded the observed birds at each encounter (chicks, adult females/males and birds of unknown age/sex), and measured the perpendicular distance in meters from the birds to the transect line. Pedersen et al. (1999) tested this procedure with radio-collared willow ptarmigan and found the technique suitable and in accordance with the assumptions of the distance sampling method. The total transect length in each survey area varied between 17 and 167 km (median=53.5, mean=58.0, SD=34.2), with estimated densities (sum of young and adult birds) between 2.1 and 132.5 birds/km^2 (median=12.4, mean=19.7, SD=25.2).

Bag records and hunting effort

We used Statskog's web-based bag record system where the hunters had to submit a mandatory and detailed bag report every 14 days of hunting in order to continue hunting. Bag records with the number of ptarmigan killed (n_{total} = 29,749) and days hunted (n_{total} = 44,875) were received from 91% to 97 % of small game hunters in all areas (Table 1), thus providing detailed information about hunters harvest and effort. We did not extrapolate the missing data, due to the small proportion that had not reported their bag, and the assumption that this group had bagged few birds (Asferg 1996). We calculated the abundance of ptarmigan in each hunting block by multiplying autumn density (young and adult birds/km^2) with the total area of suitable ptarmigan habitat (see description of habitat suitability below). We defined hunting effort as the total number of hunting days/km^2. Catch per unit effort (henceforth CPUE) was defined as ptarmigan harvested divided by the cumulative number of hunting days. Harvest rate was defined as the proportion harvested in each block, i.e. the number of birds shot divided by the estimated abundance.

Environmental variables

As proxies for hunter accessibility to ptarmigan hunting areas, we calculated the mean distance to roads and cabins within each hunting block. We included all passable (for vehicles) roads > 50 meters length extracted from the dataset Transport Networks and cabins from the Cadaster (The Norwegian Mapping Authority 2017b, c) . There are many building types in the Cadaster, but we included only those we consider as potential starting points for ptarmigan hunting trips, i.e. recreational homes, tourist cabins, rental cabins and forest huts. Slope and vector ruggedness measures were estimated from a digital elevation model (DEM) with a resolution of 30*30 meters (The Norwegian Mapping Authority 2017a). Slope describes the average steepness of the hunting block in degrees (0-90). The vector ruggedness measure (VRM) is a combination of slope and aspect from the DEM, and was calculated among nine neighboring pixels in the DEM. The VRM ranges from 0 to 1 where 1 is a complex landscape with high topographic variation commonly termed as rugged (Sappington et al. 2007). We calculated the proportion of forest cover in each block based on a digital vegetation map, NORUT (Johansen 2009) with a resolution of 30*30 meter. Lastly, we used a resource selection map developed for willow ptarmigan to calculate the aerial coverage of suitable habitat (Kvasnes and Nilsen 2017). Predictions from the resource selection function (RSF) developed by Kvasnes and Nilsen (2017) were quantile binned into five categories from low to high relative selection. The lowest ranked bin was then separated in two new bins where the 25 % lowest predictions were placed in a new bin 1 and the remaining 75 % predictions placed in new bin 2. This resulted in six categories of relative probability of willow ptarmigan selection. We considered map predictions in the lowest ranked bin (new bin 1) as unsuitable habitat for willow ptarmigan and the remaining categories (2-6) as suitable habitat.

Statistical Analysis

We used program R for handling all data and analyses (R Version 3.3.3, www.r-project.org, 2017). Willow ptarmigan density from the line transects was estimated using the program Distance (Buckland et al. 2001). We estimated mixed effects logistic regression models to model effort and CPUE using the *glmer* command in the *lme4* package (Bates et al. 2008). Each of the two global models were estimated with a Poisson family distribution and with the same explanatory variables: density, mean distance to roads, mean distance to cabins, ruggedness (VRM), mean slope in degrees and proportion of forest, with year and hunting block as a random effects (Table 2 and 5). Overdispersion was detected in the global models, and we corrected the standard errors using a negative binomial family distribution. We used the accumulated number of hunting days, with the area of suitable willow ptarmigan habitat as offset, when modeling hunting effort. We removed one outlier from the dataset because this hunting block (“Leina”) had high hunting activity due to easy access by boat despite a long distance to roads (> 5.5 km). For modeling CPUE, we used the total number of harvested birds as a response variable with the accumulated days of ptarmigan hunting as an offset. When modeling harvest rate, the response variable was the total number of ptarmigan harvested, and the total estimated ptarmigan population size was the offset variable. We performed an automated model selection with subsets of the supplied global model using the *dredge* function with a limit of five terms in a single model. To incorporate model selection uncertainty we used the function *model.avg* in the MuMin package for the top models returning a conditional and a full model (Burnham and Anderson 2003). We followed Nakagawa and Freckleton (2011) and used the full model since our aim was to determine which factors have the strongest effect on the response variable. We used a 95 % confidence level as a cut-off criterion to delineate the top model set (summed weight) according to Burnham and Anderson (2003). The performance of the models were assessed based on their AIC values (Burnham and Anderson 2003).

Results

Hunting effort

The average hunting effort in all the 162 hunting blocks during the study period was 1.27 (median=0.86, SD=2.08) days/km^2 (Table 4, in Appendix). The total hunting effort in all hunting blocks varied markedly among years; see Table 1. The best model of hunting effort included the proportion of forest cover and the distance to cabins and forest roads, (Table 2, 3 and 4). The model averaged parameter estimates showed that efforts decreased with increasing distances to roads and cabins, and decreased with increasing forest cover (Table 3 and 4). The second best model (ΔAIC; 0.49, Table 3 and 4) also included terrain steepness, with less effort the steeper the terrain. Finally, the third best model (ΔAIC = 1.86) included terrain ruggedness instead of slope, with less hunting effort in the more rugged terrain (Table 3 and 4).

Catch per unit effort (CPUE)

The average number of ptarmigan shot per hunting day (CPUE) in the 162 hunting blocks was 0.77 (median=0.71, SD=0.48, see Table 8 in Appendix). The best model of CPUE included terrain slope, ruggedness, and distance to forest roads (See Table 5, 6 and 7). The effect of terrain slope on CPUE was negative (M61, AIC; 4393.8), whereas the distance to roads had a positive effect, i.e. CPUE was higher in areas with longer distances to roads (Table 6 and 7). The second best model (M62, ΔAIC; 0.64) also included the proportion forest cover, with higher CPUE with increasing forest cover (Table 6 and 7). Finally, the third best model (M63, ΔAIC; 1.16) included distance to cabins, indicating a higher CPUE with increasing distance to cabins (Table 6 and 7). For the subset of the data with access to ptarmigan density estimates, we found a marked positive effect of density on CPUE (Fig 2).

Harvest rate

During 2013-2016 the average harvest rate was 0.076 (median= 0.055, min= 0.001, max= 0.245) in the 36 hunting blocks with density estimates (Table 8, in Appendix). In only two hunting blocks the average harvest rate exceeded 15%. Based on the models of CPUE described above, we predicted ptarmigan removal within a range of densities from 0-30. As illustrated in Fig. 3, removal increased markedly below ptarmigan densities of ca 10 birds/km^2. Hence, hunters bagged a larger proportion of the population in areas of relatively low density.

Discussion

In accordance with our prediction, hunting effort decreased with distance to roads and cabins, and similar results were reported in studies of hunting impact on ruffed grouse (Fischer and Keith 1974, Small et al. 1991), willow ptarmigan (Brøseth and Pedersen 2000) and elk (*Cervus elaphus nelson)* (Lyon and Burcham 1998). Brøseth and Pedersen (2000) found that the area around the starting point of the hunting trip had the highest hunting activity. The wide distribution of construction and forest roads in our study area provide easy access for hunters, and may result in a more homogenous and high hunting pressure in large parts of the hunting blocks. Before this infrastructure was established, much of the hunting pressure may have been concentrated close to human settlements, whereas the remote areas were probably left relatively undisturbed. With a heterogeneous distribution of hunting activity, source-sink dynamics may arise (Novaro et al. 2005). In a source-sink system, the persistence of populations in habitat sinks will depend on dispersal from high quality habitat sources (Novaro et al. 2005). Kastdalen (1992) and Willebrand and Hörnell-Willebrand (2001) found a close relationship between hunting effort and harvest rates on forest grouse. Thus, reducing the number of hunters in hunting blocks with many roads and cabins may therefore be an appropriate intervention to reduce harvest. Alternatively, allowing hunting, but restricting access to roads, may concentrate hunting efforts in smaller parts of the blocks (i.e. sinks) while more remote areas are left undisturbed (i.e. sources).

Contrary to our predictions, CPUE increased with distance to roads. An explanation may be that more dedicated hunters seek areas with few other hunters, more birds and less previous disturbance. Wam et al. (2013) showed that the most eager hunters were crowd-avoiding, and Brøseth and Pedersen (2000) found that ptarmigan hunters on average walked long distances and hunted long days, but with the lower hunting activity close to the borders of the hunting area. Furthermore, Brøseth and Pedersen (2010) showed that willow ptarmigan selected dense habitat with fewer disturbances during the hunting season. We propose that the hunters that moved further from roads may have benefitted from higher bird densities and few encounters with other hunters.

Overall, the harvest of ptarmigan on public land in Nordland and Troms counties the first three weeks of the season was found to account for < 10 % of the autumn population in the censused hunting areas. This is the same level as estimated by Hagen (1952) more than 60 years ago, but he added an additional 10% as snared during winter. Snaring is still legal but numbers harvested by this method is insignificant today. A harvest mortality of 10% in small bodied grouse such as ptarmigan is probably compensated to a large extent, as additive mortality has not been observed at harvest rates below 20% (Braun and Rogers 1971, Sandercock et al. 2011, Smith and Willebrand 1999). Hunting mortality was compensatory in northern bobwhites *Colinus virginianus* (Williams et al. 2004) and ruffed grouse *Bonasa umbellus* (Small et al. 1991) in up to 60% harvest, while for large-bodied species like greater sage-grouse *Centrocercus urophasianus Sedinger et al. (2010),* showed that hunting mortality was additive above 10–15% harvest.

Harvest rates varied greatly between hunting blocks. However, the blocks with the highest harvest rates had relatively low densities. Based on our models, the predicted daily removal of ptarmigan increased markedly when densities became lower than ca 10/km^2. A similar pattern, i.e. inversely density dependent harvest rates, was previously reported by Willebrand et al. (2011). When a red listed species is being hunted, the general public and conservation organizations tend to explain the declining population trend on overharvest. However, with the current management system, the annual harvest rates of willow ptarmigan in Nordland and Troms is relatively low and probably partially compensatory (Sandercock et al. 2011).We propose that further restrictions than at present are not needed during periods of relatively high ptarmigan densities. However, in order to reduce the risk of overharvest, ptarmigan populations need to be carefully monitored and hunting restrictions should be considered at low densities.

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Tables

Table 1. Summary showing total number of hunters, effort (total hunting days), bag (total harvested willow ptarmigan), density (mean population of ptarmigan/km^2 in 36 hunting blocks with density estimates) and CPUE (mean ptarmigan shot per hunter/day in every hunting block), the two latter with median values in parentheses, from 162 hunting blocks on state-owned land in North-Norway during September 10-30, 2013-2016.

Year	Hunters	Effort	Bag	Density	CPUE
2013	2548	9485	4012	17.60 (12.60)	0.35 (0.26)
2014	4426	15271	11647	16.58 (16.90)	0.59 (0.44)
2015	4058	12878	8355	27.59 (14.40)	0.47 (0.31)
2016	2761	7241	5735	15.97 (9.35)	0.65 (0.67)

Table 2. Results from the model selection based on Akaike information criterion (AIC) within ΔAIC ≤ 6, comparing models of how hunting effort on willow ptarmigan is affected by forest cover, mean distance to cabins, terrain slope, terrain ruggedness and mean distance to roads within 162 hunting blocks on state-owned land in North-Norway during September 10-30, 2013-2016.

