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Master's thesis in Natural Resource Management

Supervisor: Thor Harald Ringsby / Erlend Nilsen / Lasse Frost Eriksen

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Abstract

The evolutionary mechanisms and environmental factors that underlie variation in movement behaviors have remained a major challenge in population ecology. This constitutes substantial issues for wildlife managers, as the models that are currently relied upon for making sustainable harvest decisions oftentimes require state-dependent movement as a parameter. Movement is seldomly used in models, an omission which may lead to inaccurate population growth projections and consequently, advise plans of over- or underharvest. As the world faces increased biodiversity loss, unsustainable management of exploited populations can drive populations towards extinctions which may have severe consequences for ecosystems, species, and the human communities that rely on them. This study first investigated the state-specific movements of a population of willow ptarmigan (*Lagopus lagopus*) in central Norway were investigated. It was found that females moved farther distances than males in terms of seasonal movements between summer and winter season ranges. However, during spring migration no difference was found between adults and juveniles. Sex did not explain variation in breeding dispersal and both male and female adults were found to disperse short distances. Conspecific attraction in juvenile breeding site selection was also investigated, but no evidence for this behavior was found. Nevertheless, further investigation might find conspecific attraction at a finer scale. Second, a harvest model incorporating state-dependent movement patterns was constructed to explore movements effect on population growth rate (λ) estimates. Movement had a substantial effect on population growth rate, with a gradating dependency on local management area size, neighboring harvest rates, and temporal harvest strategy. In general, the larger the local management area, the less negative impact on population growth rate was seen as a consequence of neighboring regime. When local harvest rates were equal to the neighboring rate, local management area size had no effect on population growth rate. In this scenario projected growth reflected the estimations of a non-spatial population model. This study shows that when designing management plans based on growth rates projected from harvest models, movement patterns and neighboring regimes are essential factors that should be taken into account. Accordingly, strategies must be planned on a regional level to ensure persistent, sustainable local population dynamics.

Table of Contents

1	Introduction	1
2	Methods.....	4
2.1	<i>Study species</i>	<i>4</i>
2.2	<i>Study area</i>	<i>5</i>
2.3	<i>Hypotheses</i>	<i>6</i>
2.4	<i>Data collection</i>	<i>8</i>
2.4.1	Longitudinal study based on marked willow ptarmigans	8
2.4.2	Local willow ptarmigan population density estimation	9
2.5	<i>Statistical analyses on individual variation in movement</i>	<i>9</i>
2.5.1	Seasonal movement	9
2.5.2	Breeding dispersal	10
2.5.3	Juvenile spring movement.....	11
2.5.4	Conspecific attraction.....	11
2.6	<i>Harvest models.....</i>	<i>12</i>
3	Results	16
3.1	<i>Empirical movement analysis: State comparison in distance / Movement in Lierne management cells</i>	<i>16</i>
3.1.1	Seasonal movement	16
3.1.2	Breeding dispersal	16
3.1.3	Juvenile spring movement.....	17
3.1.4	Conspecific attraction.....	17
3.2	<i>Harvest models: Sustainable hunting quotas for different sized management areas.....</i>	<i>20</i>
4	Discussion	22
4.1	<i>Movement.....</i>	<i>22</i>
4.2	<i>Management implications</i>	<i>24</i>
5	Acknowledgements	27
6	References	28
7	Appendices.....	35
7.1	<i>Appendix A</i>	<i>35</i>
7.2	<i>Appendix B</i>	<i>36</i>
7.3	<i>Appendix C.....</i>	<i>36</i>

1 Introduction

Currently, there is an ongoing massive decline in global biodiversity, according to the latest Global Assessment Report on Biodiversity and Ecosystem Services (IPBES 2019). Among the most substantial drivers of biodiversity loss, the direct exploitation of organisms, including unsustainable hunting, has been ranked second (BirdLife International 2018, IPBES 2019). Hunting wild species for sport and the provision of revenue and protein serve as a core livelihood for many and carry deep rooted cultural and traditional purposes in many parts of the world. Despite this considerable value, hunting wild species isn't without penalty; studies across taxa have found that when conducted unsustainably, hunting can lead to population declines and in turn the collapse of human communities and industries that rely on them (Thiollay 1984, 2005, Kano and Asato 1994, Bennett et al. 1997, Myers et al. 1997, Peres 1997, Gien 2000, Hamilton and Butler 2001, Keane et al. 2005, Packer et al. 2011, Pöysä et al. 2013, BirdLife International 2018). Coupled with an insufficient management regime, these situations can even lead to extinctions, such as in the infamous cases of the passenger pigeon (*Ectopistes migratorius*) and great auk (*Pinguinus impennis*) (Gaskall 2000, Lagrot et al. 2008, Baisre 2013, Hung et al. 2014). However, alongside the aforementioned management failures there are a number of species threatened by overharvest that have rebounded as a result of well-informed policy backed by sustainable strategies (Keiter 1997, Heffelfinger et al. 2013, Krausman and Cain 2013, Rose and Rowe 2015). This has underscored the need for reliable tools in harvest management to curb the planet's loss of biodiversity.

Quantitative matrix population models are among the essential instruments that have repeatedly been used to establish sustainable management systems (Salo et al. 2013). Matrix population models are temporal-based analyses designed to separate a population into distinct stages (i.e. spatial, state) and illustrate the dynamic progression of the population through these phases (Deriso et al. 1991, Caswell 2001, Klanjscek et al. 2006, Salo et al. 2013). When building matrix models, vital rates determine the populations transition through the stages (Caswell 2001). An analysis of these transitions over time provides population growth rate (λ) projections, which act as a powerful diagnostic for issues such as threatened species persistence and invasive species spread (Crouse et al. 1987, Bullock et al. 2008, Ezard et al. 2010, Morris et al. 2011). Elasticity and sensitivity analyses are performed to determine the relative importance of the vital rates included in the transition matrix (Crouse et al. 1987, Benton and Grant 1999, Caswell 2001, Stevens 2010, Morris et al. 2011). In addition to the inclusion of empirical estimates of vital rates, such models may also account for harvest. This

has been successfully implemented in many studies assessing the influence of hunting on the growth rates and demographic structure of wildlife species (Bunnell and Tait 1980, Cooke et al. 2000, Brooks and Lebreton 2001, Nilsen et al. 2005, Novaro et al. 2005, Stoner et al. 2006, Besnard et al. 2010, Wielgus et al. 2013). Despite their success as an applicable tool in harvest design, matrix models are not a panacea. Stunted by limitations such as an inability to account for changing vital rates in unpredictably transient environments, matrix models are only meant to guide harvest management rather than make exact predictions (Bunnell 1989, Van Mantgem and Stephenson 2005). Accordingly, a balance must be struck between simple and complex models so that enough detail is included to represent the system for management goal applicability and provide insight into system dynamics, all without attempting to mirror reality where understanding is lost due poorly understood interactions (Bunnell 1973, 1974, 1989, Bunnell and Tait 1980). Nonetheless, it has been argued that the inclusion of details on spatial and temporal distribution of harvest is essential when designing matrices for the management of hunted species (Ling and Milner-Gulland 2008). Therefore, demographic movement patterns are relevant parameters to analyze when building accurate models for directing harvest strategy.

Relatively few harvest models used hitherto have explicitly considered movement, thus making the implicit assumption that the managers are dealing with a closed population (Ling and Milner-Gulland 2008, Gervasi et al. 2015). For instance, a review by Novaro et al. (2000) highlighted that a number of studies in the tropics do not consider space in sustainable hunting research but rather compare population production or growth to harvest rates to determine sustainability (Robinson and Redford 1991, Alvard et al. 1997, Slade et al. 1998). Nevertheless, it is already well known that movement patterns (e.g. seasonal movement, migration, and natal dispersal) have major implications on species distribution and population dynamics, especially considering that variation in individual state will influence movement behavior (Madsen and Fox 1995, Clobert et al. 2012, Olsen et al. 2012). State-specific movement is of particular interest because it exposes different subgroups of individuals to factors (e.g. predation, harvest, and environmental conditions) that vary across a spatiotemporal landscape (Bjørnstad et al. 1999, Kendall et al. 2000, Lundberg et al. 2000, Willebrand and Hörnell 2001). Moreover, when movements take individuals beyond the boundaries of a management unit and over a heterogeneous landscape, the dynamics within the units will to some extent be altered. As a result, this will affect the extent and distribution of harvest pressure across a population, potentially undermining strategy intentions with implications for population growth (Pulliam

1988, Novaro et al. 2000, Naranjo and Bodmer 2007, Gervasi et al. 2015). Harvest models that exclude movement as a parameter are vulnerable to inaccurate hunting mortality projections and may misguide policy makers into over- or underharvest (Csányi 1992, Boyce et al. 1999, Jonzén et al. 2001, Willebrand and Hörnell 2001).

