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Effects of forestry, predators and weather on capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) in South-East Norway

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Abstract

The European populations of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) have declined the last 50 to 100 years. The decline has happened at the same time as changes in forestry practices, predation pressure and climate, but the specific drivers of the decline are still not clear.

The aim of this thesis was to test the main drivers for population dynamics of the forest grouse species; capercaillie and black grouse. In South-East Norway, over a period of 41 years in Sjøliseterberget (1975-2016) and 19 years in Hobøl (1987-2016), data were collected each autumn by a line transect method. By this method capercaillie and black grouse abundance and reproduction, in addition to habitat (forest age classes) were registered. My main goal was to reveal if the reproduction of forest grouse had changed over time and what the main causes could be. I therefore, specifically tested the habitat preferences of forest grouse, if these habitats had changed during time of study and if the preference of forest grouse had changed accordingly, to establish whether forestry could be affecting the reproduction. In addition, annual drivers of forest grouse reproduction like weather in the summer ("The Weather Hypothesis") and difference in predation pressure ("The Alternative Prey Hypothesis") were tested.

I found declining reproduction of capercaillie in Sjøliseterberget and black grouse in Hobøl. While the capercaillie preferred the oldest succession stages of the forest, the black grouse preferred younger forest. The proportion of medium old and old forest did not change in neither area over time, and nor did the forest grouse preferences. The reproduction was thus declining despite a stable age structure of the forest. I further found that temperature in June and differences in fox population from one year to another explained most of the variation in reproduction in Sjøliseterberget based on AICc model selection, while no factors explained the variation in reproduction in Hobøl. Lack of significant results in Hobøl was possibly caused by a smaller sample size. The alternative prey hypothesis was confirmed as a large vole population increased the fox population the next year, and this fox population decreased reproduction of forest grouse. Despite this two-step link between voles and forest grouse, no significant covariation between vole abundance and forest grouse reproduction was detected, even in periods with a high fox population. The weather hypothesis was partially confirmed as increase in temperature in June had a large positive effect on reproduction, while increase in precipitation in the same month did not have a negative effect as first predicted. Further analyses showed that also seasonal NAO affected the reproduction.

This study contributes to the understanding of short-term fluctuations and long-term trends in population dynamics of capercaillie and black grouse. In addition, knowing how forest-dwelling species respond to variation in forestry, predation pressure and weather can help us understand how these species will persist in a future with extensive forestry and a changing climate.

Sammendrag (in Norwegian)

De europeiske populasjonene av storfugl (*Tetrao urogallus*) og orrfugl (*Lyrurus tetrix*) har sunket de siste 50 til 100 årene. Denne nedgangen har skjedd samtidig med endringer i skogbruk, predasjonstrykk og klima, men de spesifikke driverne er fortsatt utydelige.

Målet med denne oppgaven er derfor å teste hva som er hoveddriverne for populasjonsdynamikken til skogsfuglene; storfugl og orrfugl. I Sør-Norge har det over en periode på over 40 år (1975-2016) i Sjøliseterberget og 19 år i Hobøl (1987-2016) blitt samlet data med en linjetransektmetode som inkluderer registreringer av skogsfuglartene og habitatregistreringer (hogstklasse). Jeg ønsket å undersøke om reproduksjonen til skogsfuglen har gått ned, og hva årsakene kan være. Jeg testet derfor habitatpreferansene til skogsfuglene, om dette habitatet hadde endret seg gjennom studieårene og om preferansene til skogsfuglen hadde endret seg i samme mønster, for å kunne bekrefte om skogbruk hadde påvirket reproduksjonen. I tillegg testet jeg de årlige drivere av skogsfuglreproduksjon, slik som været i juni ("Vær-hypotesen") og forskjell i predasjonstrykk ("Alternativ byttedyrhypotesen").