Model	Forest cover	Distance to cabins	Terrain slope	Terrain ruggedness	Distance to roads	df	AIC	ΔAIC	w_i
52	x	x			x	7	5469.9	0.00	0.34
56	x	x	x		x	8	5470.3	0.49	0.27
60	x	x		x	x	8	5471.7	1.86	0.13
51		x			x	6	5472.9	3.06	0.07
50	x				x	6	5473.7	3.83	0.05
54	x		x		x	7	5474.4	4.54	0.04
55			x		x	7	5474.5	4.60	0.03
59		x		x	x	7	5474.8	4.95	0.03
49		x			x	5	5475.6	5.76	0.02
58	x			x	x	7	5475.7	5.87	0.02

Table 3. Parameter estimates for the three best models (i.e. lowest AIC values) in the global set of models presented in Table 2. Parameters are estimated based on maximum likelihood.

Model/term	Parameter	Parameter value (SE)
52	Forest cover	-0.16 (0.07)
	Distance to cabins	-0.18 (0.08)
	Distance to roads	-0.31 (0.09)
56	Forest cover	-0.19 (0.07)
	Distance to cabins	-0.19 (0.08)
	Terrain slope	-0.09 (0.02)
	Distance to roads	-0.34 (0.10)
60	Forest cover	-0.17 (0.07)
	Distance to cabins	-0.19 (0.08)
	Terrain ruggedness	-0.03 (0.07)
	Distance to roads	-0.32 (0.10)

Table 4. The relative importance of parameters presented in tables 2 and 3 based on the sum of Akaike weights across all models where the parameter is present (Burnham & Anderson 2002), and model averaged parameter estimates.

Parameter	Relative importance	Model averaged parameter (SE)
Distance to roads	1.00	-0.32 (0.10)
Distance to cabins	0.88	-0.16 (0.09)
Forest cover	0.84	-0.14 (0.09)
Terrain slope	0.34	-0.03 (0.06)
Terrain ruggedness	0.18	0.00 (0.03)

Table 5. Results from the model selection based on Akaike information criterion (AIC) within ΔAIC ≤ 6, comparing models of how CPUE on willow ptarmigan is affected by forest cover, mean distance to cabins, terrain steepness, terrain ruggedness and mean distance to roads within 162 hunting blocks on state-owned land in North-Norway during September 10-30, 2013-2016.

Model	Forest cover	Distance to cabins	Terrain slope	Terrain ruggedness	Distance to roads	df	AIC	ΔAIC	w_i
61			x	x	x	7	4393.8	0.00	0.27
62	x		x	x	x	8	4394.4	0.64	0.19
63		x	x	x	x	8	4394.9	1.16	0.15
53			x		x	6	4395.3	1.54	0.12
55		x	x		x	7	4395.8	2.03	0.10
54	x		x		x	7	4396.5	2.75	0.07
56	x	x	x		x	8	4396.9	3.18	0.05
47		x	x	x		7	4397.7	3.97	0.04
39		x	x			6	4399.3	5.57	0.02

Table 6. Parameter estimates for the three best models (i.e. lowest AIC) values in the global set of models presented in Table 5. Parameters are estimated based on maximum likelihood.

Model/term	Parameter	Parameter value (SE)
61	Terrain slope	-0.22 (0.08)
	Terrain ruggedness	-0.11 (0.07)
	Distance to roads	0.22 (0.10)
62	Forest cover	0.07 (0.08)
	Terrain slope	-0.20 (0.03)
	Terrain ruggedness	-0.12 (0.07)
	Distance to roads	0.26 (0.11)
63	Distance to cabins	0.06 (0.08)
	Terrain slope	-0.19 (0.03)
	Terrain ruggedness	-0.03 (0.07)
	Distance to roads	-0.32 (0.11)

Table 7. The relative importance of parameters presented in tables 5 and 6 based on the sum of Akaike weights across all models where the parameter is present, and model averaged parameter estimates.

Parameter	Relative importance	Model averaged parameter (SE)
Terrain slope	1.00	-0.23 (0.07)
Distance to roads	1.00	-0.21 (0.05)
Terrain ruggedness	0.69	-0.08 (0.07)
Distance to cabins	0.36	0.02 (0.05)
Forest cover	0.26	0.02 (0.03)

Figure captions

Fig 1. Map of the study area showing 162 hunting blocks for small game on state-owned land in Nordland and Troms Counties, Norway. We have willow ptarmigan density estimates from the 36 areas marked in black.

Fig 2. The relationship between hunting effort and density in the 36 hunting blocks with density estimates on state-owned land in North-Norway, 2013-2016. A logarithmic regression line showing the trend is included in the graph.

Fig 3. Predicted proportions of the ptarmigan population shot per day on 36 hunting blocks in North-Norway, 2013-2016. Daily removal rates are estimated by dividing predicted CPUE values with estimated densities.

Figure 1

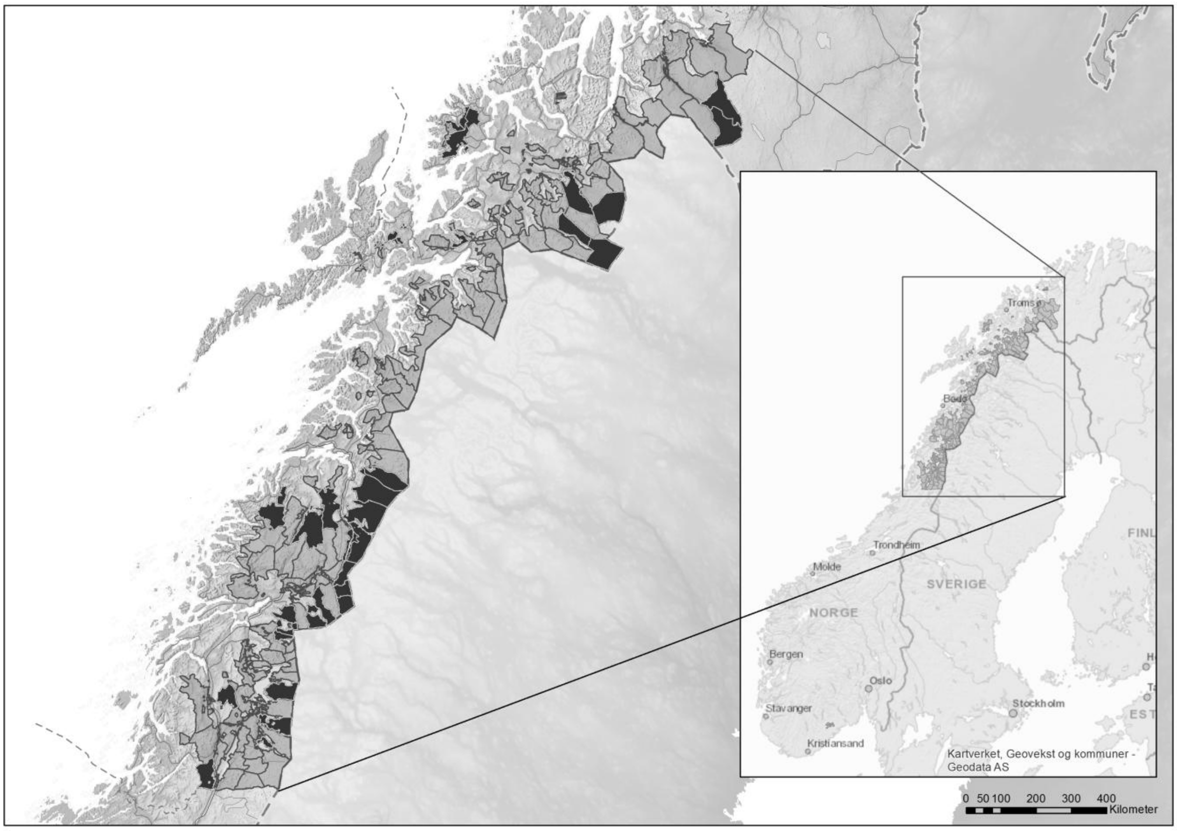

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Figure 2

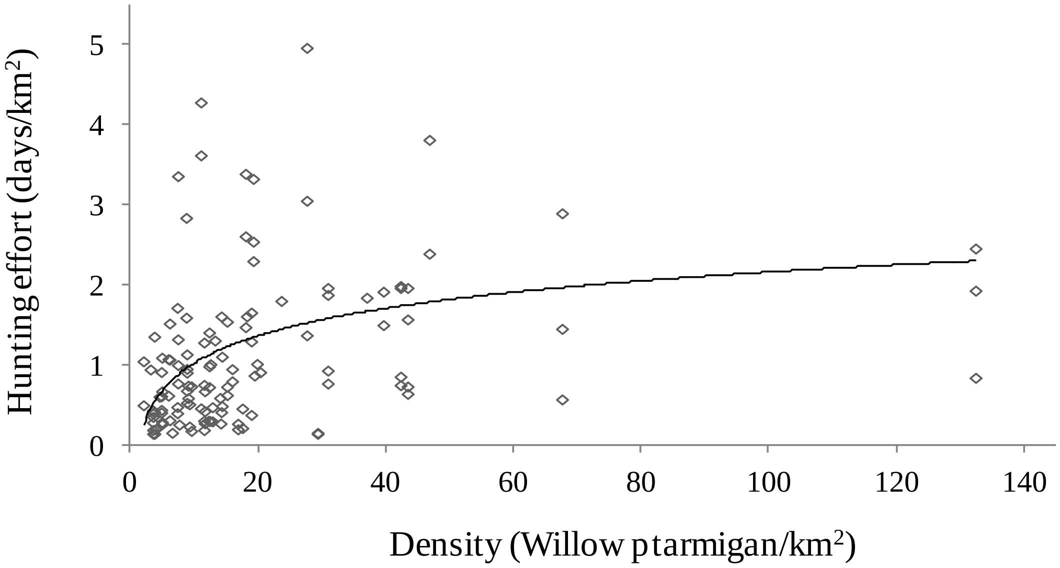
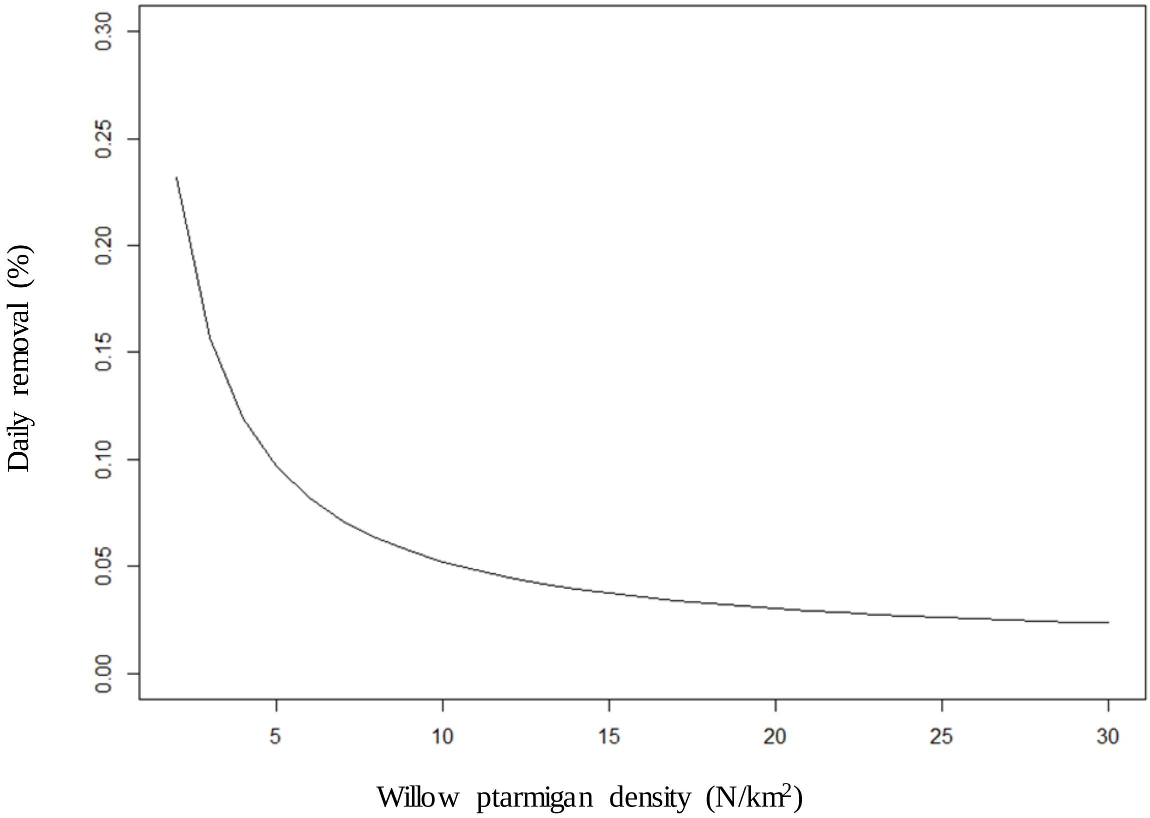


Figure 3



Appendix

Table 8. Summary of variables included in the models analyzing hunting effort, hunter efficiency (catch per unit effort) and harvest rate, on state-owned land in North-Norway, September10-30, 2013– 2016. Data are stratified by hunting blocks (A) and presented as averages (A), with mean, median, max and min estimates from the same 36 hunting blocks (B). The four last rows (C) shows the average estimates, median, max and min from all the 162 management areas.