As one of Norway's most popular game species, the willow ptarmigan (*Lagopus lagopus*) is harvested throughout much of its range, entrenching the species within the country's culture and traditions (Storch 2007). However, over the last decades Norway's population has displayed an alarming decline, resulting in the species' introduction to the Norwegian Red List for Species (Henriksen and Hilmo 2015). This has prompted an increased emphasis on developing sustainable harvest strategies. Despite the need for well-informed management, aspects of ptarmigan movement biology and its resulting effects on harvest management remain unknown (Breisjøberget et al. 2018). Global research has shown that although the state-specific movement patterns (i.e. seasonal movement and breeding dispersal) of grouse species follow general trends in behavior, there is variation between species, populations, and individuals (Bendell and Elliott 1967, Eng and Schladweiler 1972, Brøseth et al. 2005). Dispersal is made up of two distinct seasonal movements: the autumn movement from breeding to wintering grounds and vice versa in the spring movement (Moss et al. 2006). These movements may influence spatiotemporally explicit population dynamics with the potential to redistribute populations across borders, consequently distorting management strategy predictions and consequence. Accordingly, further investigations into willow ptarmigan migration and dispersal patterns are important if movement is to be quantified and included in harvest models that explore sustainable harvest design.

In this study I investigated two questions:

1. How does individual state (i.e. sex and age) influence variation in movement and conspecific attraction in willow ptarmigan?
2. To what extent are spatiotemporal harvest strategies for willow ptarmigan influenced by state-specific movement patterns?

To answer these questions, I first used data from ongoing field projects in Lierne, central Norway to test specific hypotheses (see Hypotheses chapter 2.3) regarding explanations for variations in ptarmigan state-specific movement patterns. Second, I estimated key distance-specific movement rates which, along with survival and recruitment rates, were used as parameters in a novel two-season population matrix model. The model was built to allow for seasonal movements across the boundaries of hypothetical management areas and acted as a

foundation for stochastic simulations designed to investigate population growth rate response to gradating local harvest rates. I explored scenarios comprised of different neighboring harvest rates and local management area sizes. To shed light on the importance of considering movement in sustainable harvest, I compared the resulting trends to trends projected from a model that used the same survival and fecundity rates but excluded movement parameters.

2 Methods

2.1 Study species

The willow ptarmigan is a medium-sized bird species of the subfamily Tetraonidae, commonly known as grouse. This species is widely distributed within Scandinavia, primarily inhabiting mountainous regions (Lehikoinen et al. 2014, Kvasnes et al. 2015). Willow ptarmigans are unique among other tetraonids in that males continue to help with parental care after eggs are laid, which typically occurs at the end of May (Hannon et al. 1998). The monogamous pair will have 1 clutch each year but might renest if eggs are preyed on (Munkebye et al. 2003). By the beginning of summer, 6 – 12 eggs normally hatch with a highly variable breeding success which, by some long-term studies, has been estimated to between 0.5 – 6 nestlings per pair (Marcstrom et al. 1988, Myrberget 1988, Munkebye et al. 2003, Steen and Haugvold 2009). This variability in breeding success is due in most part to high predation rates of eggs and chicks by mammals, corvids, and raptors (Munkebye et al. 2003, Sandercock et al. 2011, Breisjøberget et al. 2018, Israelsen et al. 2020). Comparably, survival rates in a central Norwegian population averaged 0.43 after the first year of life (Israelsen et al. 2020). Predation by raptors, particularly Gyrfalcon (*Falco rusticolus*) and Northern goshawk (*Accipiter gentilis*), is the most frequent cause of natural death year-round (Smith and Willebrand 1999, Brøseth and Pedersen 2010, Breisjøberget et al. 2018). Accordingly, the willow ptarmigan's life cycle is characterized by short generation time, high adult mortality rates, and large reproductive potential.

Previous empirical studies on ptarmigans primarily show that movement patterns are state-dependent and vary between populations and individuals (Hannon et al. 1998, Rorvik et al. 1998, Brøseth et al. 2005, Hörnell-Willebrand et al. 2014). In migratory populations, generally males display short seasonal movements while females migrate longer distances between summer and winter territories (Gruys 1993, Hörnell-Willebrand et al. 2014). However, some studies however have found populations to be non-migratory and the difference between distance moved to vary between years (Bergerud 1970, Mossop 1988,

Gruys 1993). Both sexes often return to the same breeding grounds from previous years – ergo, a minimal and similar breeding dispersal distance (Schieck and Hannon 1989, Hannon et al. 1998, Brøseth et al. 2005, Hörnell-Willebrand et al. 2014). Juvenile dispersal in the spring settlement period has been hypothesized by Kvasnes et al. (2015) to be influenced by an attraction to areas with a high abundance of conspecifics, as this may indicate superior habitat quality resulting in high survival rates.

2.2 Study area

The data for this study was collected across the Lierne municipality in Eastern Central Norway – primarily, in the administrative management areas of Lifjellet (64°25′–64°30′N, 13°11′–13°24′E and Guslia (64°15′–64°18′N, 13°25′–13°37′E) (Fig. 1). These areas are state-owned common land and are open to the public for hunting willow ptarmigan. The landscape is characterized by a diverse subalpine landscape of mountains, valleys, lakes, forests, open mires, and tundra ranging from elevations of 459 – 757 m above sea level spanning from subalpine to alpine bioclimatic zones (Moen 1998). The area covers 1350 km² in total, whereas suitable willow ptarmigan area is calculated to 980 km² (Eriksen et al. 2017). The patches of forest community in the subalpine zone are dominated by spruce (*Picea abies* L.), Scots pine (*Pinus sylvestris*), and scatterings of mountain birch (*Betula pubescens* spp. *czerepanovii*). The shrubbery, interspersed amongst these patches, consists of dwarf birch (*Betula nana* L.) and willows (*Salix* spp.). In the lowest elevations, grasses and sedges blanket the mires and ericaceous plants (Ericaceae spp.) cover the forest floors. Higher altitude vegetation comprises of heath, sedges, and lichens. The climate of the last climatological normal period (1961 – 1990) in the area saw, on average, annual temperatures of 0 °C and annual precipitations of 920 mm. In most years, the ground is snow-covered between late October and May.

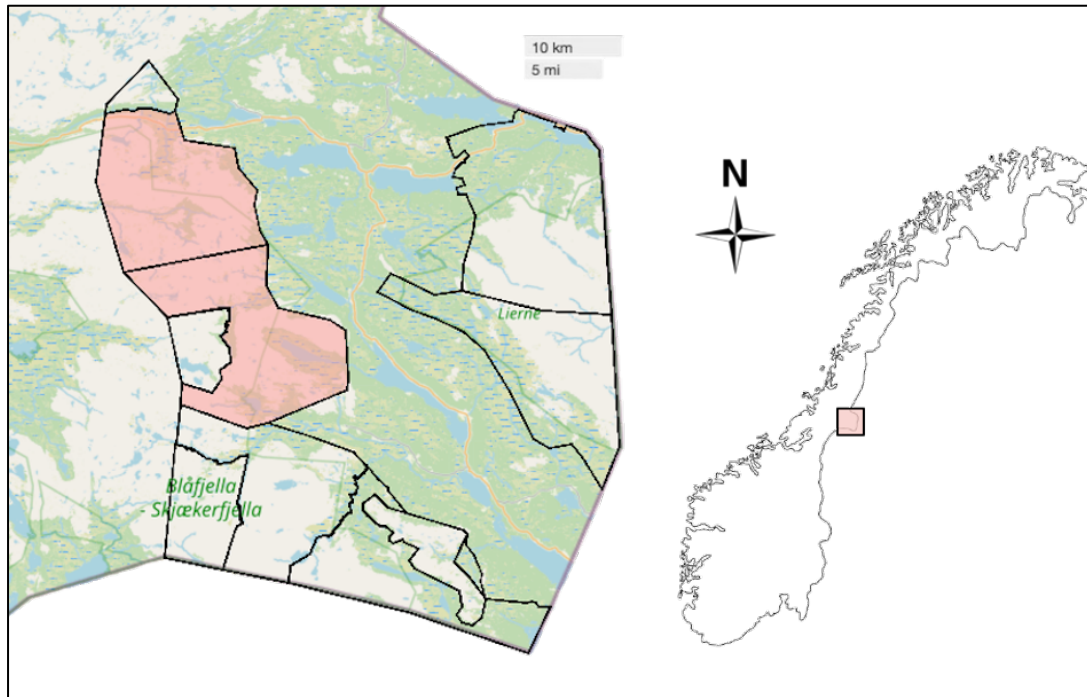


Fig. 1. Map of the Lierne municipality in eastern central Norway with management cells outlined in black. The Lifjellet and Guslia study areas are highlighted in red as is the location of Lierne on the map of larger Norway.

2.3 Hypotheses

In order to address whether individual state, such as sex and age, influenced the variation in movement and conspecific attraction of willow ptarmigan in the study area (referring to question 1 in the introduction) I predicted to find the following in regard to the three types of behavior that were investigated in this study:

Hypothesis H1: Based on empirical knowledge and life-history and movement theory, movement behavior will likely differ among the individual states of sex and age (Hannon et al. 1998, Brøseth et al. 2005, Lebigre et al. 2008, Hörnell-Willebrand et al. 2014, Kvasnes et al. 2015).

Prediction P1.1: Seasonal movement: Adult females will move farther distances than adult males during seasonal movements between wintering and breeding grounds (Gruys 1993). Accordingly, more adult females than males will move outside their respective management area during these transition periods.

Prediction P1.2: Adult breeding dispersal: Both male and female adults will re-use breeding sites from the previous year resulting in no

difference between sexes in breeding dispersal distance (Hannon et al. 1998, Brøseth et al. 2005). Consequently, individuals from neither sex will be found occupying a management area different from the preceding breeding season.