Jeg fant nedgang i reproduksjon av storfugl i Sjøliseterberget og orrfugl i Hobøl. Mens storfuglen foretrakk de eldste suksesjonstrinnene i skogen, foretrakk orrfugl yngre skog. Andelen mellom gammel og gammel skog endret seg ikke i noen av områdene i løpet av studieperioden, og det gjorde heller ikke preferansene til skogsfuglene. Dette studiet viser at temperatur i juni og endring i revebestand fra et år til et annet forklarer mest av variasjonen i reproduksjon hos skogsfugl i Sjøliseterberget basert på AICc modellseleksjon. I Hobøl forklarte ingen faktorer variasjonen i reproduksjon, antageligvis på grunn av mindre datagrunnlag. Den alternative byttedyr hypotesen ble bekreftet av at en stor musepopulasjon resulterte i økt revepopulasjon året etter, og at denne revepopulasjonen førte til nedgang i reproduksjonen til skogsfugl det samme året. På tross av denne to-steps forbindelsen mellom mus og skogsfugl, fant vi ingen direkte samvariasjon mellom mus og skogsfugl, selv i perioder med mye rev. Vær-hypotesen ble delvis bekreftet ettersom temperatur i juni hadde stor, positiv effekt på reproduksjonen, mens økning i nedbør den samme måneden ikke hadde noen negativ effekt, som først antatt. Videre analyser viste at en økning i sesong-NAO økte reproduksjonen.

Dette studiet bidrar til forståelse av kortvarige svingninger og langvarige trender i populasjonsdynamikken til storfugl og orrfugl. I tillegg kan kunnskap om hvordan skogslevende arter reagerer på variasjon i skogbruk, predasjonstrykk og vær, hjelpe oss å forstå hvordan disse artene vil overleve i en framtid med mye hogst og klimaendringer.

Table of contents

Acknowledgements	I
Abstract	III
Sammendrag (in Norwegian)	V
Table of contents.....	VII
1 Introduction.....	1
2 Materials and Methods	4
2.1 Study Areas	4
2.2 Study Species	5
2.3 Data Collection.....	5
2.4 Statistical Analyses.....	9
3 Results	12
3.1 Temporal Trends in Forest Grouse Reproduction.....	12
3.2 Habitat Selection and Temporal Trends in Logging in Sjøliseterberget and Hobøl	13
3.3 Factors Explaining Annual Variation in Forest Grouse Reproduction	16
4 Discussion	23
4.1 Population Size and Dynamics	23
4.2 Habitat Selection and Temporal Trends in Logging in Sjøliseterberget and Hobøl	24
4.3 Factors Explaining Annual Variation in Forest Grouse Reproduction	26
5 Conclusions.....	30
6 References	31
7 Appendices	36
Appendix A.....	36
Appendix B	39
Appendix C	40
Appendix D.....	41

1 Introduction

Forest grouse are worldwide confined to the Palearctic boreal forests, characterized by coniferous forests dominated by species like spruces (*Picea*) and pines (*Pinus*) (Jönsson et al. 1991). During the last 50 to 100 years there has been a dramatic decrease in the European populations of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) (Kurki et al. 2000; Storch 2000). The Norwegian populations are no exception, and bags of forest grouse clearly show that the population density today is at a much lower level compared to the 1970s (Gregersen & Gregersen 2009). The specific drivers of this decline are unclear, but the decline has happened in parallel to changes in forestry practices, predation pressure and climate (Ludwig 2007). These are all elements that can cause temporal short-term fluctuations in the population dynamics (Angelstam et al. 1985; Ludwig et al. 2006), as well as negative long-term trends (Jahren et al. 2016; Ludwig et al. 2006).

Human activities have long been known to cause severe damage to wildlife; both to smaller populations and to whole groups of species (Myers 1993; Singh 2002). Degradation and fragmentation of forest due to modern forestry or change in agricultural land can change the forest as wildlife habitat. Fennoscandian boreal forests are included, as they are currently largely exposed to commercial forestry causing extensive changes in forest structure (Esseen et al. 1992). Despite both species being confined to the boreal forest, capercaillie and black grouse differ in preference for specific successional stages of the forest. While black grouse prefer the earliest succession stages with moor-like and less productive forest (Baines 1996; Swenson & Angelstam 1993), capercaillie is mainly found in the oldest succession stages which often contains well-developed field layers of bilberry (*Vaccinium myrtillus*) (Rolstad & Wegge 1987; Storch 1993; Swenson & Angelstam 1993). As commercial forestry reduce the area of old forest, the capercaillie are seen as the most vulnerable species of the forest grouse to modern forestry (Mikoláš et al. 2015).