Paper II

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Research Article

Ptarmigan Hunting Restrictions: Effects on Hunters' Opinions and Harvest

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ABSTRACT In Norway, willow (*Lagopus lagopus*) and rock ptarmigan (*Lagopus muta*) populations and harvests have declined during the last few decades, and the 2 species are considered as near threatened on the Norwegian Red List. The Norwegian State-Owned Land and Forest Enterprise (Statskog) is a main provider of ptarmigan hunting on public lands, and has recently introduced harvest restrictions in Nordland County. We investigated the relationship between hunters' opinions and the effects of restrictions on hunters and ptarmigan harvest using online structured questionnaires (2012, $n = 570$) and bag reports (2009–2011, $n = 8,795$). A majority of hunters (66%) supported harvest restrictions, and 89% were willing to shoot fewer birds to increase population size. However, opinions towards specific management alternatives were more negative and disparate. Residency of the hunters (local or non-resident) was the most influential factor on hunter opinions, and this reflected a tendency to approve of restrictions with the smallest effect on their own hunting practice. Our study indicates that access and the opportunity to hunt are more important to hunters than bag size. Daily and annual hunting bags were small, averaging 1.7 and 5.8 ptarmigan, respectively, and the daily bag limit of 4 birds was reached during 5.8% of hunting days. A harvest reduction of 50% implied a daily bag limit of 1 bird and a seasonal bag of 4, which were lower than what hunters found as acceptable. Hence, although hunter opinions may provide useful guidelines for the development of management practices, their opinions need to be evaluated for the actual effects they may have on the game populations.

KEY WORDS bag limits, harvest restrictions, *Lagopus lagopus*, *Lagopus muta*, Nordland County, rock ptarmigan, willow ptarmigan.

Willow (*Lagopus lagopus*) and rock ptarmigan (*L. muta*) are the most popular game birds in Norway, with annual harvests of 120,000 to 365,000 birds during the last decade (Statistics Norway 2016*a*). In Fennoscandia, ptarmigan populations have declined during the last decades along with several other montane bird species (Kålås et al. 2014, Lehikoinen et al. 2014). The 2 species are now considered near threatened on the Norwegian Red List (Henriksen et al. 2015). The causes and the extent of the population declines are unclear, but several studies emphasize the negative effect of range contractions and altered floral and faunal composition due to climate change (Lehikoinen et al. 2014, Elmhagen et al. 2015). The population declines have triggered a debate on the effect of hunting and the necessity of imposing more conservative hunting restrictions. In recent years, different types of harvest restrictions on small game have been introduced by managers to reduce the risk of over-harvesting. Some restrictions are daily bag limits, seasonal bag limits, shortened hunting season, prohibition of the use of dogs, or the use of source-sink systems with networks of hunted and protected area units (Tamisier 1985, Connelly et al. 2003, Novaro et al. 2005, Pedersen and Karlsen 2007, Sandercock et al. 2011).

In a study of the effect of hunting restrictions on the harvest of bobwhite quail (*Colinus virginianus*), Guthery et al. (2004) reported that bag limits generally affected hunting opportunities and harvest rates only when population levels were high. At low population levels, few hunters reached the bag

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limit, but the ratio of hunters to bobwhites increased. Thus, the proportion of birds harvested increased during periods of low population levels, rendering the restrictions insufficient at times when hunting control was most important. A somewhat similar pattern has been observed in Scandinavian ptarmigan hunting (i.e., an inverse density-dependent impact of hunting; Willebrand et al. 2011). Harvest rates were higher when ptarmigan populations were low, and Willebrand et al. (2011) concluded that effective control of hunting pressure was most important during these periods. Guthery et al. (2004) and Willebrand et al. (2011) demonstrated that knowledge about the actual effects of harvest restrictions on harvest rates is vital when introducing new management systems.

Wildlife agencies and managers are facing a desire from the public to be more involved in the management of wildlife (Decker and Enck 1996, Decker et al. 1996, Chase et al. 2000). The effectiveness of restrictions on harvests is assumed to depend on the acceptance and satisfaction of hunters (Wam et al. 2013, Andersen et al. 2014), 2 social concepts that are closely linked (Fulton and Manfredo 2004). Hence, several scientific studies have investigated factors associated with hunters' attitudes to different management regimes (Fulton and Hundertmark 2004, Fulton and Manfredo 2004, Collier and Krementz 2006, Mangun et al. 2007, Brunke and Hunt 2008). Schroeder et al. (2014) report that perceptions of new hunting regulations differ markedly among hunters and may change over time. Differences in acceptance could be related to the levels of experience among hunters; motivations and attitudes may change during a progressive development in their degree of hunting specialization (i.e., recreational specialization; Kuentzel and Heberlein 1992, Scott and Shafer 2001).

Statskog (The Norwegian State-Owned Land and Forest Enterprise) is responsible for providing ptarmigan hunting to a maximum number of hunters while ensuring a sustainable harvest of the resource (Statskog 2016). Securing hunting access for a large number of hunters may require smaller quotas than the hunters find acceptable, especially during periods of low population density. Alternatively, access can be restricted by reducing either the number of hunters or the timing or the duration of the hunting season (Peterson 2001, Angulo and Villafuerte 2004). Currently, little information exists about the relationship between restrictions imposed on hunters, their attitudes, and the actual impact on the harvests. We explored these relationships by analyzing data from bag records and a survey of hunters collected in a large state-owned mountain range in northern Norway. First, we investigated factors associated with hunter opinions about the different management systems and hunting restrictions. Second, we analyzed data on hunting practices and performances to recognize to what extent hunters are affected by the restrictions.

STUDY AREA

We conducted this study on Statskog's land in the 3 municipalities of Grane, Vefsn, and Hattfjelldal in Nordland County, in north Norway (65°10′–65°88′ N, 12°76′–14°62′E). Statskog has ownership of 66% of the 6,623 km^2 of land in these municipalities (Fig. 1). During the study period, the area had

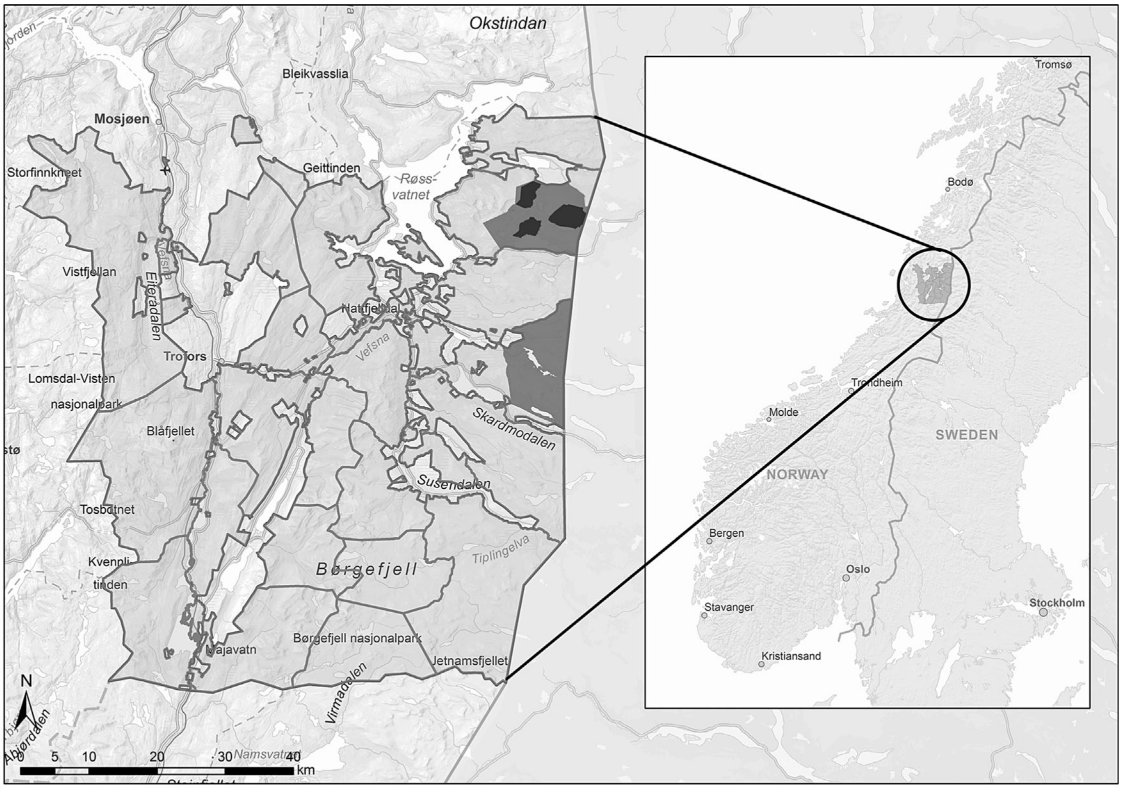

Figure 1. Twenty-five hunting blocks for ptarmigan on state-owned land in 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway. The 2 dark gray polygons are experiment area (north) and control area (south) for the source-sink experiment. The 3 black areas are refuges.

16,354 inhabitants living mainly in towns and villages (Statistics Norway 2016*b*). The study area was situated in a rugged landscape in the northern boreal birch (*Betula* spp.) forest and alpine tundra, with elevations ranging 200–1,450 m above sea level. The vegetation below the treeline was dominated by bilberries (*Vaccinium myrtillus*), mountain birch (*B. pubescens tortuosa*), and some Norway spruce (*Picea abies*). At higher elevations, vegetation was dominated by alpine heath, sedges, willows (*Salix* spp.), and patches of dwarf birch (*B. nana*). The higher fauna consisted of relatively dense populations of moose (*Alces alces*), domestic reindeer (*Rangifer rangifer*), and resident lynx (*Lynx lynx*) and wolverine (*Gulo gulo*). Main predators on ptarmigan were red fox (*Vulpes vulpes*), stoat (*Mustela erminea*), and large raptors (golden eagle [*Aquila chrysaetos*] and gyrfalcon [*Falco rusticolus*]). Before winter snowfall, willow ptarmigan resided in the subalpine zone, overlapping slightly with rock ptarmigan, which occupied the alpine zone. In winter, both species used the subalpine birch forest zone (Pedersen and Karlsen 2007). The climate was humid with an average annual precipitation between 1,200 mm and 1,500 mm, and 171 days with precipitation of >1 mm/day. The average temperature was 1.4°C with snow cover of 1–3 m depth during a period of approximately 200 days from October to late May between 1961 and 1990 (Norwegian Meteorological Institute 2016).

METHODS

Harvest Regulations

Statskog introduced harvest restrictions after a long tradition of unregulated sale of hunting permits. A new system termed accumulated hunter days (AHD) was introduced in 2009, where 25 hunting blocks were closed to ptarmigan hunting when the hunting effort exceeded 3 accumulated days of hunting/km^2. The size of the hunting blocks ranged from 41 km^2 to 425 km^2 ($\bar{x} = 201$ km^2) with an area of 4,130 km^2. There was a daily bag limit of 4 ptarmigan/hunter, no annual quota, and no restrictions in the use of dogs. The hunters had to report their daily harvests to Statskogs managers every 10 days of hunting to continue their hunt. Most (92%) hunters reported their harvest under this system.