Prediction P1.3: Juvenile spring movement: Juveniles will move farther distances than adults during spring when transitioning from wintering to breeding territories (Badyaev et al. 1996, Marjakangas and Kiviniemi 2005).

Hypothesis H2: An area with a higher density of adults may demonstrate high survival rates or promising reproductive opportunities, thereby influencing breeding settlement preference for first year reproducers (Schieck and Hannon 1989, Kvasnes et al. 2015).

Prediction P2.1: Conspecific attraction: Juveniles will move into areas with higher conspecific abundance when establishing their first breeding territory (Kvasnes et al. 2015).

To test the extent to which spatiotemporal harvest strategies for willow ptarmigan are influenced by state-specific movement patterns (referring to question 2 in the introduction) the following hypothesis was put forward:

Hypothesis H3: State-specific movement of a local population across a heterogenous landscape of neighboring and local harvest regimes will influence population growth rates (Boyce et al. 1999, Hörnell-Willebrand et al. 2014).

Prediction P3.1: Harvest model: The annual growth rate of the local population will be influenced by the local area's management zone size and harvest rate and neighboring harvest rates.

The hypotheses were preregistered in the Open Science Framework (OSF) with the Center for Open Science (COS) and have remained the same but have been reworded from their original phrasing for clarity (Eichholz et al. 2019). Refer to Appendix A for the original descriptions.

2.4 Data collection

2.4.1 Longitudinal study based on marked willow ptarmigans

Willow ptarmigan were captured during winter in the two study areas of the Lifjellet and Guslia between 2015 and 2020 in Lierne municipality, central Norway, by the Norwegian Institute for Nature Research (NINA) in collaboration with Nord University and local area managers. Each winter approximately 35 – 45 new birds were captured; over the course of the study period 188 birds, including five cohorts, had been marked. The capture method has been to search the study area during winter nights, in February and March. Ptarmigans were detected and captured at random. They were detected from astride snowmobiles using spotlights, which would temporarily stun the birds that looked into the bright light. This would allow the capturers to trap them using long-handled dip nets (Brøseth and Pedersen 2010, Sandercock et al. 2011). Once in-hand, the birds were sexed and aged as either juveniles (<1 year) or adults (>1 year) depending on the researcher's assessment of plumage coloration, weight, size, and pigmentation patterns of the outer primaries (Stavnås 2018). In addition, sex assignment for most birds was confirmed by DNA-analysis using sex-specific microsatellites. The birds were fitted with either a Holohil R1-2B or RI-2D VHF-collar radio transmitter and an identification leg ring. The radio-transmitters were expected to run for 24 months and each weighed 15 grams and have been shown to have little to no influence on tetraonid survival and reproduction rates (Cotter and Gratto 1995, Thirgood et al. 1995). After capture, the birds were monitored using VHF telemetry triangulation, normally at least once each month (with the exception of December and January due to weather and daylight limitations) since February 2015 by NINA biologists and trained land managers and rangers. The transmitter would send a mortality signal after 12 hours of inactivity, at which point researchers would locate the ptarmigan and diagnose the cause of death. Birds were monitored until mortality occurred, or until they were censored (e.g. due to collar failure). The combined set of data collected from the live captures, radio telemetry, and camera traps was used to detail individual variation in ptarmigan life history, phenology, movement, birth and mortality rates, and reproductive success (Smith and Willebrand 1999, Sandercock et al. 2011). Summer season was defined as May 25th to September 25th, and winter season as January 15th to April 15th. Refer to Fig. 2 for willow ptarmigan phenology and seasons.

2.4.2 Local willow ptarmigan population density estimation

Each August, trained personnel from the national monitoring program Hønsfuglportalen surveyed line transects placed across state-owned common land in Lierne municipality to collect data used to estimate local population densities. During the field season, teams of two walked along a predetermined transect while a trained pointing dog searched both sides of the line. When a ptarmigan was flushed by the dog and observed by the volunteer, the species, age, sex, and perpendicular distance from the transect line was noted. The volunteers then took coordinates of the flush site with a GPS and recorded the time of day (Nilsen et al. 2020). Using this suite of information, distance sampling models (Buckland et al. 2001) that incorporate the likelihood of detection and observed distance were produced using the R-package “Distance” (Miller et al. 2019) to estimate ptarmigan density. This study used the results of these models based on distance sampling data collected between 2015 and 2019. In the analysis, I stratified by area and year to obtain annual estimates of density for each management unit. I used a half-normal detection function as a basis for the detection model, being a common approach in distance sampling studies (Buckland et al. 2001).

2.5 Statistical analyses on individual variation in movement

The program R version 3.5.1 was used in all statistical analyses (R Core Team 2018). The package “lme4” was used for generalized linear mixed effect model (GLMM) analyses (Bates et al. 2015); “sm” for constructing density plots (Bowman and Azzalini 2014); “ggplot2” for plots (Wickham 2016); and “optiRum” to back transform predictions to their natural scale (Locke 2018). See Appendix B for a map displaying the locations of summer and winter season observations used in the analysis.

2.5.1 Seasonal movement

In order to determine the extent to which adults performed seasonal migration, I first analyzed whether adults moved into new management areas (intercell movement = 1) or remained within the bounds of the subsequent season’s management area (intercell movement = 0) (relating to P1.1). Thus, among 95 observations of a subsample of adults (N = 91) that performed spring migration, a GLMM (binomial family) was composed where intercell movement (0/1) was included as response variable, while an intercept and individual identity as random effect were included as explanatory variables. To test whether adult seasonal movement across management boundaries differed among sexes (P1.1), a GLMM analysis (binomial family) was

built using the same observations and individuals with intercell movement (0/1) as a response variable, sex as an explanatory variable, and individual identity as a random effect.

In order to address whether willow ptarmigan movement distance among adults differed between sexes (addressed in P1.1) a GLMM analysis (gamma family) was conducted using the same subsample of individuals. Rather than fitting a normal linear model to the logs of the data, the gamma family was a more appropriate and effective choice due to the nonsymmetrical and skewed nature of the data (Fu and Moncher 2004). Distance was included as a response variable, sex as a fixed explanatory variable, and individual identity as a random effect. Distance was defined as the distance (km) between an individual's recorded latitude and longitude coordinates during the summer season and their recorded coordinates during the winter season. If an individual was observed multiple times within a single season, then the coordinates used were that of the observation that was most centralized, meaning that it had the shortest cumulative sum distance to all other observations of that individual within the season. To estimate the gamma distribution of seasonal movement distances of males and females and to further illustrate differences in the sexes a kernel model (gamma family) was built using the same variables.

To illustrate the distances moved and the differences between the sexes, the proportions of birds moving farther than 1, 5, and 10 kilometers by sex were estimated from the raw data. In order to test the statistical significance, generalized linear models (GLMs) (binomial family) were used where movement beyond the respective distance was included as a binomial response variable (beyond = 1, within = 0), in addition to sex as a fixed explanatory variable, and individual identity as a random variable (N = 87).

2.5.2 Breeding dispersal

To determine the extent to which willow ptarmigan adults either returned to or remained in the management area during subsequent breeding seasons (intercell dispersal = 0) or established breeding territories in another management area (intercell dispersal = 1) (P1.2), a GLMM model (binomial family) was composed. 33 observations from 29 adults were used. Intercell dispersal (0/1) was included as a response variable, and individual identity as a random variable. To determine whether adult breeding dispersal across management boundaries differed among sexes (P1.2), a GLMM analysis (binomial family) was constructed using the same subset of individuals with intercell dispersal (0/1) as a response variable, sex as an explanatory variable, and individual identity as a random effect. A kernel model (gamma

family) was built using the same variables to again estimate the gamma distribution of breeding dispersal distances of males and females and to highlight differences in the sexes.

To analyze the difference in breeding dispersal between the sexes (P1.2), a GLMM (gamma family) was used where distance (km) was included as the response variable, sex the explanatory variable, and individual identity the random variable (N = 29). The proportions of adults that dispersed farther than the benchmarks of 1, 5, and 10 kilometers were assessed with GLMs (binomial family), using dispersal beyond the respective distance as the response variable (beyond = 1, within = 0), sex the explanatory variable, and individual identification as a random variable (N = 25). The same model was used to test for a significant difference between the sexes in the proportions of adults dispersing beyond each distance benchmark by back transforming the resulting intercepts for both sexes.

2.5.3 Juvenile spring movement

A GLM (gamma family) with movement distance (km) as the response variable and age as the explanatory variable was conducted to test if juveniles moved farther distances than adults post-winter (P1.3). A total of 159 observations of 149 individuals were used in the analysis. To better display the distribution and compare spring movement distances between the two age classes, a kernel model (gamma family) was used with distance (km) as the response variable and age as the explanatory variable.

The proportions of adults and juveniles moving beyond the 1, 5, and 10 km distances were estimated using GLM models (binomial family), where distance moved beyond the respective benchmark was used as a binomial response variable (1/0), age class as the explanatory variable, and individual identification as the random variable.

2.5.4 Conspecific attraction

To test if juveniles would move into management areas with higher conspecific abundance during the spring movement (H2), a GLM (binomial family) was used with conspecific attraction as a response variable. The binomial variable, conspecific attraction, identified if a juvenile has moved into a Lierne management area with higher breeding density than the density of the management area occupied by the same individual during the subsequent winter season (1) or not (0). A GLM (binomial family) was constructed to determine if there was a significant deviance between sexes in individuals displaying conspecific attraction by using conspecific attraction as a response variable and sex as an explanatory variable.