The changes in habitat can be a threat to the populations as lack of nest cover or change in distribution of food can be detrimental factors to forest grouse populations (Kurki et al. 2000; Storch 2000). Also, increased predation caused by higher densities of generalist predators such as red fox (*Vulpes vulpes*), as a result of intensified agricultural activities (Kurki et al. 1998), are expected to affect the forest grouse negatively (Kurki et al. 2000). A further reason for increase in number of predators, may be the increased proportion of younger succession stages after clear-cutting. This results in a grass-dominated field layer, which is highly suitable for voles of the genus *Microtus* (Hansson 1992). These voles are preferred prey of several generalist predators, and may therefore results in larger fox populations (Henttonen 1989). A high predation pressure can be severe to small populations. Chicks, in particular, are easily a target for predators (Marcstrom et al. 1988). In Norway

earlier findings show an average egg loss of 70 % in Varaldskogen, and the losses were especially high right before and after peaks in the small rodent cycle for both capercaillie and black grouse (Wegge & Storaas 1990). This suggests that predators like red fox and mustelids switch to grouse when the small rodent populations collapse year after a peak. This is commonly known as The Hypothesis of Alternative Prey and states that the generalist predators shift diet in dissimilar phases of the vole cycle (Kurki et al. 1997). According to the alternative prey hypothesis, the short-term fluctuations in forest grouse in the autumn is caused by the varying predation pressure on mainly eggs, chicks and juveniles (Angelstam et al. 1984; Hagen 1952). The effect of the red fox as a generalist predator on grouse population dynamics has been further confirmed by Lindström et al. (1994) during outbreaks of sarcoptic mange. This epizootic mange was caused by the itch mite (*Sarcoptes scabiei*) and reduced the red fox population to less than half its former number in Sweden and Norway (Lindström 1989). The reduced fox population lead to increased forest grouse populations (Lindström et al. 1994).

Studies have confirmed weather to influence capercaillie and black grouse's productivity (Slagsvold & Grasaas 1979; Summers et al. 2004). This is especially the case when it comes to rainfall and temperature in June and corresponds with the first few weeks after the chicks have hatched. Hens nest in many different habitats (Storaas & Wegge 1987), but at least capercaillie chooses habitats that are moist, like close to mires (Rodem et al. 1984). Here the density of insects is higher, which the chicks utilize on a large scale (Wegge et al. 2005), before they later in the summer or in the beginning of autumn move to habitats that are richer on blueberries (Selas 2001). The time of hatching have been found to correlate with the maximal amount of moth larvae (Baines et al. 1996), which then again is related to the weather (Moss et al. 2001). Not only local weather can affect forest grouse reproduction, also the weather phenomenon North Atlantic oscillation (NAO) is acknowledged to affect especially survival of willow ptarmigan (*Lagopus lagopus*) chicks (Kvasnes et al. 2014).

Few studies have investigated drivers of forest grouse dynamics using long-term data (more than a decade). Hence, the objective of my study was to examine if there has been a change in the forest grouse reproduction success in two data series from south-eastern Norway covering 3 and 4 decades respectively. To investigate possible causes, variation in reproduction was studied in relation to changes in availability of key habitat types and changes in other annual environmental drivers (predation, alternative prey and summer weather). I predict that reproduction of capercaillie and black grouse have declined in my study areas (**P1**). Due to intensive forestry in the study areas, I further predict that the key habitats of capercaillie and black grouse in the study area have changed (**P2**), with decreasing old forest and increasing clearcuts (**P2a**), and that this has caused an increase in the use of the remaining old forest (**P2b**), in particular for capercaillie.