In 2007, an experimental area of 110 km^2 was set aside to test the source-sink system, where dispersal of ptarmigan from high quality habitats with no hunting (sources, refuges) was intended to counteract higher mortality in areas with unrestricted hunting (sinks). In this area, hunting was unrestricted in terms of hunting bags and access within 72% of the area, whereas hunting was banned in the remaining 28%. Three refuges (30.5 km^2) were placed within the experimental area of 110 km^2 (Fig. 1). Near the experimental area, a control area of 118 km^2 had no refuges and no bag limit. In the source-sink experimental area, the hunters had to report their bag 3 times during the hunting season. The hunting season for ptarmigan was open from 10 September to the end of February.

Hunter Survey

We conducted the survey using 2 data sets. First, we evaluated hunter opinions concerning ptarmigan management based on a structured questionnaire that was distributed to all small-game permit holders after the hunting season (2011–2012) ended. We also used this data set to investigate factors associated with daily and annual bag sizes of the hunters. Second, we used bag records from the years 2009–2011 (i.e., 8,795 hunting days, see description above) to evaluate the potential reduction in harvest that could have been obtained with more restricted seasonal and daily bag limits.

To evaluate the hunters' opinions, we used a digital online questionnaire administered by QuestBack Ask&Act^{TM} (Oslo, Norway). We were granted permission by the Norwegian Data Protection Official for Research (permit 33455) to distribute the questionnaire and obtain information on the permit holders. We distributed the questionnaire (Table 1) to all small-game permit holders by e-mail ($n = 693$) or as a link in a text message ($n = 213$). We used text messages when e-mail addresses were not available. Thirty-six of 942 small-game license holders did not receive the questionnaire because of missing e-mail addresses or cell phone numbers. We sent a notice to optimize response rates prior to the questionnaire as recommended by Dillman (2000), and sent reminders 1 and 2 weeks after the delivery of the questionnaires according to Schaefer and Dillman (1998). Among the 906 distributed questionnaires, 543 were returned giving a preliminary response rate of 60%. After 14 weeks, we contacted 100 of the 362 non-respondents to investigate if their opinions differed from the respondent group. We obtained 27 responses from this group, and chi-squared tests showed that their answers did not differ significantly. We therefore pooled the results from the 2 groups, giving a final response rate of 63% ($n = 570$). Respondents answered categorical questions with a 5-point Likert scale (Likert 1932) from strongly agree to strongly disagree. None of the questions were mandatory. When relevant, the respondents were given the opportunity to answer "I do not know/unknown" or "other, please specify."

The questionnaire was part of a larger survey of hunter satisfaction and opinions about the ptarmigan management system at Statskog. Among 53 primary questions with 33 sub-questions, we selected 9 questions (Q1–9) that were the most relevant for our study (Table 1). These included a question regarding the necessity to regulate hunting pressure (Q1), and opinions regarding different alternatives to regulate hunting pressure (Q2–9). These alternatives included the AHD system (Q2), the source-sink system (Q3), bag reduction (Q4–6), periodic ban of hunting at low ptarmigan densities (Q7), and shortening the hunting season (Q8–9). We selected questions that were specific for this new management system, and excluded questions just relevant for Statskog.

Statistical Analysis

We used program R for handling all data and analyses (R Version 3.3.0, www.r-project.org, accessed 6 May 2016). We examined factors affecting hunters' opinions towards different harvest regulations and scenarios with generalized linear models (binomial family) using the prettyR package. Response variables were the binary answers (i.e., agree vs. disagree and neutral) to 9 different questions (Table 1). We used the same set of explanatory variables in all full models. These were age, education (years of education), hunting dog

Table 1. Parameter estimates and test statistics from generalized linear models of factors associated with attitudes towards ptarmigan harvest restrictions in Nordland County, Norway, 2011–2012. We transformed responses in a 5-point Likert scale to binary response variables (disagree or neutral vs. agree). The explanatory variables were age, hunting dog (whether or not a dog was used during the hunt), target species (willow or rock ptarmigan), bag size (number of ptarmigan shot/day), residency (whether the hunter resided in the same municipality as the hunting area, or in another municipality within the same county, or out-of-county), and source-sink (whether the hunt had taken place in a source-sink experimental area).

Question[a]	Predictor	Logit estimate	SE	χ^2	*P*
Is it necessary to regulate hunting pressure? (Q1)	Intercept	−0.17	0.34		
	Age	0.02	0.01	7.06	0.008
	Target species			7.16	0.007
	Willow ptarmigan	0.00			
	Rock ptarmigan	−1.10	0.42		
Is accumulated hunter days (AHD) a management tool that reduces risk of over-harvest? (Q2)	Intercept	−0.98	0.22		
	Residency			58.81	≤0.001
	Local	0.00			
	Regional	0.20	0.26		
	Out-of-county	1.51	0.26		
Is the use of refuge areas a management tool that reduces risk of over-harvest? (Q3)	Intercept	−0.64	0.09		
	Source-sink			4.99	0.025
	Hunted outside source-sink	0.00			
	Hunted inside source-sink	0.74	0.33		
Are you willing to accept a seasonal quota of 10 ptarmigan? (Q6)	Intercept	0.61	0.20		
	Residency			6.68	0.035
	Local	0.00			
	Regional	−0.10	0.25		
	Out-of-county	−0.52	0.24		
Should hunting be banned during periods of low ptarmigan density? (Q7)	Intercept	−0.30	0.26		
	Hunting dog			8.04	0.005
	With	0.00			
	Without	0.53	0.19		
	Daily bag	−0.09	0.04	5.78	0.016
	Residency			7.39	0.025
	Local	0.00			
	Regional	−0.09	0.25		
	Out-of-county	0.43	0.25		
Are you willing to accept a 2-week delay in the opening of the hunting season? (Q8)	Intercept	0.25	0.38		
	Age	0.02	0.01	5.34	0.021
	Residency			22.72	≤0.001
	Local	0.00			
	Regional	−0.05	0.27		
	Out-of-county	−0.96	0.26		
Are you willing to accept that the hunting season is shortened and ends 3 months earlier? (Q9)	Intercept	−0.93	0.22		
	Residency			66.17	≤0.001
	Local	0.00			
	Regional	0.53	0.26		
	Out-of-county	1.78	0.26		

[a] The responses for the questions "Are you willing to shoot fewer birds to increase the ptarmigan population?" (Q4) and "Are you willing to accept a daily bag limit of 1 ptarmigan?" (Q5) were not influenced by any of the explanatory variables we tested.

(whether or not a dog was used during the hunt), target species (willow or rock ptarmigan), daily bag (no. ptarmigans shot/day), residency (whether the hunter resided in the same municipality as the hunting area, in another municipality within the same county, or out-of-county), and source-sink (whether the hunt had taken place in the source-sink experimental area). These variables (except source-sink) had been included in previous Scandinavian studies of hunter performance and attitudes (Asmyhr et al. 2012, Kaltenborn et al. 2012). We excluded gender from the analyses because of the very small number of female respondents. We used backwards selection to identify the most parsimonious model (i.e., a model with only significant terms at $P < 0.05$). We used the lsmeans package to calculate average proportions and 95% confidence limits of the responses.

We used generalized linear models (GLM) to identify factors associated with bag sizes. We obtained the data from the questionnaires, and the response variables were average daily bag of each hunter and total annual bag of each hunter. The explanatory variables were the same as listed in the previous paragraph. We used a quasi-poisson error structure in the models of annual bags because of data overdispersion, and a normal error structure in the models of daily bag size. In the latter, we normalized the response variable using ln-transformation.

RESULTS

Respondents from the questionnaire survey averaged 46 (range = 17–81, SD = 12.58) and 41 (range = 24–59, SD = 9.00) years of age for men and women, respectively. Only 4% of the respondents were female. Hunters averaged 23 ± 13.68 (SD) years of hunting experience and had completed 13.4 ± 4.36 years of education (equivalent to high school and some college education). Most hunters did not use dogs while hunting (60.5%), and the majority (57.6%) had hunted in the same area for >3 years. Almost all hunted for willow ptarmigan or both species (95.1%), and 4.9% had hunted rock ptarmigan only. Most of the hunters came from Nordland County (59.6%) of which 19.2% came from the municipality they were hunting. Forty (7.0%) of 570 respondents had hunted in the source-sink experimental area.

Hunter Opinions

Sixty-six percent of the respondents agreed that it was necessary to regulate hunting pressure, 20.0% were neutral, and 14.3% disagreed. Logistic regression models revealed that older respondents were more likely to support regulating the hunting pressure (Table 1). Furthermore, respondents who had hunted only rock ptarmigan were less supportive of regulating the hunting pressure.

The only variable with a significant influence on the opinion on whether AHD reduces risk of over-harvesting was hunter residency (Table 1). Out-of-county hunters residing outside Nordland County were more likely to agree (63% agree, 95% CI = 57–69%) than local hunters residing in the municipality of the hunting blocks (27% agree, 95% CI = 19–37%) and regional hunters residing within Nordland County (32% agree, 95% CI = 26–38%).

The only significant factor influencing the response on the use of refuge areas to reduce risk of overharvest was whether the respondents had actually hunted in areas with this source-sink management practice (Table 1). These hunters were positive (53% positive, 95% CI = 37–67%) compared to other hunters that had not hunted on the experimental source-sink areas (35% positive, 95% CI = 31–39%).

There was a strong willingness to kill fewer birds, if necessary (i.e., 89% agreed). Hence, we found no factors influencing this opinion (Table 1), probably because of the small proportion of neutral (8%) and disagreeing hunters (3%). Only 16% of the hunters were willing to accept a daily bag of 1 bird. None of the explanatory variables had any significant effect on the acceptance of this restriction (Table 1). On average, 58% agreed that a seasonal quota of 10 ptarmigan was an acceptable bag restriction. The most parsimonious model explaining opinions on a seasonal quota included only 1 significant term: the hunter's residency (Table 1). Out-of-county hunters were less likely to agree (52% positive, 95% CI = 45–59%) than local (65% positive, 95% CI = 55–73%) and regional (62% positive, 95% CI = 56–69%) hunters.

Fifty-one percent of the hunters agreed to a prohibition of hunting when ptarmigan densities are low. A significantly larger proportion of hunters without dogs agreed to this statement (55%, 95% CI = 49–60%) than hunters with dogs (41%, 95% CI = 34–49%). Furthermore, local (45%, 95% CI = 35–56%) and regional (43%, 95% CI = 36–50%) hunters were less positive than out-of-county hunters (56%, 95% CI = 49–62%). We also found a significant effect among the hunters regarding the number of birds shot/day. The more birds shot/day, the more likely the hunters would disagree (Table 1).

Sixty-four percent of the hunters were willing to accept a 2-week delay in the opening of the hunting season. Opinions on this restriction depended on the age and residency of the hunters (Table 1). Older respondents were more likely to agree. Furthermore, local (74%, 95% CI = 64–81%) and regional hunters (72%, 95% CI = 66–78%) were more positive than out-of-county hunters (51%, 95% CI = 45–58%).

The attitudes toward closing the hunting season 3 months earlier to avoid over-harvest at low densities differed according to the residency of the hunters (Table 1). A far larger proportion of out-of-county hunters were supportive of this restriction (70%, 95% CI = 64–76%) than local (28%, 95% CI = 21–38%) and regional hunters (41%, 95% CI = 34–47%).

Hunting Quotas

The questionnaire respondents reported average daily bags of 1.7 ± 2.93 (SD) ptarmigan/hunter and GLMs revealed a significant effect of whether or not a hunting dog had been used (Table 2). Hunters with dogs shot more birds (2.5 ± 3.77) than hunters without dogs (1.3 ± 2.13). None of the other predictor variables had a significant effect. Regarding seasonal bags, the respondents reported an average of 5.8 ± 7.60 (SD) ptarmigan/hunter. Also in this case, the only predictor with a significant effect was whether or not a hunting dog had been used (Table 2). Hunters using dogs shot more birds (8.7 ± 9.47) than hunters who did not use dogs (4.0 ± 5.27).