2.6 Harvest models

In order to understand the effects of the movement patterns analyzed above on ptarmigan response to harvest, I integrated these findings, along with other previously analyzed data and stochasticity, into predictive models that simulated different management strategies and circumstances. Of the several families of harvest model framework, the proportional model type was used in this study because the static nature of the strategy best illustrated how long-term growth was influenced by different movement behaviors (Lande et al. 1995). Each situation that was analyzed comprised of one of six local management area sizes and one of three neighboring hunting regimes. The six local management zone sizes in the model had a radius of 1, 2, 3, 5, 7, and 9 kilometers (areas of 3.1, 12.6, 28.3, 78.5, 153.9, and 254.5 km² respectively). The four neighboring harvest rates that were used to contrast the local management zone were 0, equal to the harvest rates within the local management zone, 0.14, and 0.20. These 24 different management situations were each subjected to 20 different local harvest quotas ranging between 0 – 0.25.

The simulation (Equation 1), was initiated with a local population vector separated into age and sex demographics (juvenile female, adult female, juvenile male, adult male) (Equation 1. Stage 1). This vector was representative of the local population at the end of summer season prior to harvest and ready to begin the seasonal movement to winter grounds from breeding sites. The population was then split into two by multiplying each demographic in the vector by its respective seasonal movement rate (Equation 1. Stage 2a, b). That migration rate was the proportion of the demographic that, during a seasonal movement, would move farther than the radius of the management zone in the particular test (Equation 1. Stage 2a). This resulted in a demographic vector of migrants (Equation 1. Stage 3a). The resident rates, which were representative of the proportion of each demographic that did not move beyond the distance of the management cell radius ($1 - \text{migration rates}$), were also multiplied by the summer population vector which resulted in a vector of residents (Equation 1. Stage 3b). The two vectors were then put through either the resident or migrant autumn transition matrix (Equation 1. Stage 4a, b). These matrices were made of survival rates. A study by Israelsen et al. (2020) shows that although demographic's survival rates of willow ptarmigan in central Norway vary from year to year, those rates are largely similar over long-term periods and lack any substantial difference between sexes. Accordingly, each demographic had the same survival rate of 0.62 ± 0.04 (Israelsen et al. 2020). The harvest rate used in the resident matrix was one of the 20 harvest levels between 0 and 0.25 and the harvest rates for migrants were one of the four

neighboring harvest levels: 0, equal to the local management area, 0.14, and 0.20. Each transition resulted in a new set of vectors representative of the philopatric and dispersing subpopulations that survived to the end of autumn (Equation 1. Stage 5a, b). These new population vectors went through another set of transition matrices (Equation 1. Stage 6a, b). These matrices, similar to the autumn transitions, included winter survival from natural mortality ($.73 \pm 0.03$) and local or neighboring harvest rates (Israelsen et al. 2020). The winter matrices also included stochastic breeding rates to introduce new recruits into the system. The results of these transitions (Equation 1. Stage 7a, b) were added together to simulate the seasonal movement of ptarmigans to breeding grounds within the local management area. This combination was a vector containing the total size of each demographic within the local area prior to the subsequent year's hunting season (Equation 1. Stage 8).

Altogether, the winter and autumn transitions were equivalent to one year. The model ran this cycle 20 times and during each timestep the total population size was recorded. Population sizes from time steps six through 20 were used to calculate the population growth rate under that simulation's particular set of circumstances (management zone size and neighboring harvest strategy) and local harvest quota. Timesteps 1 – 5 were excluded because the original demographic sizes would influence the population growth rate if not given space to stabilize into appropriately representative numbers. The simulation was also run with all seasonal movement rates equal to 0 to provide a reference population growth rate indicative of non-spatial model estimates.

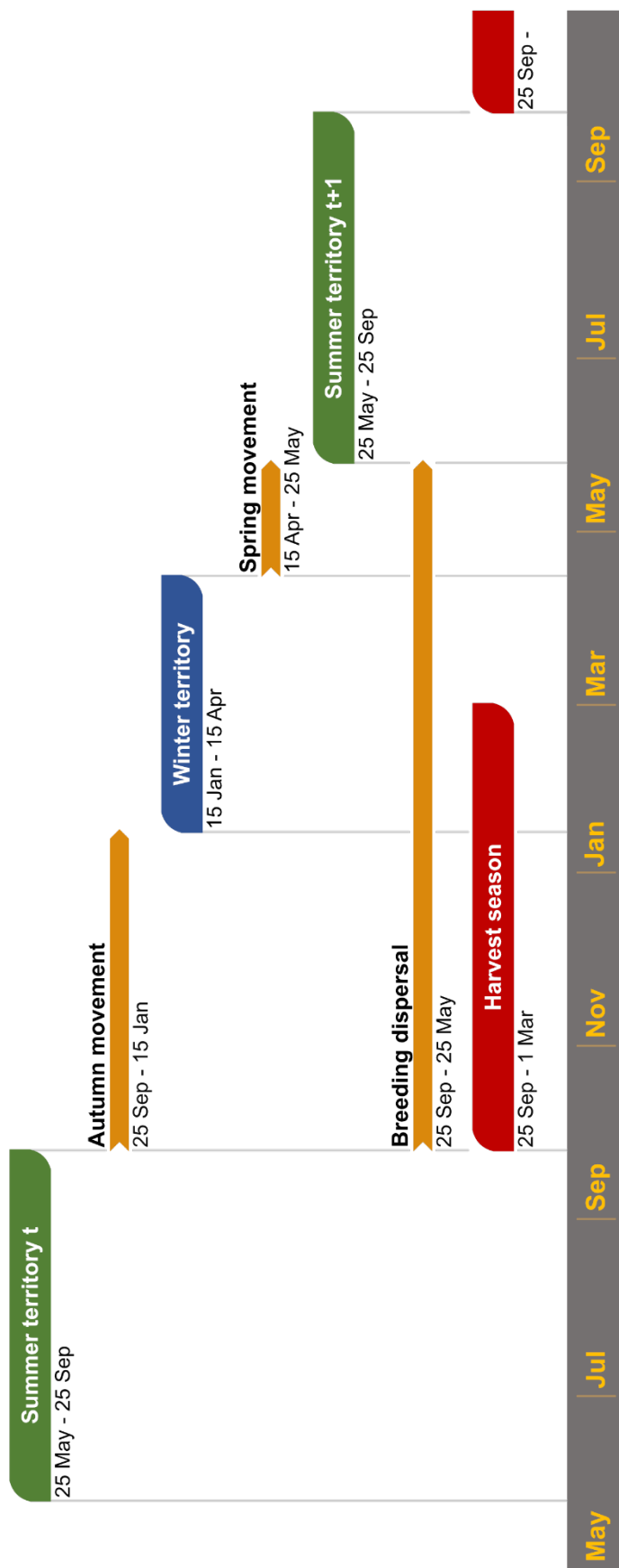
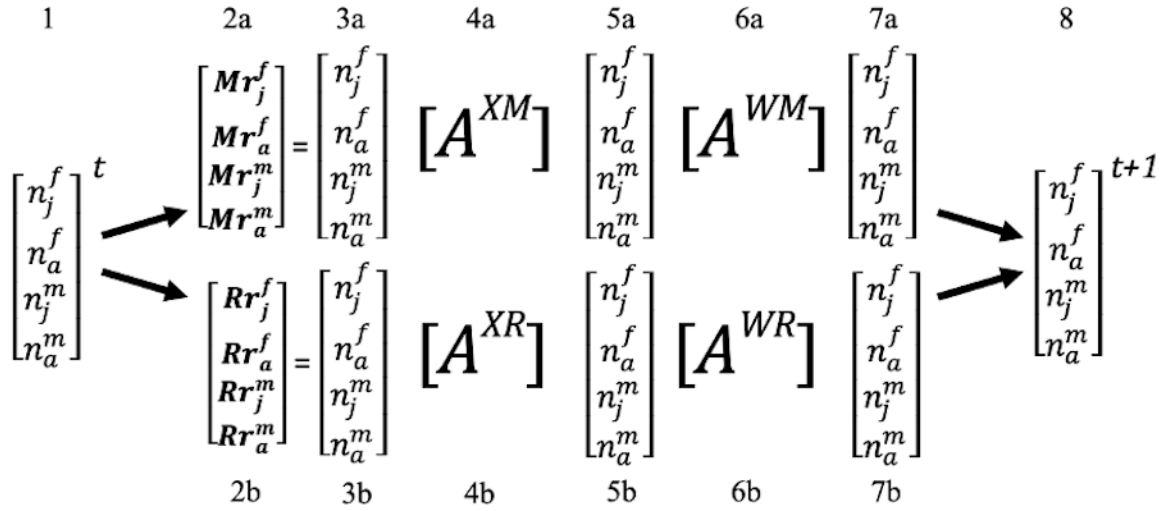


Fig. 2. Timeline of willow ptarmigan phenology and hunting season in Norway.