The alternative prey hypothesis was tested with several predictions. Since *Microtus* voles are preferred prey for many generalist predators, including the red fox (Henttonen 1989), that occur in large numbers in peak years, I predict that fox population have a negative effect on forest grouse reproduction (**P3**) where **P3a**) a large vole population in year t increases breeding success and number of red foxes (that increase the hunting bag of foxes the following autumn and winter of year $t+1$). Peak vole abundance last only one year. Therefore, **P3b**) the high fox population in year $t+1$ will coincide with low vole abundance and foxes will switch to prey on forest grouse reflected in a decreased forest grouse reproduction in the same year ($t+1$). Transfer of the population effect from voles to forest grouse, depends on a responsive fox populations (Angelstam et al. 1985; Lindström et al. 1987). The sarcoptic mange outbreak provided a natural experiment when the fox population was at a continuous low for more than 10 years (year 1983 to 1994; a time period covered by my study period). The forest grouse population increased during this period (Lindström et al. 1994). I therefore predict that **P4**) covariation between voles and forest grouse reproduction is dependent of a high fox population, meaning there will be no co-variation during outbreaks of sarcoptic mange (**P4a**) and covariation before and after outbreaks of the sarcoptic mange (**P4b**).

The weather hypothesis can be divided into particular local weather parameters that can affect the reproduction directly and large-scale climate variation as NAO, that affects the local weather, which in turn can affect the forest grouse. As the chicks hatches in June, and both rainfall and temperature in this month have been showed to be important for survival (Slagsvold & Grasaas 1979; Summers et al. 2004), I predict that weather influence the reproduction of forest grouse (**P5**) and that **P5a**) a high summer temperature gives a direct positive effect on reproduction and **P5b**) a high summer precipitation gives a direct negative effect on reproduction. I further predict that **P5c**) seasonal NAO-index for May, June and July gives a direct positive effect on reproduction, since positive seasonal NAO-index for these months have been showed to correlate with high temperatures and accelerated plant growth (Kvasnes et al. 2014), which in turn can affect viability of young chicks through its effect on availability of important insect prey species (Erikstad & Spidsø 1982).

2 Materials and Methods

2.1 Study Areas

This study was conducted south east of Norway in two different areas (Figure 1); Sjøliseterberget (Figure 1A) and Hobøl (Figure 1B). Sjøliseterberget is located 60°76'N, 12°05'E in Hedmark county, right next to the border of Sweden. Here moraine soil dominates with scots pine (*Pinus Sylvestris*) and species from the Ericaceae family, like blueberries (*Vaccinum Myrtillus*) and calluna (*Calluna Vulgaris*). The forest has well-drained soil and in moist areas Norway spruce (*Picea abies*) is common.

Hobøl is located at 59°59'N 10°96'E in Østfold county. Hobøl has, in contrast to moraine soil, marine deposits in the lower altitudes with the Norway spruce dominating the forests. In higher altitudes, we find more shallow soil with basement rocks and more fine-grained sedimentations dominated by scots pine. Recent data show the productive forest composition in Østfold, Akershus, Oslo and Hedmark combined, to consist of 41% Norway spruce, 41% scots pine and the remaining percentage of deciduous trees with a site quality consisting of 32.7 % low, 44.8% medium, 20.7 % high and 1.8 very high forest (Granhus et al. 2012). While Hobøl represents a fragmented forest landscape split by roads, agricultural land and buildings, Sjøliseterberget is part of the large, continuous forest at Finnskogen.