According to the bag records from the period 2009 to 2011, no birds had been shot in a large proportion of the hunting days ($n = 8{,}795$, 67%; Fig. 2). Furthermore, the daily bag limit of 4 birds had been reached in a relatively small proportion of the hunting days (5.8%; Fig. 2). Hence, a pronounced reduction in daily bag limit would have been required to obtain a noticeable reduction in the total harvest. A bag limit of 3 birds would lead to a reduction of <10% and to reduce total harvest by 50%, the bag limit would need to be 1 bird/day (Fig. 3). Furthermore, a large proportion of the hunters (51%) did not shoot a single bird during the whole season, and a small proportion (5%) shot ≥15 birds (Fig. 4). Accordingly, only a relatively small seasonal quota would lead to a marked reduction in the number of birds harvested (Figs. 4 and 5). A seasonal quota of 15 birds would reduce the harvest by only 8.6%, whereas a seasonal quota of 10 birds would produce a 19.2% reduction and a seasonal quota of 4 birds would produce a 48.2% reduction (Fig. 5).

DISCUSSION

Previous literature suggests that hunters may agree about wildlife management aims but disagree concerning the strategies to accomplish them (Cornicelli et al. 2011). Our study concurs with this inference; the majority of hunters agreed to regulate hunting pressure and shoot fewer birds, if necessary, but the questions focusing on specific alternatives to

Table 2. Parameter estimates and test statistics from generalized linear models of factors associated with ptarmigan hunting bags in Nordland County, Norway, 2011–2012. The response variables were daily hunting bags per hunter and seasonal bags (no. birds shot during the season per hunter).

Response	Predictor	Logit estimate	SE	χ^2	*P*
Daily bag	Intercept	0.93	0.05		
	Hunting dog			27.34	≤0.001
	With	0.00			
	Without	−0.34	0.06		
Seasonal bag	Intercept	2.13	0.08		
	Hunting dog			36.76	≤0.001
	With	0.00			
	Without	−0.73	0.12		

achieve this outcome revealed more negative opinions and disagreement among the hunters. These results may be partially explained by the relatively short time frame of the management experiments; the AHD and source-sink systems had been introduced only 3 and 5 years prior to the questionnaire survey, respectively. Opinions about the introduced systems in our study may change; introduced hunting regulations have been reported to gain legitimacy over time (Schroeder et al. 2014). Hence, the negative responses may reflect a general skepticism towards unfamiliar management systems. An example of the effect of familiarity with management was revealed in the opinions concerning the source-sink system. In this case, respondents that had actually hunted within these experimental areas were more supportive of the management technique than those that had not.

A relationship between hunting specialization and environmental orientation could potentially explain the more positive attitudes of older hunters to regulate hunting pressure in our study. According to the recreation specialization concept, hunters are assumed to progress over time from novice to expert (Bryan 1977, Donnelly et al. 1986, Ditton et al. 1992). In this process, attitudes, satisfaction levels, management preferences, and hunting bags have been observed to change (Kuentzel and Heberlein 1992, Scott and Shafer 2001). Rather than being bag oriented, more specialized hunters are assumed to be motivated by the quality of the experience in terms of social and nature appreciation (Bryan 1977, Kuentzel and Heberlein 1992). Hunting with dogs suggests a high degree of specialization among the hunters. Still, in our study, hunters with dogs shot more birds/day and thus appeared more bag oriented than hunters without dogs. A possible explanation may be that bags are larger simply because hunting dogs find more dead and wounded birds, and not because of a different attitude among the hunters.

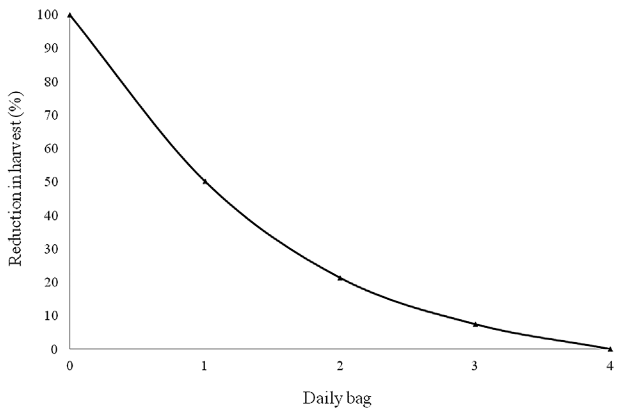

Figure 3. Proportional reductions in harvest given daily bag limits from 4 to 0 ptarmigan. The estimates are based on reported bags from 8,795 hunting days on state-owned land in 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway, during hunting seasons in 2009–2010, 2010–2011, and 2011–2012. We calculated estimates as the ratio between the number of ptarmigan that could have survived given a reduced bag limit ($\sum$ of current bags − $\sum$ of reduced bags) and the number of birds shot with the current bag limit of 4 birds.

In our study, hunter age affected only the opinion about the need for hunting restrictions, but it was not the most important factor affecting opinions about the specific management alternatives. Instead, hunter residency was more important. A study of hunter perceptions and opinions about management of white-tailed deer (*Odocoileus virginianus*) in Minnesota, USA, revealed strong site fidelity among the hunters, and an approval of management strategies that first and foremost secured access to their hunting areas, even if quotas were

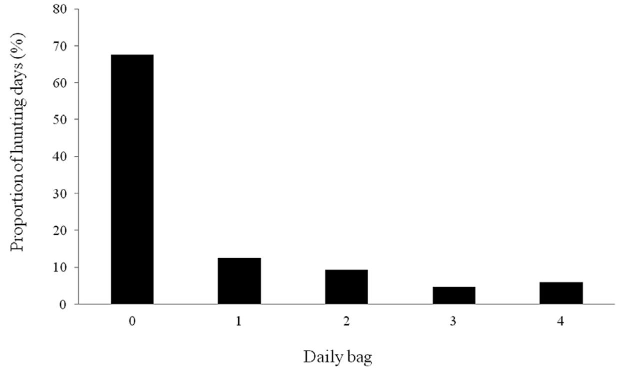

Figure 2. Proportions of hunting days with daily bags of 0–4 ptarmigan within areas with an accumulated hunter days management system and daily bag limit of 4 birds. Data are based on reported bags from 8,795 hunting days on state-owned land in the 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway, during hunting seasons in 2009–2010, 2010–2011, and 2011–2012.

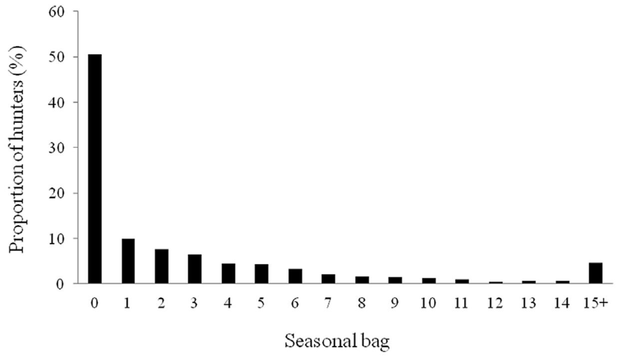

Figure 4. The proportion of hunters obtaining bags of 0 to >15 ptarmigan during the hunting season within areas with an accumulated hunter days management system and daily bag limits of 4 birds. Data are based on reported bags from 8,795 hunting days on state-owned land in 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway, during hunting seasons in 2009–2010, 2010–2011, and 2011–2012.

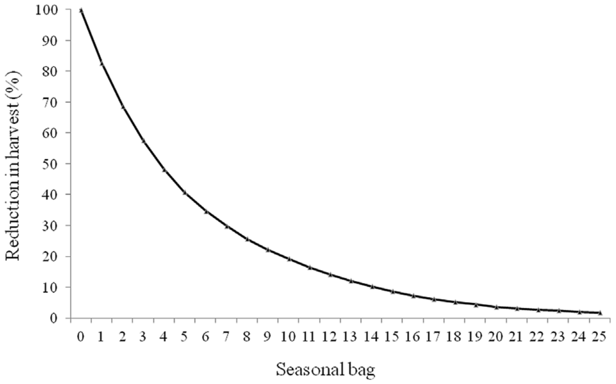

Figure 5. Proportional reductions in harvest given seasonal bag limits from 25 to 0 ptarmigan. Estimates are based on reported bags from 8,795 hunting days on state-owned land in 3 municipalities: Grane, Vefsn, and Hattfjelldal, Nordland County, Norway, during hunting seasons in 2009–2010, 2010–2011, and 2011–2012. We calculated estimates as the ratio between the number of ptarmigan that could have survived given a reduced bag limit and the number of birds shot with the current system of no seasonal bag limits.

limited (Cornicelli et al. 2011). In our case, a combination of site fidelity and fear of losing hunting opportunities may also explain the relationship between the opinions about the AHD system and the residency of the hunters. Out-of-county hunters were more positive than local hunters, and the majority of hunters from other counties visit these areas in the very beginning of the season. At this time, most of the blocks are open for hunting, but as time progresses, some blocks are closed for hunting because of the imposed limit of 3 accumulated hunting days per km^2. Hence, the restrictions are likely to affect the hunting opportunities of local residents later in the season when few out-of-county visitors are present.

The line of reasoning above may also explain why the residency of the hunters was an important factor determining the opinions towards bag restrictions and shortening the hunting season. Local hunters were more positive towards a 2-week delay in the opening of the hunting season, less positive towards closing the season 3 months earlier, and less positive towards a ban of hunting at low population densities. A 2-week delay in the opening of the hunting season would probably reduce hunting access for out-of-county hunters more than for local hunters, whereas the opposite would be the case if hunting was closed 3 months earlier. Likewise, the difference in attitudes towards a ban of hunting may be explained by higher site fidelity among local hunters.

Results indicate bag size had no influence on the opinions of hunters towards the different systems of harvest restriction. These results may reflect that hunting bags in general were small (i.e., below the daily bag limit of 4 birds). Possibly, the majority of the hunters therefore have no incentive to reduce their own impact on the ptarmigan population. Daily bag limit is a commonly used harvest restriction among managers of ptarmigan hunting in Scandinavia (Asmyhr et al. 2012, Andersen et al. 2014), but its effect on bag size and harvest rates have not been studied before. According to Peterson (2001) and Guthery et al. (2004) daily bag limits are regressive (i.e., harvest rates are only affected at high population densities when they are least needed). Hence, in many cases, daily bag limits will restrain the hunting practice and not affect the actual harvest. In our study area, a substantial reduction in bag limits to only 1 bird would have been needed to obtain a 50% reduction in the harvest, and this low bag limit was not found acceptable by the hunters.

MANAGEMENT IMPLICATIONS

In our study, we have shown that although most hunters were positive to hunting restrictions in general, it was difficult to find management alternatives that hunters find acceptable and that have an actual impact on harvest rates. Hunter opinions may provide useful guidelines for the development of management practices, but the opinions need to be evaluated in view of the actual effect on the game populations (Peterson 2001). The negative attitudes towards the specific management alternatives may imply that other options should be evaluated. However, it may also reflect insufficient information on the necessity of hunting restrictions and the potential impact of the different restriction alternatives. This is not unexpected, as there is no unified consensus in the Scandinavian scientific community regarding the effect of hunting on ptarmigan populations or concerning which management options are best suited for reducing harvest. An improved knowledge of hunting effects and management options is clearly needed, and this information needs to be effectively communicated to the stakeholders to gain valuable insight into their attitudes towards management alternatives and factors associated with their satisfaction.