STAGE



Equation 1. Harvest model. A – Transition matrix, X – Autumn, W – Winter, M – Migrant, R – Resident, n – Population size, f – Female, m – Male, j – Juvenile, a – Adult, r – Seasonal migration rate, S – Survival, F – Breeding rate, h – Harvest rate.

$$\begin{bmatrix} S_j^x(1 - Mh) & 0 & 0 & 0 \\ 0 & S_a^x(1 - Mh) & 0 & 0 \\ 0 & 0 & S_j^x(1 - Mh) & 0 \\ 0 & 0 & 0 & S_a^x(1 - Mh) \end{bmatrix}$$

Equation 1. Stage 4a. $[A^{XM}]$ Autumn transition matrix for migrants.

$$\begin{bmatrix} S_j^x(1 - Rh) & 0 & 0 & 0 \\ 0 & S_a^x(1 - Rh) & 0 & 0 \\ 0 & 0 & S_j^x(1 - Rh) & 0 \\ 0 & 0 & 0 & S_a^x(1 - Rh) \end{bmatrix}$$

Equation 2. Stage 4b. $[A^{XR}]$ Autumn transition matrix for residents.

$$\begin{bmatrix} S_j^w(1 - Mh)\left(\frac{F}{2}\right) & S_a^w(1 - Mh)\left(\frac{F}{2}\right) & 0 & 0 \\ S_j^w(1 - Mh) & S_a^w(1 - Mh) & 0 & 0 \\ S_j^w(1 - Mh)\left(\frac{F}{2}\right) & S_a^w(1 - Mh)\left(\frac{F}{2}\right) & 0 & 0 \\ 0 & 0 & S_j^w(1 - Mh) & S_a^w(1 - Mh) \end{bmatrix}$$

Equation 3. Stage 6a. $[A^{WM}]$ Winter transition matrix for migrants.

$$\begin{bmatrix} S_j^w(1 - Rh)\left(\frac{F}{2}\right) & S_a^w(1 - Rh)\left(\frac{F}{2}\right) & 0 & 0 \\ S_j^w(1 - Rh) & S_a^w(1 - Rh) & 0 & 0 \\ S_j^w(1 - Rh)\left(\frac{F}{2}\right) & S_a^w(1 - Rh)\left(\frac{F}{2}\right) & 0 & 0 \\ 0 & 0 & S_j^w(1 - Rh) & S_a^w(1 - Rh) \end{bmatrix}$$

Equation 4. Stage 6b. $[A^{XR}]$ Winter transition matrix for residents.

3 Results

3.1 Empirical movement analysis: State comparison in distance / Movement in Lierne management cells

3.1.1 Seasonal movement

In general, females moved farther than males (GLMM Gamma, $\beta = -1.48 \pm 0.37$, $t = -3.95$, $P < 0.001$, Fig. 3a), with a model-predicted movement distance of 4.2 kilometers (95% CI = 2.5 – 7.0 km) for females and 1.0 kilometers (95% CI = 0.6 – 1.7 km) for males. Most males moved less than 1 kilometer while almost all females moved farther than 5 kilometers. Fewer than a tenth of males moved that far, while virtually none moved farther than 10 kilometers. Almost half of all females moved beyond 10 kilometers (Fig. 4a). There was a significant difference in the proportion of females to males that moved beyond these three benchmarks (Table 1a, see Appendix C Table 2 for descriptive statistics).

The proportion of adult willow ptarmigans that crossed the boundaries of Lierne management cells during their seasonal movements was estimated to be 21.1% (SD = 4.0, Fig. 5a). Significantly more willow ptarmigans in Lierne remained within the boundaries of their respective management cell during seasonal movements (GLMM Binomial, $\beta = -11.53 \pm 2.04$, $Z < 0.01$, $P < 0.001$). There was a significant difference between adult males and females in their propensity to leave the management area during seasonal movement (GLMM Binomial, $\beta = -3.54 \pm 1.16$, $Z = -3.048$, $P < 0.01$), and 95% of the birds that left their respective management area were females. Accordingly, these results were consistent with previous studies that found substantial differences in seasonal movement distances between the sexes, as addressed in P1.1.

3.1.2 Breeding dispersal

No significant difference was found between the breeding dispersal distances of adult females and males (GLMM Gamma, $\beta = 0.34 \pm 0.81$, $t = 0.42$, $P > .05$, Fig. 3b). Females moved a model-predicted distance of 0.8 kilometers (95% CI = 0.2 – 2.4 km), and males 0.6 kilometers (95% CI = 0.2 – 1.7 km). In general, about half of females moved beyond 1 kilometer, while slightly less males did (Table 1b, see Appendix C Table 2 for descriptive statistics). Much fewer birds moved farther than 5 kilometers and even less moved more than 10 kilometers (Fig. 4b). There was no substantial difference in the deviance between sexes in the proportions of individuals moving beyond each benchmarked distance supporting P1.2.

Only one individual (3.0%, SD = 1.0) moved to another management area between years (Fig. 5b). Because there were almost no birds that were intercell dispersers, there was accordingly no difference between sexes (GLMM Binomial, $\beta = 191.50 \pm 580.70$, $Z = 0.33$, $P > .05$).

3.1.3 Juvenile spring movement

During spring, the differences in movement distance between the age classes were mostly similar and not statistically significant (GLM Gamma, $\beta = -0.08 \pm 0.22$, $t = -0.35$, $P > 0.05$, Fig. 3c). Adult and juvenile model predicted movement distances were 1.7 kilometers (95% CI = 1.3 – 2.4 km) and 2.5 kilometers (95% CI = 1.8 – 3.4 km) respectively. Most juveniles and adults moved beyond 1 kilometer. About half of the birds that moved farther than 1 kilometer also moved more than 5 kilometers. Slightly less moved more than 10 kilometers (Fig. 4). There were no significant differences between age classes in the proportion of individuals moving beyond each of the specified distances rejecting P1.3 (Table 1c, see Appendix C Table 2 for descriptive statistics).

3.1.4 Conspecific attraction

Significantly fewer than 50% of the juveniles (4.0%, SD = 1.4) moved into a new management area with a higher abundance of conspecifics during the spring movement (GLMM Binomial, $\beta = -14.15 \pm 6.59$, $Z = -2.15$, $P < 0.05$), a result not in accordance with P2.1. Additionally, there was no difference between the sexes (GLM Binomial, $\beta = -18.12 \pm 3546.07$, $Z = -0.005$, $P > 0.05$).

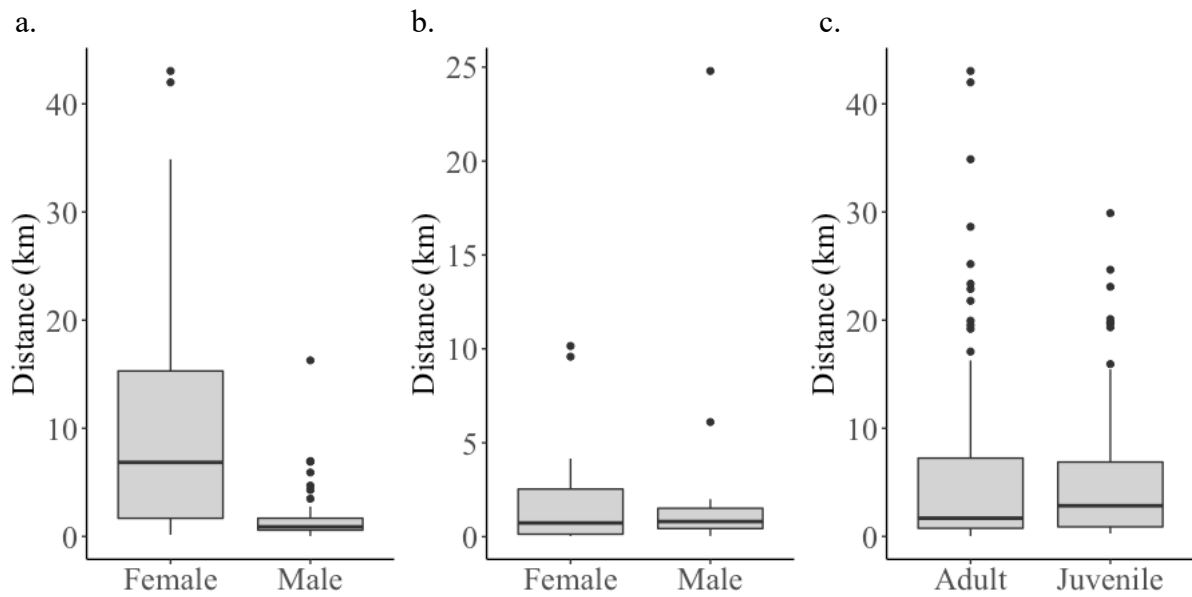


Fig. 3. Distribution of state-specific movement distances regarding (a) seasonal movement (b) breeding dispersal (c) spring movement. Visualized in Tukey's box-and-whisker plots. The horizontal split line = median, 2 hinges = interquartile range (25 – 75% quantiles), vertical whiskers = highest/lowest observations larger/smaller than or equal to the upper/lower hinge $\pm 1.5 \times$ interquartile range. Data points outside the whiskers = outliers plotted individually.