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Paper III

The alternative prey hypothesis revisited: still valid for Willow Ptarmigan population dynamics

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Abstract

The Alternative Prey Hypothesis (APH) predicts that the interaction between generalist predators and their main prey is a major driver of population dynamics of alternative prey species. In Fennoscandia, changes in climate and human land use are assumed to alter the dynamics of cyclic small rodents (main prey) and lead to increased densities and range expansion of an important generalist predator, the red fox *Vulpes vulpes*. In order to better understand the role of these potential changes in community structure on an alternative prey species, willow ptarmigan *Lagopus lagopus*, we analyzed nine years of population census data from SE Norway to investigate how community interactions affected their population dynamics. The ptarmigan populations showed no declining trend during the study period, and annual variations corresponded with marked periodic small rodent peaks and declines. Population growth and breeding success were highly correlated, and both demographic variables were influenced by an interaction between red fox and small rodents. Red foxes affected ptarmigan negatively only when small rodent abundance was low, which is in accordance with APH. Our results confirm the important role of red fox predation in ptarmigan dynamics, and indicate that dampening small rodent cycles may lead to decline in ptarmigan and other alternative prey species due to elevated predation pressure.

Introduction

During the last decades faunal range shifts, population declines and changes in community structures and interactions have been attributed to climate warming in Scandinavia (Elmhagen et al. 2015). Concern has been raised about range expansions of typical “southern species” (e.g. red fox, European brown hare *Lepus europaeus*, European badger *Meles meles*), range contractions and decline of “northern species” (e.g. willow ptarmigan, rock ptarmigan *Lagopus muta*, mountain hare *Lepus timidus*, arctic fox *Vulpes lagopus*) and disruption of small mammal population cycles (Elmhagen et al. 2011, Elmhagen et al. 2015, Henden et al. 2009, Henttonen and Wallgren 2001, Hörnfeldt 2004, Hörnfeldt et al. 2005). Particularly strong impacts of climate change are expected in mountainous habitats, partially due to an above average temperature increase in higher altitudes (Parmesan and Yohe 2003, Post et al. 2009) and an inevitable contraction of habitat area following an elevated tree line. It is, however, difficult to disentangle the relative effects of climate change and other environmental stressors (e.g. changes in human land use). An example of this is the red fox, whose increase in density and range expansion in Scandinavia has been attributed to several forms of anthropogenic influence, including climate change, mesopredator release, ungulate overabundance, human land use, and altered human hunting pressure (Elmhagen and Rushton 2007, Hersteinsson and Macdonald 1992, Ims et al. 2007, Killengreen et al. 2011). Irrespective of the cause, the expansion of red foxes towards higher altitudes may entail direct negative impacts on mountain wildlife communities through increased competition and predation (Linnell et al. 1999, Tannerfeldt et al. 2002). Furthermore, more complex negative effects may arise as a consequence of dampened small rodent cycles, as the interaction between generalist predators (e.g. red fox) and their main prey (small rodents) may exert strong influence on alternative prey species (The alternative prey hypothesis – APH; Angelstam et al. 1984, Hagen 1952, Lack 1954).

Further increase in mammalian generalist predators in the Scandinavian mountains are expected in the future due to the facilitative effect of rising temperatures (Elmhagen et al. 2015), along with disturbances in the dynamics of small rodents due to altered winter conditions (Aars and Ims 2002, Kausrud et al. 2008). In order to predict the potential consequences of environmental changes on mountain wildlife communities we need to enhance our current knowledge of the direct and indirect community interactions. Hence, in this paper, we analyzed nine years of population census data to investigate whether the population growth of a declining alternative prey species, the willow ptarmigan, depends on the interaction of abundance of red foxes and their main prey, small rodents.

Originally, APH was presented as an explanation of the synchronous population cycles of small rodents and other small herbivores. That is: generalist predators synchronize herbivore prey dynamics through prey switching during the crash phase of their main prey, with less influence on alternative prey species at high main prey densities (Angelstam et al. 1984). Numerous studies support the hypothesis (see e.g. Dahl 2005, Kjellander and Nordström 2003, Lindström et al. 1987, Small et al. 1993, Wegge and Storaas 1990), and some of the strongest evidence stem from studies of mammalian generalist predators, mainly red fox and pine marten, boreal forest grouse (capercaillie and black grouse) and mountain hares: Angelstam et al. (1984) found support for APH-based predictions, i.e. that red fox shifted diet when vole abundances declined, and inverse correlations between vole abundance and the mortality rates of black grouse and mountain hares. In addition, predator removal experiments conducted by Marcstrom et al. (1988) showed that the synchrony between vole abundance and grouse breeding success vanished once red foxes and pine martens were removed.

Somewhat similar patterns were observed in another experiment, where supplemental feeding of generalist predators during vole decline prevented a reduction in forest grouse chick production (Lindström et al. 1987).

Regarding willow ptarmigan population dynamics, the general impact of predation and its relationship with rodent cycling has been disputed. Kausrud et al. (2008) observed a strong link between the collapse of small rodent cycles and climate change mediated by altered snow conditions during winter. Parallel changes in the dynamics of ptarmigan and other bird communities were attributed to "shared predators being an important part of the cyclic and synchronous behavior of the system". Later, Selås et al. (2011) stated that "increased predation on eggs and chicks as the causal link between climate change and grouse density as proposed by Kausrud et al. (2008) may be incorrect". Selås et al. (2011) argued that although predation may enhance cycle amplitudes in grouse, fluctuations in food plant quality is a major influential factor generating synchronized dynamics in rodents and grouse. Furthermore, Selås et al. (2011) suggested that negative impact of climate change on grouse could be caused by the elevated plant chemical defense following warmer summers which, in turn, could negatively affect grouse reproduction. Still, other factors and mechanisms have been proposed as important drivers of grouse dynamics and population trends. Over a 4-year study period, Henden et al. (2011b) did not observe an anticipated positive response in a willow ptarmigan population during one rodent peak. Based on this, and observed effects on ptarmigan habitat occupancy patterns, Henden et al. (2011b) concluded that factors other than changing rodent population dynamics may be responsible for the declining trend in Scandinavian ptarmigan. Then again, Kvasnes et al. (2014) observed a pronounced large-scale spatiotemporal synchrony in ptarmigan recruitment that corresponded with variation in rodent abundance. However, an effect of spring/summer climate (NAO-index) had a stronger effect on recruitment of ptarmigan than rodents and Kvasnes et al. (2014) concluded that the link between rodent and ptarmigan dynamics had been weakened following the collapse of rodent cycles during the 1990ies, and as a consequence the importance of environmental perturbations had increased.

Interpretations and conclusions concerning the ptarmigan-rodent-predator relationship has been weakened by a lack of information of one of the main actors in the system; the predators. The fact that no studies of ptarmigan population dynamics have yet included predator abundance as a predictor variable is an obvious limitation in our knowledge of how the system works. In our study, we combined census data on ptarmigan, rodents and red fox to examine spatiotemporal patterns in ptarmigan population growth. We addressed the APH-hypothesis and evaluated its relevance for ptarmigan dynamics by testing the following prediction: that ptarmigan population growth depends on an interacting effect of abundances of rodents and mammalian generalist predators. According to APH, predation impact from generalist predators should be limited during periods of high availability of main prey, and thus, we expect that ptarmigan growth is determined by an interaction between rodents and predators.

Material and methods

Study area

Our study was carried out in Hedmark County (27 400 km^2, 61° N 11° E), southeastern Norway (Fig 1), in the boreal zone (Moen 1999). The southern part of the county consists of a mosaic of farmland and commercially managed conifer forests, whereas fragmented alpine areas are in the northern part, covering approximately19 % of the county (Blumenrath and Hanssen 2010) (Fig 1). Suitable habitat for ptarmigan at and above treeline is characterized by presence of willows (Salix spp.), dwarf birch (*Betula nana*) and ericaceous shrubs. The treeline is situated at elevations of approximately 800-1000 m, and the highest mountain peak ("Rondslottet") is 2178 meters above sea level. The climate is classified as semi-continental with mean temperatures of -13 °C in January and 13 °C in July in the northern parts of the study area (Norwegian Meteorological Institute). Potential mammalian predators present in the study area are the red fox, pine marten (*Martes martes*), stoat (*Mustela erminea*), least weasel (*Mustela nivalis*) and wolverine (*Gulo gulo*). Common avian predators are hooded crow (*Corvus cornix*), raven (*C. corax*), rough-legged buzzard (*Buteo lagopus*), gyrfalcon (*Falco rusticolus*) and golden eagle (*Anquila chrysaetos*). Prevailing small rodent species are Norwegian lemmings (*Lemmus lemmus*), tundra voles (*Microtus oeconomus*) and bank voles (*Myodes glareolus*).

Census data

Line transect surveys of willow ptarmigan were conducted in early August 2005-2014 by the use of pointing bird dogs. During this period, an average of six annual counts (SD = 2.6) were conducted in 48 different survey areas. The size of the survey areas averaged 56.0 km^2 (SD = 61.1), and in each area, an average of 15.4 (SD=10.9) transect lines ($\overline{x}$ = 3.2 km ± 1.1 SD) with a total length of 47.1 km (SD=34.5) per survey area were monitored. The dog handlers noted all observations of willow ptarmigan (i.e. group size and location), and whether or not small rodents had been observed along the transect lines.

We estimated predator track frequencies along 2.95 km (SD=0.5) long snow tracking transect lines in January in the period 2006 to 2014 (Fig 1). The transect lines were part of a nationwide monitoring program for Eurasian lynx (*Lynx lynx*) and were based on voluntarily work from members of the Hedmark Chapter of the Norwegian Association of Hunters and Anglers. All tracks crossing the transect lines were recorded, including red fox. The transect line density was 3-4 lines per 100 km^2 (Tovmo and Brøseth 2011). Of a total of 621 different lines, 281 to 484 lines were surveyed annually during favorable snow conditions, i.e. 2-5 days after snowfall.

Statistical analysis

For each survey area and year, we calculated a density index for willow ptarmigan by dividing the total number of flushed birds by the total length of the surveyed transect lines (i.e. birds per km of survey). Willow ptarmigan population growth rates (r) were defined as the logarithm of the density index in year t divided by density index in year t-1 ($r= \ln(N_t/N_{t-1})$). As indices of breeding success, we used the proportion of juvenile ptarmigan among all counted birds per survey area. The surveys were conducted prior to brood break-up, and thus, single birds or pairs were most likely adults that had lost eggs or chicks. The numbers of juveniles per brood was estimated by subtracting two adults from each group of birds. For each survey area and year, we calculated small rodent density indices by dividing the number of transect lines where rodents had been observed with the total number of surveyed transect lines. Although the line transects varied in length; transects with rodent observations were on average 56 m shorter than transects with no observations, we observed no effect of this variation on the probability of detecting small rodents (t= 0.59, p=0.557).

From the snow tracking transects, we calculated track frequency indices for red fox by dividing the number of tracks per km with the number of days since last snowfall. Because the predator sampling took place some distance from the ptarmigan areas, we used the inverse-distance weighting (IDW) method for spatial interpolation of predator tracks. This gave predicted index values for red fox per survey area and year. The basic assumption for this method is that the value of a non-sampled location is the average of known values within neighboring surveyed points, inversely weighted with the distances between sampled and non-sampled locations. All variables were assessed by the use of ArcGIS .

We analyzed the data using linear mixed effects models (LME) from the lme4 package (Bates et al. 2008). Willow ptarmigan growth rate and breeding success were used as dependent variables and track indices of red fox and small rodent indices as explanatory variables. All independent variables were from year t, i.e. from January for red fox and August in the same year for rodents. Hence, the survey data included in the models were collected 6-7 months apart. Despite the different timing of the surveys, we argue that the data were valid for testing APH predictions: Red fox have been shown to affect forest grouse mainly through predation of eggs and chicks, i.e. during May-June (Angelstam et al. 1984, Hagen 1952, Hörnfeldt 1978, Marcstrom et al. 1988, Storaas and Wegge 1987). Our red fox density index data were collected prior to the reproduction period, and probably corresponded quite well with the relative distribution of predators during the following spring. If red fox had been surveyed after reproduction, the data would probably reflect spatial differences in red fox breeding success rather than relative abundances and predation impact during the most critical period for ptarmigan. Following this argument, the optimal timing of rodent would be spring rather than late summer. We did not have access to spring data, and our only alternative would be using rodent data from the preceding august survey. However, due to the very high and unpredictable winter mortality in Scandinavian small rodents (Aars and Ims 2002, Hansson and Henttonen 1985, Johnsen et al. 2017, Korslund and Steen 2006), we considered that survey data from August the same year served as a better proxy to spring densities. Willow ptarmigan survey area was set in the models as a random term. We used the same sets of models to analyze variation in breeding success and growth rates (Table 1). The data was analyzed using R (R Core Team 2017). We selected the most parsimonious model using Akaike Information Criterion (AIC) values and Akaike weights (Anderson et al. 1998).

Results

The ptarmigan population density index varied markedly between years and between areas (Fig 2). During the study period, three clear peaks occurred: in 2007 (8.0 per km, SD=5.9), 2011 (7.0 per km, SD=5.3) and 2014 (4.7 per km, SD=3.2). The lowest average densities were observed in 2009 (2.8 per km, SD=1.6) and 2012 (2.9 per km, SD=2.7). Population growth rates were strongly and positively correlated with breeding success ($R^2 = 0.42$) (Fig 3). The rodent abundance indices exhibited high amplitudes that corresponded with ptarmigan density: i.e. markedly low densities in 2009 (0.02, SD=0.1) and 2012 (0.01, SD=0.02), and peaks in 2011 (0.80, SD=0.2) and 2014 (0.65, SD=0.3), see (Fig 3). The red fox index varied less among years (Fig 3).

For both ptarmigan population growth and breeding success, the best models included the interaction between rodent and red fox abundance, as expected (Tables 1 and 2). As shown in Figs 3 a) and b), the negative impact of red fox on ptarmigan appeared when small rodent densities were low. During years of high rodent density, breeding success and population growth of ptarmigan were high, presumably because the impact of red fox was low. Markedly higher AIC-values were obtained from models with only one predictor variable (Table 1).

Discussion

In our study, population growth and breeding success of willow ptarmigan were highly correlated, and both variables were influenced by an interaction between the red fox (a generalist predator) and small rodents. This similarity emphasizes the close relationship between variation in population growth and recruitment rates. This is a typical feature of the so called high reproductive species, whose low annual survival, high fecundity and early maturity produces high population fluctuations that are typically determined by variation in recruitment (Sæther et al. 1996). Few ptarmigan fail to produce a clutch (Martin et al. 1989), and therefore recruitment rates in autumn are mainly determined by nest losses and juvenile survival (see e.g. Hannon and Martin 2006, Munkebye et al. 2003, Sandercock et al. 2005, Steen and Erikstad 1996). Our results indicate that predation from mammalian generalists - especially red fox - is a significant influence in this stage, and this is in accordance with previous research on willow ptarmigan in North America (see e.g. Sandercock et al. 2005).

In Fennoscandia, data on nest losses and chick survival in willow ptarmigan are somewhat limited, but some evidence suggests that predation is highly variable and partially caused by mammals (Munkebye et al. 2003, Parker 1984, Smith and Willebrand 1999, Steen and Haugvold 2009, Wiebe and Martin 1998). The role of predation on forest grouse (capercaillie and black grouse) is better known, and mammalian generalists are identified as the main threat to eggs and chicks in previous studies (Angelstam et al. 1984, Brittas and Willebrand 1991, Lindström et al. 1994, Storaas et al. 1999, Storaas and Wegge 1987, Wegge and Kastdalen 2007). Furthermore, a stronger impact on recruitment rates than on adult survival of forest grouse was demonstrated in two generalist predator removal experiments in Scandinavia (Kauhala et al. 2000, Marcstrom et al. 1988). Our study demonstrates that mammalian generalist predators may exert a comparable impact on willow ptarmigan. Still, somewhat different patterns of predation impact could be expected between prey species in alpine- and woodland habitats due to differences in carnivore community composition. Regarding predators, the most pronounced difference is the relatively lower abundances of mammals versus birds in alpine areas, and thus, mammalian predator impact on ptarmigan could be lower than for forest grouse (Hannon et al. 2003, Sandercock et al. 2011, Smith and Willebrand 1999). However, several studies suggest that mammalian predator influence is increasing in Scandinavian mountains (Elmhagen and Rushton 2007). In particular, the red fox has received attention due to its increasingly negative impact on the arctic fox (Hersteinsson and Macdonald 1992, Tannerfeldt et al. 2002). The particular importance of red fox predation was demonstrated by the marked population increase in several small game species during an epizootic of sarcoptic mange that significantly reduced red fox abundance during the 1970ies and 1980ies (Lindström et al. 1994, Smedshaug et al. 1999).

According to our analyses, red fox had a negative effect on ptarmigan growth rates and breeding success only when rodent abundances were low. This is in accordance with APH, as the predators are assumed to exert little influence on alternative prey species, e.g. ptarmigan, when the main prey densities are high. The

APH predicts that a change in predation impact on alternative prey is mainly caused by a functional response of the predators. In our case, it is difficult to disentangle the relative effect of a functional or a numerical response based on the generalist predator snow tracking index, as the number of crossing tracks on transects is a product of the number of individuals present (numerical) and their individual travel distances (functional). Hence, the index may therefore better reflect the total response of the predators. Nevertheless, our analyses suggest that the functional component of the predator response plays an important role in their impact on ptarmigan, as the best models show an interaction between red fox and small rodent abundance on ptarmigan growth. The positive relationship between red fox and ptarmigan at high rodent densities, and the negative association at low rodent densities, would probably not occur unless there was a diet shift among the predators.

Conclusions

In this paper, we have shown a clear relationship between the breeding success and growth rate of willow ptarmigan and its dependency on the interaction between the abundance of small rodents and a mammalian generalist predator; the red fox. Our results suggest that changes in the dynamics of small rodents and increase in predator abundance may contribute to further decline in ptarmigan and other alternative prey species. Still, although we have demonstrated linkages among a generalist predator and its main and alternative prey, more research is needed to document and quantify predation impact, the relative importance of different predator species, and the potentially interactive effects of predation and other influential factors. Furthermore, the relative influence of climate change versus other types of human influence on community dynamics in mountain ecosystems warrants further attention.

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The following Supporting Information is available for this article online:

Data set.

Tables

Table 1. Akaike information criterion (AIC), ΔAIC and AIC$_w$ selection summary of four models examining the contribution of the following explanatory variables to willow ptarmigan growth rate and breeding success: Effects of rodent abundance (ROD) and red fox density index (RF).

		Growth rate			**Breeding success**		
Model	**Explanatory variables**	**AIC**	**ΔAIC**	**W**	**AIC**	**ΔAIC**	**W**
M1	ROD*RF	586.1	0	0.97	-461.0	0	0.92
M2	ROD+RF	593.5	7.4	0.02	-456.1	4.9	0.08
M3	ROD	602.7	16.6	<0.01	-439.4	21.6	<0.01
M4	RF	626.6	40.5	<0.01	-400.6	60.4	<0.01
M0	NULL	635.5	49.4	<0.01	-381.3	79.7	<0.01

Data were collected in Hedmark county, SE Norway in 2006-2014. The most parsimonious model (M1) is marked with bold font.

Table 2. Parameter estimates explaining population growth and breeding success in willow ptarmigan.

	Growth rate			**Breeding success**		
Predictor variable	**Estimate**	**SE**	**t-value**	**Estimate**	**SE**	**t-value**
Intercept	0.24	0.10	2.34	0.72	0.02	39.12
ROD	-0.03	0.25	-0.14	0.04	0.04	1.12
RF	-0.92	0.20	-4.60	-0.17	0.03	-5.18
ROD*RF	1.54	0.50	3.10	0.21	0.08	2.65

Parameter estimates from the best model explaining population growth and breeding success in willow ptarmigan in Hedmark county, Norway, 2006-2014 (see Table 1).

Figure captions

Fig 1. Overview of locations of ptarmigan survey areas and predator snow tracking transect centroids within the county of Hedmark, southeast Norway.

Fig 2. Temporal patterns of willow ptarmigan population density indices (birds observed per km ± 2SE error bars) obtained from 48 survey areas in Hedmark county, SE Norway.

Fig 3 a, b, c and d. Temporal patterns of willow ptarmigan (WP) breeding success, population growth ($r = \ln(\lambda)$), rodent abundance and red fox abundance indices obtained from 48 survey areas in Hedmark county, SE Norway. Each column contains the extreme of the lower whisker, the lower quartile, the median (black line), the upper quartile and the extreme of the upper whisker for each year. Breeding success was expressed as the proportion grouse chicks, i.e. the number of chicks divided by the total number of bird observations. Rodent abundance indices were calculated for each survey area by dividing the number of ptarmigan transect lines where rodents had been observed with the total number of surveyed transect lines (i.e. max=1.0 and min = 0.0). We used the inverse-distance weighting (IDW) method for spatial interpolation of red fox tracks based on data from 621 snow tracking transect lines that were distributed throughout the county (see Fig 1). Outliers are exluded from the box plot.

Fig 4 A and B. Predicted values from a model of growth rate (r), and breeding success of willow ptarmigan expressed as the proportion of juveniles among observed birds in August transect counts (see Table 2). Explanatory variables were indices of red fox (tracks per km transect lines/days since last snowfall) and rodent abundance. The lines depict predicted growth rates and breeding success given rodent indices (ROD_{ind}) from 0-1, and red fox indices from 0-1.6.