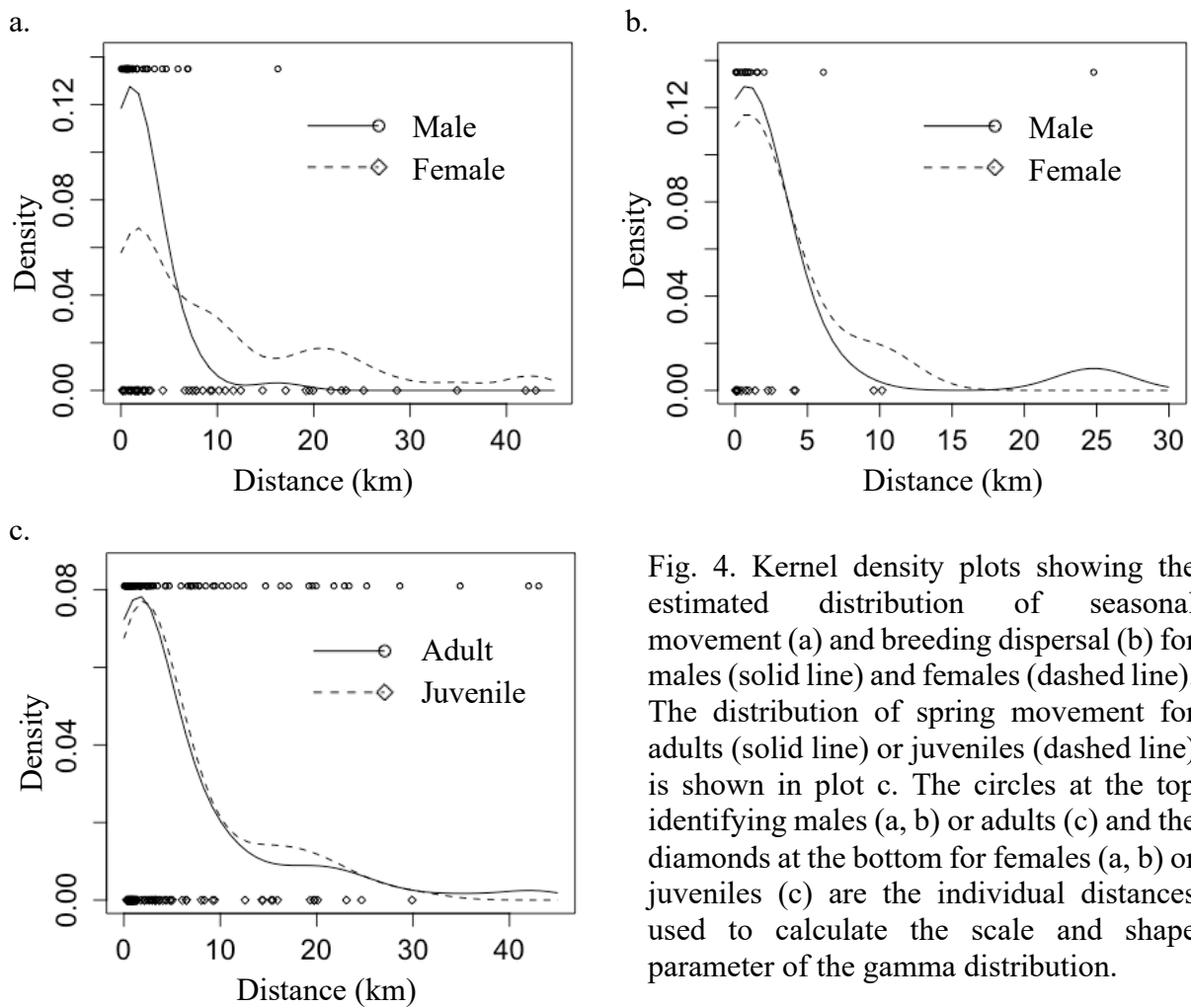


Fig. 4. Kernel density plots showing the estimated distribution of seasonal movement (a) and breeding dispersal (b) for males (solid line) and females (dashed line). The distribution of spring movement for adults (solid line) or juveniles (dashed line) is shown in plot c. The circles at the top identifying males (a, b) or adults (c) and the diamonds at the bottom for females (a, b) or juveniles (c) are the individual distances used to calculate the scale and shape parameter of the gamma distribution.

Table 1. Proportion of ptarmigans that moved beyond 1, 5, and, 10 km during (a) seasonal movement (b) breeding dispersal (c) spring movement separated by sex or age class. Z-statistics represent the deviance in probability of movement between states. Significance levels are indicated by an asterisk, where *; $P < 0.05$, **; $P < 0.01$ and ***; $P < 0.001$. Analysis (a) included 43 males and 44 females, (b) 12 males and 13 females, and (c) 91 adults and 68 juveniles.

		1 km	5 km	10 km
a. Seasonal movement	Male	44.2%	9.3%	2.3%
	Female	86.4%	56.8%	38.6%
	Z-value	-3.88***	-4.21***	-3.10**
b. Breeding dispersal	Male	41.7%	16.7%	8.3%
	Female	53.9%	15.4%	7.7%
	Z-value	0.81	0.09	0.06
c. Spring movement	Adult	65.8%	28.1%	19.0%
	Juvenile	72.6%	28.2%	19.1%
	Z-value	0.92	0.05	0.03

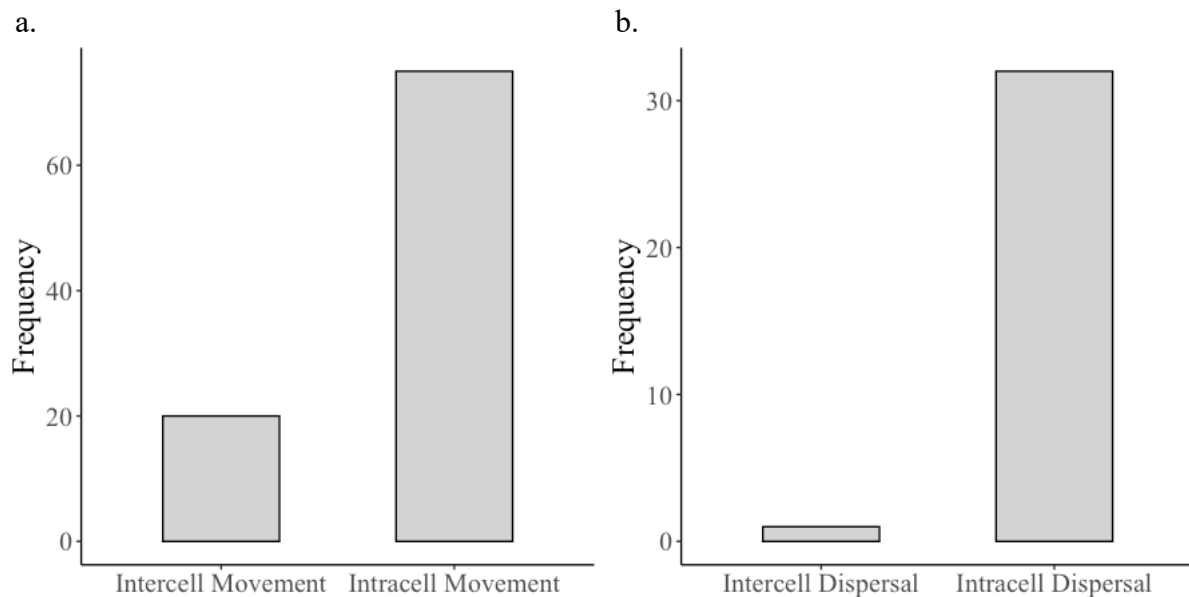


Fig. 5. Frequency of adults that displayed intercell (i.e. those that crossed the management area borders) and intracell (i.e. those that remained within the management area borders) movement behaviors. (a) Seasonal movement (b) Breeding dispersal.

3.2 Harvest models: Sustainable hunting quotas for different sized management areas

Introducing management strategies to the population matrix models had substantial consequences for the local population growth rate. The results based on the simulations revealed that the local population growth rate was strongly dependent on the harvest rate in the neighboring management area as well as on the size of the local management area.

When the harvest rate in the neighbor management area was equal to the local harvest rate (Fig. 6a), the local population growth rate was not dependent on the size of the local area.

In the scenario with a more intensive neighboring harvest rate (0.14) (Fig. 6b), increasing the rate of local harvest strongly affected population growth rate. The strength of this effect was strongly dependent on the size of the local management area. In general, the larger the local area (indicated by the colored slopes in Fig. 6), the less negative impact on population growth was seen as a consequence of the higher neighboring harvest rate (0.14). This was because as local area size increased less individuals moved beyond the area's boundaries during autumn movement to establish wintering territories where they were exposed to neighboring winter harvest. Consequently, larger management areas saw more harvest mortality from local hunting, thus increasing the influence of local harvest rates on population growth. When the local harvest quota was below neighboring rates, the largest management areas saw the highest levels of population growth and smaller areas saw the lowest. As local harvest rates approached the neighboring rate (0.14), the effect of local management area size on population growth rate decreased, and the predicted growth more closely reflected the predictions of a non-spatial population model, i.e. where movement was not taken into consideration (indicated by the black slopes in Fig. 6). This was due to the fact that ptarmigans that crossed management borders would be hunted to a similar extent, making a moot point of transboundary movement. When local rates were higher than neighboring quotas the effects of size were reversed, and larger management areas saw growth rates lower than smaller management areas. Increasing the neighboring harvest rate to 0.20 (Fig. 6c) showed a similar pattern to the preceding scenario but highlighted that an increase in neighboring rates garnered a stronger negative effect on population growth. This pattern would be seen in all management areas with the exception of one theoretically large enough to encompass all ptarmigan movement within the area, effectively closing the system.

Next, in a situation where there was no neighboring harvest (Fig. 6d), increasing local harvest rates had the steepest negative effect on population growth rates in the largest management areas. This effect lessens as management area size decreases, considering that the smallest areas would have the most ptarmigans leaving its boundaries into unhunted refugia.