Figure 1

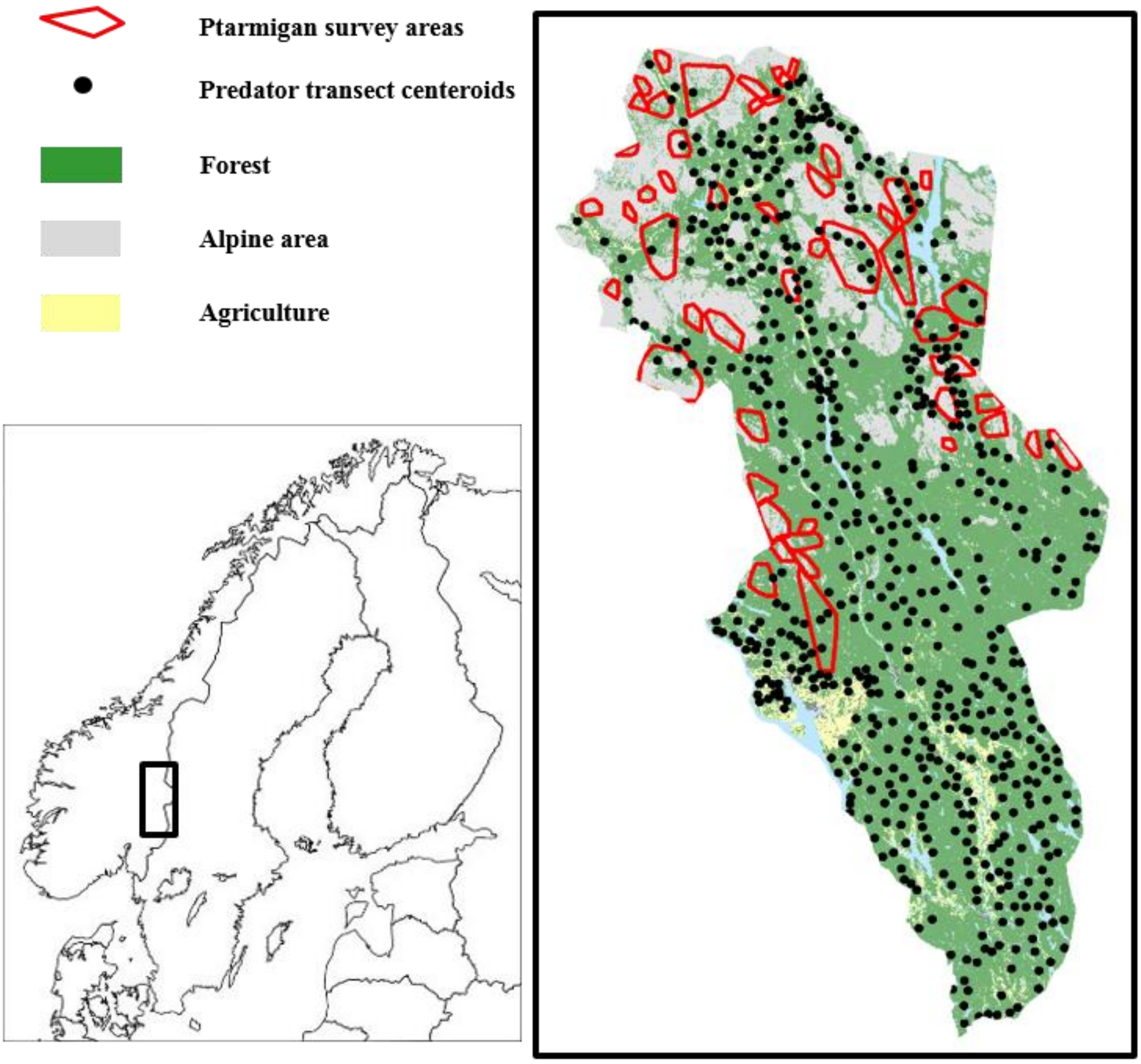


Figure 2

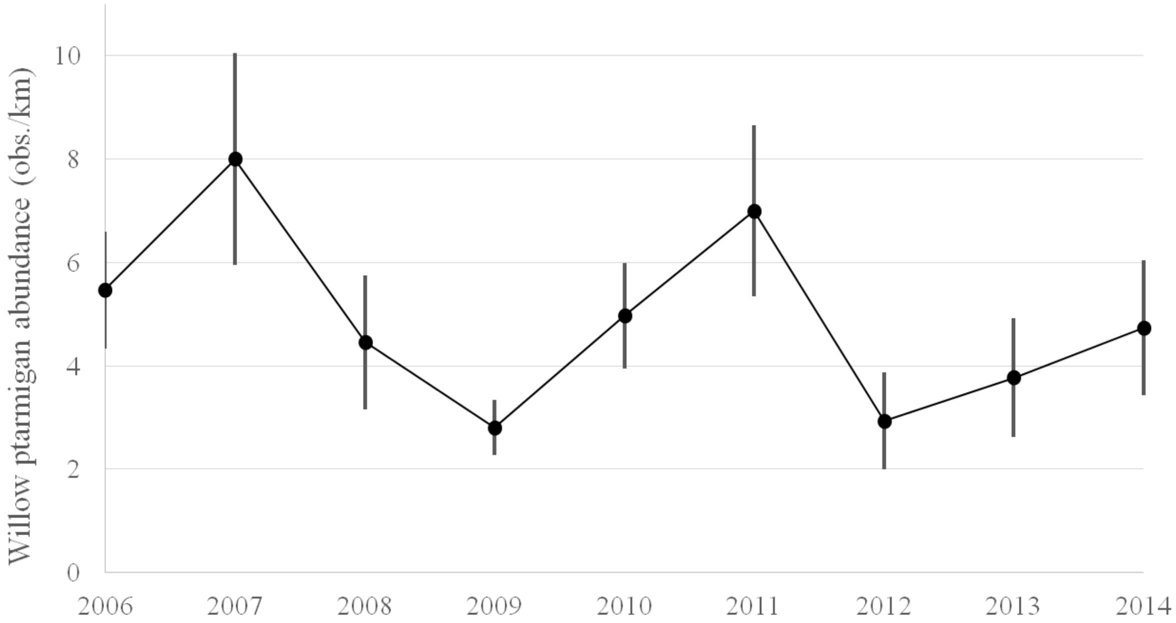

Willow ptarmigan abundance (obs./km)
0
2
4
6
8
10
2006
2007
2008
2009
2010
2011
2012
2013
2014

Figure 3

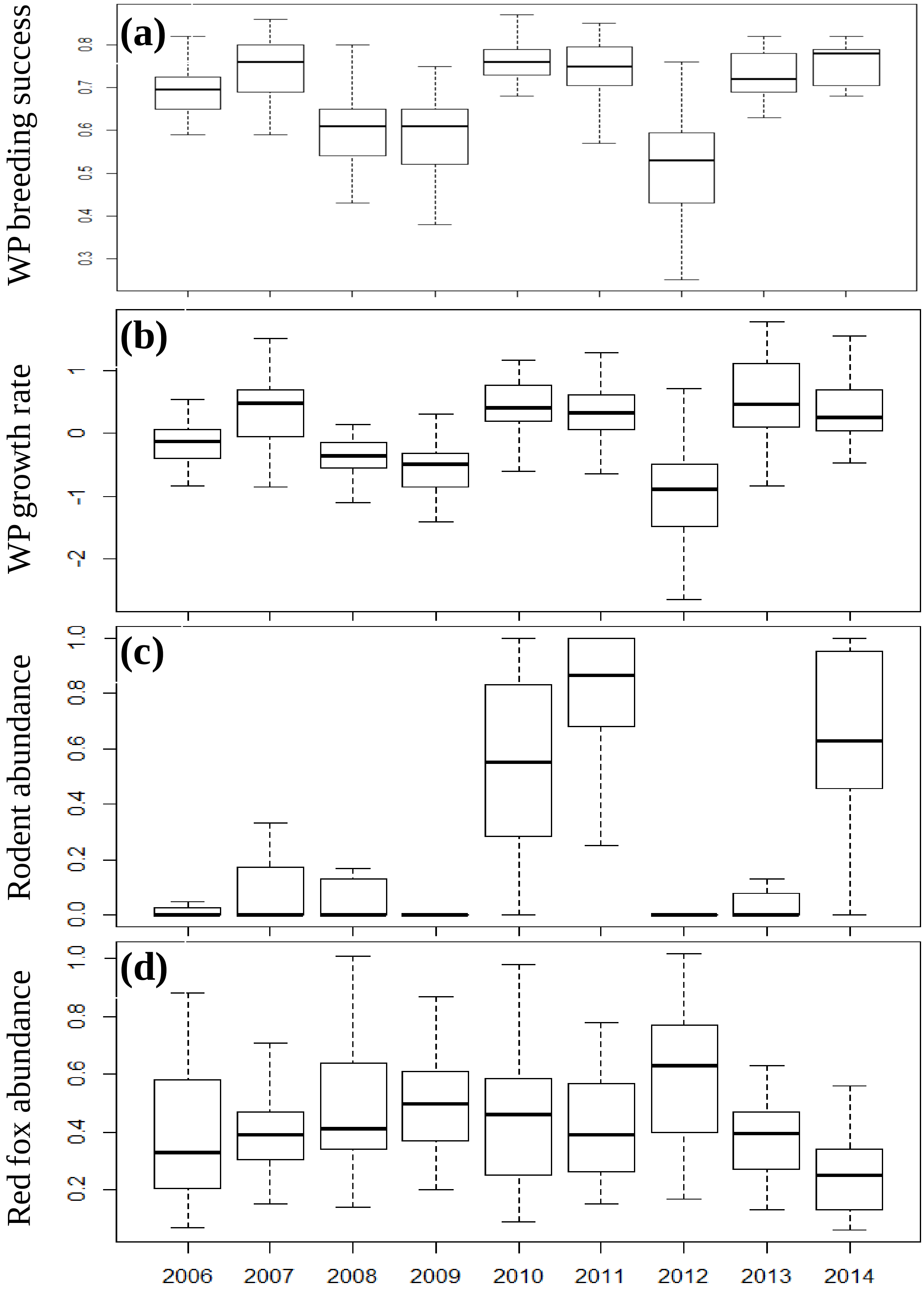
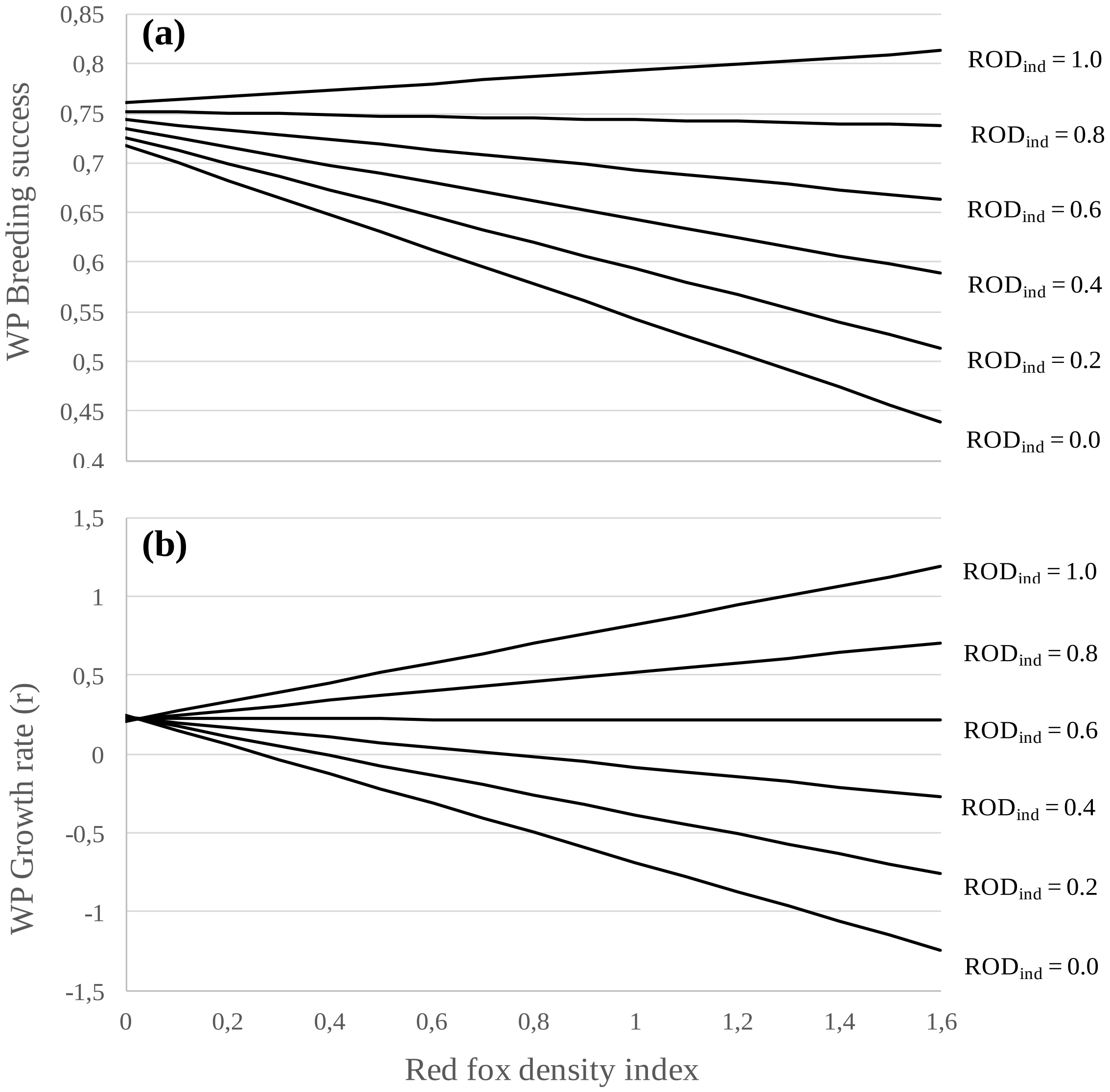

(a)
WP breeding success
0.3
0.4
0.5
0.6
0.7
0.8
(b)
WP growth rate
-2
-1
0
1
(c)
Rodent abundance
0.0
0.2
0.4
0.6
0.8
1.0
(d)
Red fox abundance
0.2
0.4
0.6
0.8
1.0
2006
2007
2008
2009
2010
2011
2012
2013
2014

Figure 4


(a)
WP Breeding success
0,85
0,8
0,75
0,7
0,65
0,6
0,55
0,5
0,45
0,4
ROD_{ind} = 1.0
ROD_{ind} = 0.8
ROD_{ind} = 0.6
ROD_{ind} = 0.4
ROD_{ind} = 0.2
ROD_{ind} = 0.0
(b)
WP Growth rate (r)
1,5
1
0,5
0
-0,5
-1
-1,5
ROD_{ind} = 1.0
ROD_{ind} = 0.8
ROD_{ind} = 0.6
ROD_{ind} = 0.4
ROD_{ind} = 0.2
ROD_{ind} = 0.0
0
0,2
0,4
0,6
0,8
1
1,2
1,4
1,6
Red fox density index