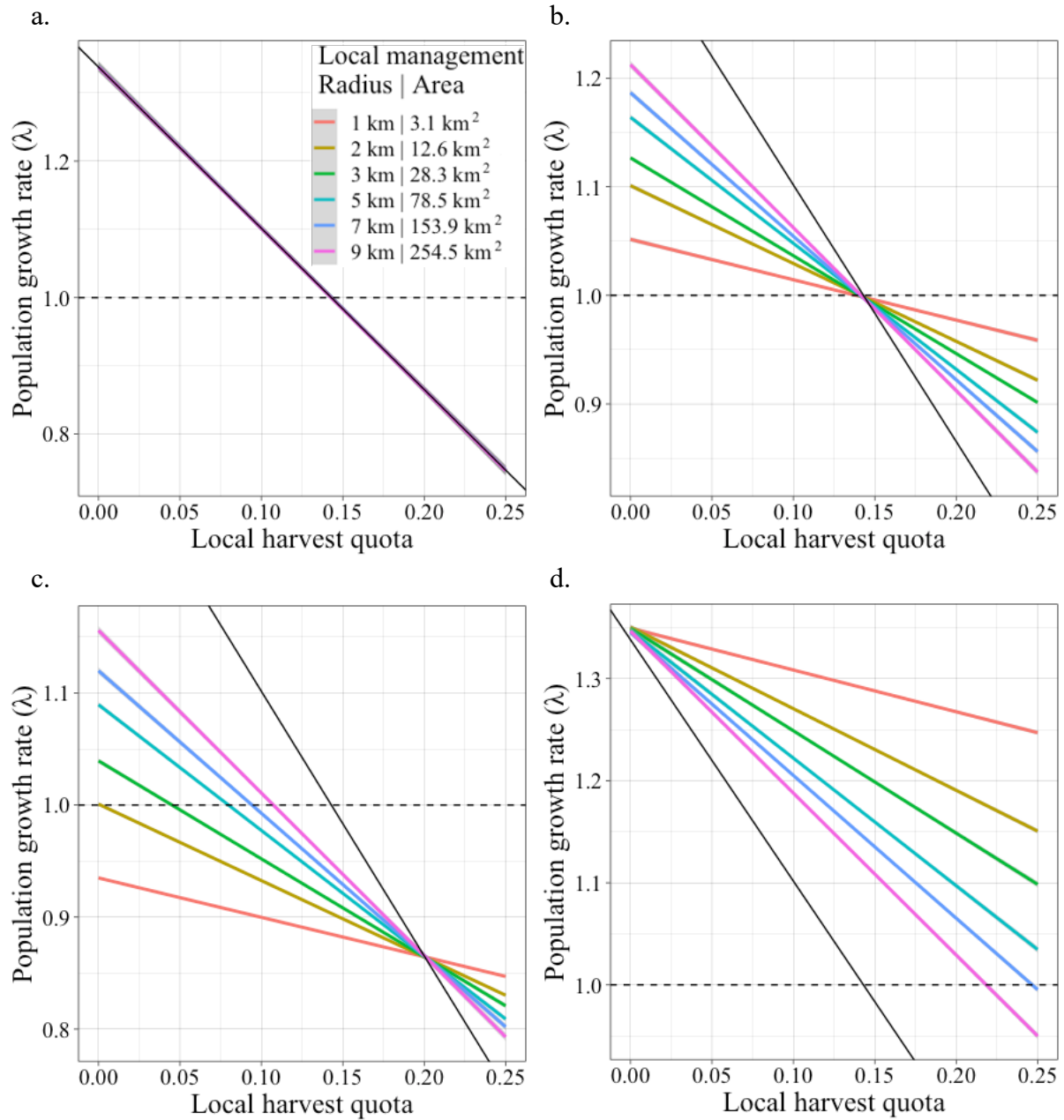


Fig. 6. Response on local population growth rate (λ) to local harvest quotas for different sized management areas with a neighboring harvest rate of (a) an equal value to that of local regimes; here each colored line has overlapped one another as would be expected in a closed population, (b) 0.14, (c) 0.20, and (d) 0. Along the x-axis is a scale of local hunting rates between 0 and 0.25. The y-axis represents the population growth rate (λ). Six of the colored lines are representative of local management area size. The black line illustrates what the population growth rate would be if movement was not included in the model. The dashed line (Population growth rate = 1) indicates a separation between population sizes that are increasing (Population growth rate > 1) or declining (Population growth rate < 1).

4 Discussion

In this study, a clear sexual difference in seasonal movement distance was found with females moving larger distances than males. However, there was no sexual bias found regarding breeding dispersal distance. There was also no difference found in movement distances between adult and juvenile classes during the spring movement. Based on a simulation model, these movements were found to create dependency between the local and neighboring harvest regimes; further, the extent of the dependency was itself dependent on the size of the management areas and the chosen harvest quota. Accordingly, the study has revealed that making sustainable management plans benefits from including specific knowledge of vital rates and movement patterns. Movement incentivizes corporation across management units and plans that ignore this potentially risk over- or underharvest. These consequences carry a particular weight in heavily harvested, red-listed species, as is the case of the willow ptarmigan in Norway.

4.1 Movement

Understanding the factors that shape variation in state-dependent movement strategies (i.e. seasonal movement and breeding dispersal) has been a major challenge in population ecology (Clobert et al. 2012). The present study revealed that seasonal movements differed between sexes, with females moving greater distances than males (as predicted in $H_1P_{1.1}$). At least three different hypotheses might explain the observed sex-biased patterns. First, males might remain close to breeding territories over the winter in order to ensure their occupancy in subsequent breeding seasons (Forero et al. 1999, Alerstam et al. 2003). Second, males may be adapted to philopatry because they are larger and able to sustain themselves for longer periods with lower resources, but for the smaller females it may be advantageous to move during winter in search of more favorable conditions (Alerstam et al. 2003, Guillaume and Perrin 2009). The third potential explanation is that the longer movement of adult females during spring is a learned behavior (Rogers 1969). Because juvenile females tend to have longer natal dispersal distances between summer and winter ranges potentially to avoid intersexual competition, (Pusey 1987) it is possible that they might then continue to repeat that behavior as adults.

Many bird species display strong breeding-site fidelity (Andersson 1980). In the present study, most male and female adult ptarmigans reused to the same breeding grounds from the preceding year, naturally resulting in minute breeding dispersal distances with no influence from sex, supporting $H_1P_{1.2}$. This is consistent with behaviors seen in other ptarmigan

populations (Hannon et al. 1998, Brøseth et al. 2005), bird species, and taxa such as mammals and amphibians (Andersson 1980, Matthiopoulos et al. 2005, Smith and Green 2005, Baker et al. 2013). Similar to the retracing of seasonal movement routes, the reuse of previously occupied breeding grounds could increase individual fitness by exposing individuals to habitats with which they are already familiar, which would in turn facilitate antipredator and foraging strategies (Greenwood 1980, Pärt 1991). However, the variation in movement behavior may change over time as environmental conditions change, thereby altering the benefits of a philopatric strategy (Smith and Green 2005, Clobert et al. 2012, Abrahms et al. 2018).

Studies have suggested that for populations that move between winter and breeding areas, older individuals with higher social status and physiological advantages as well as a local familiarity tend to move shorter distances and more quickly settle in suitable breeding habitats (i.e. the dominance hypothesis (Badyaev et al. 1996))(Johnson and Gaines 1990, Badyaev et al. 1996). Consequently, it is expected that younger, subordinate individuals will move farther than adults in search of breeding territories. It is likely that seasonal movement in willow ptarmigans may increase mortality risk due to increased physiological exhaustion and exposure to avian predators such as gyrfalcon (*Falco rusticolus*) and northern goshawk (*Accipiter gentilis*) (Johnson and Gaines 1990, Smith and Willebrand 1999, Alerstam et al. 2003). Thus, shorter distance movements may reduce the probability of mortality. Considering the aforementioned dominance hypothesis, there is potential for age-bias in willow ptarmigan spring movement distance (Johnson and Gaines 1990). However, in the current study no difference was found between age classes in the distances moved during the spring movement, rejecting $H_{1P1.3}$.

Studies on black tailed-deer (*Odocoileus hemionus columbianus*), ruffed grouse (*Bonasa umbellus*) and collared flycatcher (*Ficedula albicollis*) have shown that individuals that reuse sites with which they are familiar have increased survival probabilities (Pärt 1995, Yoder et al. 2004, Forrester et al. 2015). It has been suggested that this advantage explains why individuals in some species (e.g. spruce grouse (*Falcipennis canadensis*)) seemingly retrace routes taken as juveniles (Schroeder 1985, Hörnell-Willebrand et al. 2014). Retracing was not explicitly investigated in the current study, but this behavior might explain account for the lack of difference found between age classes regarding seasonal movement distances.

Based on a study exploring the spatial dynamics of willow ptarmigan in Norway Kvasnes et al. (2015) suggest that juveniles are attracted to areas of high conspecific abundance during the spring settlement period. In contrast, most juveniles observed in the present study

did not move into areas with higher conspecific abundance after leaving their first-year winter settlement; in fact, only two individuals moved into management cells with higher densities. These results seem to contradict Kvasnes' suggestion as well as findings in studies on songbird species in which individuals exhibited an affinity towards conspecifics by settling in high-density sites using high abundance as a cue for habitat quality (Stamps 1988, Muller et al. 1997, Ward and Schlossberg 2004, Ahlering et al. 2010, Kvasnes et al. 2015). However, a limitation of this study is that conspecific attraction would not have been detected in the analysis if juveniles were in fact using density as a cue but just at a smaller spatial scale than the size of the management area. In light of this limitation, the present study's results are not conclusive. Thus, the idea suggested by Kvasnes et al. (2015) might still hold even if it were not supported on the scale investigated in this analysis.

4.2 Management implications

The present study, which illustrates a harvested population with state-dependent seasonal movement and high breeding-site fidelity, is exemplary of a system in which population growth rates are highly dependent on both local and neighboring management regimes due to potential cyclic movement across management area boundaries. This study used the proportional harvest model, but because the results are general trends on growth rate response to movement and harvest strategy, the findings could be incorporated into other harvesting models. While using alternative harvest regime strategies would influence the model's projections of the population growth rate, its principles would remain unchanged.

The incorporation of state-dependent seasonal movement patterns into harvest models revealed that the consideration of movement had an effect on population growth estimates across a heterogenous landscape (Fig. 6). Depending on an area's size, a frequency of each demographic group was liable to migrate outside its boundaries during seasonal movement where individuals were influenced by the surrounding regime prior to return. This affected local population growth differently than when the entire population was exposed to a single harvest strategy (Fig. 6a). According to Novaro et al. (2000), Gervasi et al. (2015) and Ling and Milner-Gulland (2008), non-spatial models with this intrinsic assumption of uniform harvest are oftentimes used. These types of models have the potential to misinform managers, ultimately resulting in overharvest. When neighboring harvest rates were higher than local rates (Fig. 6b, c) this resulted in a lower local population growth compared to predictions from the non-spatial model (the black line, Fig. 6). This was especially true when local management

area was small, resulting in local population growth rates well below 1 (the dashed line, Fig. 6b, c), indicating a decline in local population size. The findings here align with other studies conducted across harvested taxa (e.g. mammals, fish, birds), which emphasized that individuals entering the breeding population in the spring may largely be individuals returning from their seasonal movement, as opposed to compensatory immigrants from neighbor populations (Boyce et al. 1999, Kokko 2001, Novaro et al. 2005, Gervasi et al. 2015). This dynamic may attribute to growth rate estimation differences between spatial and non-spatial models (Novaro et al. 2005). The degree to which the local population growth rates were lower changed in direct response to local management area size. Accordingly, managers of smaller areas must be more conscientious of neighboring strategies than managers of larger areas whose regimes have a comparably greater influence on population growth rates. Conversely, non-spatial models can also miss possibilities for greater harvest. When neighboring harvest rates were lower than local rates (i.e. to the right of 0.14 and 0.20 in Fig. 6b and c, respectively, and in Fig. 6d) the local population growth rates were higher than growth rates estimated by the non-spatial model predictions (indicated by black slopes in Fig. 6b, c and, d). In such cases, including movement in harvest models can further optimize harvest, generating more income from fee-paying hunters and avoiding prospective environmental damage from an overpopulated species, (e.g. overbrowsing from ungulates) (Clutton-Brock et al. 2002, Milner-Gulland et al. 2004). Although spatially explicit harvest models can help optimize harvest management decisions, the model in this study is best used to understand general principles rather than act as a predictive framework. To more accurately reflect potential for further harvest, other parameters such as spatial heterogeneous population distribution and local density dependence should be taken into account.

In addition to demonstrating the effects of hunting regimes, the population projection model approach used in the present study could also shed light on aspects related to conservation. The local management area may be viewed as a protected zone when the local harvest rate equals 0. Accordingly, projections from the spatial model demonstrated that when mortality outside the protected area was higher than inside (Fig. 6b, c), local population growth rate decreased correspondingly with protected area size. This aspect of the model can be useful for estimating the optimal biologically relevant size for protected areas and their buffer zones (McCullough 1996, Willebrand and Hörnell 2001, Schaub et al. 2010). For instance, such a situation has been described for the wolverine (*Gulo gulo*) in Scandinavia (Gervasi et al. 2015), in which movement between hunted (in Norway) and non-hunted (in Sweden) areas created a

source-sink dynamic. If a protected area is not appropriately sized this dynamic could bias movement from the protected area to areas with higher mortality, potentially diminishing conservation goals (Gervasi et al. 2015).

The present study demonstrates how the consequences of harvesting in heterogeneous management landscapes can be analyzed in realistic population projection models by combining essential life history data from various sources. In expanding this work there should be an emphasis on collecting more data on the influence of phenotypic variation determining both variation in movement and the survival of migrants. For instance, in some species, individuals with higher body mass have an increased overwinter survival, which influences the frequency distribution regarding quality and size of the breeding individuals after a particularly harsh winter (Newton 1993, Festa-Bianchet et al. 1997, Schorr et al. 2009). Additionally, the size of individuals in some migratory bird species has been shown to affect migration distance (Alerstam et al. 2003, Gray et al. 2014). If individual variation in size is correlated with movement distance in willow ptarmigan, this would potentially add a size bias to the portion of the population exposed to neighboring management regimes. These factors could influence both the phenotypic distribution of the adult breeding population as well as the phenotypic distribution of the new cohort and other factors possibly linked to body size (e.g. clutch size, and onset of breeding (Hannon et al. 1988, Elks et al. 2012)), which may consequently impact management goals. Nevertheless, the key message of the findings in the present study is the dependency on neighboring regimes which is subject to change with the size of the local management area. This dependency is also affected by the time of harvest. For populations with strong breeding site fidelity, adjusting harvest to exclude winter would exempt seasonal migrants from the influence of neighboring harvest. These principles underscore the necessity of effectively communicating and coordinating strategies with neighbors for the benefit of wild species and the human communities reliant upon their harvest for revenue and sustenance.

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7 Appendices

7.1 Appendix A

Hypothesis H1: *Willow ptarmigan movement is influenced by state (i.e. sex, age).*

Prediction P1.1: Seasonal movement: Adults will remain in their breeding territory, only migrating out of it during the winter months (Kvasnes et al. 2015).

Prediction P1.2: Adult breeding dispersal: Adults will return to their breeding territory from the preceding year (Hannon et al. 1998).

Prediction P1.3: Juvenile spring movement: Juveniles will move farther distances than adults during the seasonal movement between winter and summer territories (Brøseth et al. 2005).

Hypothesis H2: *Willow ptarmigan movement is influenced by conspecific attraction.*

Prediction P2: Juvenile post winter dispersal: Juveniles will move into areas with higher conspecific abundance after leaving their first year settlement to establish a breeding territory (Kvasnes et al. 2015).

Hypothesis H3: *The consequences of different harvest strategies are influenced by the age-specific movement pattern of the willow ptarmigan population.*

Prediction P2: I expected the outcomes of testing different harvest regimes in a spatially explicit predictive harvest model to be influenced by the results from the predicted movement patterns indicated in Part 1 (Boyce et al. 1999, Hörnell-Willebrand et al. 2014).

7.2 Appendix B

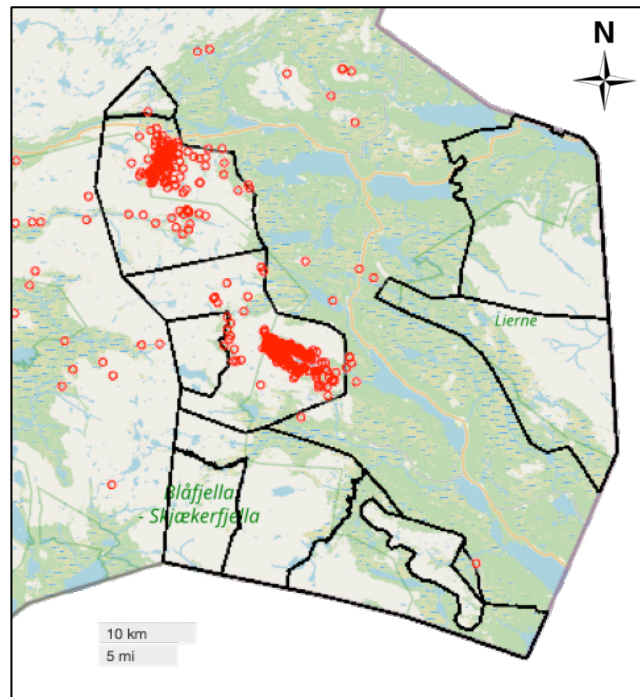


Fig. 7. Map of the Lierne municipality in eastern central Norway with management cells outlined in black. Each ptarmigan observation is represented by a red circle.

7.3 Appendix C

Table 2. Descriptive statistics for movement distance analyses. Quantile ranges, mean, SD = Standard deviation in kilometers. N = Sample size.

		25%	Median	75%	Mean	SD	N
Seasonal movement	Male	0.6	0.9	1.7	1.9	2.8	45
	Female	1.8	7.2	16.5	10.3	11.2	46
Breeding dispersal	Male	0.4	0.8	1.4	2.8	6.5	14
	Female	0.1	0.9	3.3	2.4	3.3	15
Spring movement	Adult	0.8	1.8	7.6	6.2	9.2	91
	Juvenile	0.9	2.8	6.9	5.7	7.1	68