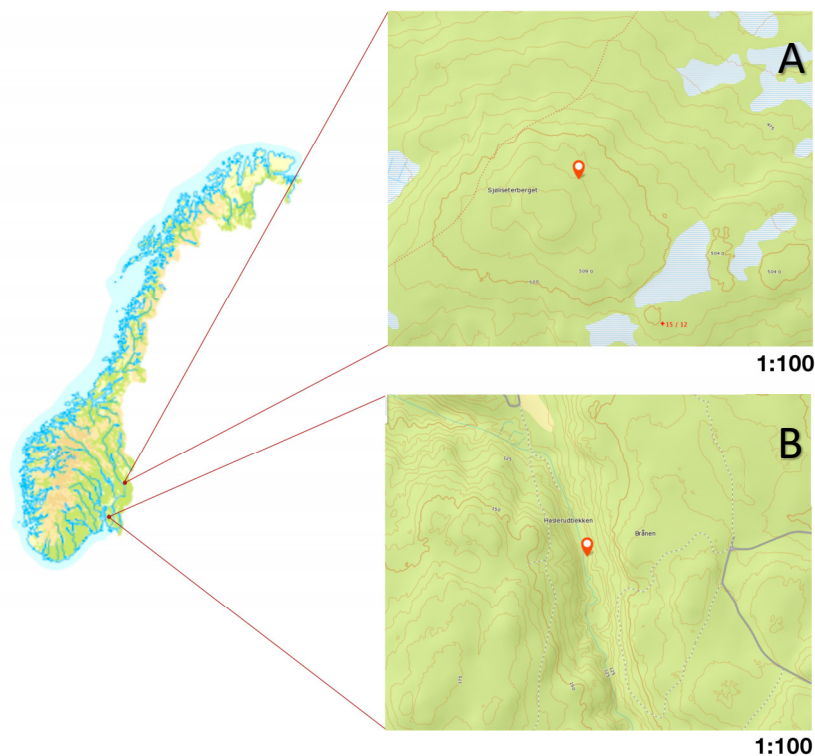


Figure 1 The study was conducted in **A**) Sjøliseterberget and **B**) Hobøl. Both areas are in south east of Norway. The enlarged maps show the terrain the line transect method was conducted in.

2.2 Study Species

There are five grouse (order Galliformes, Family tetraonidae) species occurring in Norway; black grouse, capercaillie, hazel grouse (*Bonasa bonasia*), willow ptarmigan and rock ptarmigan (*Lagopus mutus*). The three first species are considered as the true forest grouse species. In this study, I only deal with two of these species; black grouse and capercaillie.

Forest grouse are popular birds for hunting and in Norway and the hunting season takes place between 10th of September and 23rd of December. The hunting in some areas has recently been regulated with daily quotas, of usually one or two forest grouse per hunter per day in 2016 (Statsskog 2016). According to Shimmings and Øien (2015) breeding population of capercaillie is estimated to be approximately 80 000 – 100 000 individuals, whereas breeding population of black grouse is estimated to be between 100 000 and 200 000 in Norway (Shimmings & Øien 2015).

2.3 Data Collection

2.3.1 The “Man-hour” Method for Estimating Abundance

The field work took place each September (just before hunting season) between 1975-2016 in Sjøliseterberget and 1987-2016 in Hobøl. The data was gathered by students by a line transect method. The method involved students searching the forest by walking out with a 100 meters' gap between them. They followed a straight line if it was possible, and used a compass to follow a determined compass course. After 1,5 hours, the students turned to the left with an angle of 90 degrees. They walked 50 meters before they once again turned 90 degrees to the left and walked parallel with the line they came from. In addition to compass, the students used GPS to mark the spots where the species was observed and for track logs (Figure 2). The use of GPS was only done in the later years (from 2011), while in earlier years this was marked on a printed map. If two or more students walked together, they were counted as one observer. An average 29,6 transect lines were censused per year in Sjøliseterberget, ranging from 14 lines at the least and 44 at the most. Each observer walked an average of 2 hours and 57 minutes. In Hobøl, an average of 27,9 transect lines were censused per year, ranging from 10 lines at the least and 38 at the most. Each observer walked an average of 2 hours and 40 minutes.



Figure 2 Example of track log obtained from GPS showing how the students walked in the terrain. Figure shows Sjøliseterberget in 2015.

2.3.1.1 Species Registration

If the students could recognize the species, black grouse and capercaillie, and the sex of the species, this was recorded. If several birds were seen in one place, this was recorded as well. If the students could not identify the grouse species, this was recorded as unknown forest grouse. Observations with more than one bird in a group were registered as juveniles. This is not always the case, but sometimes single birds are not adults and therefore the two sources of error can be expected to cancel each other. There were new students each year and the general level of experience was therefore the same over time. Few of the students had a lot of experience with species determination, and all students got a lecture in the characteristics and determination of the different forest grouse before the field work took place.

2.3.1.2 Habitat Registration

In addition to species, what type of habitat the forest grouse were observed in was registered. This was based on height of trees dominating 1 acre of the surrounding landscape from where the forest grouse was flushed. In addition, habitat was registered on random locations, where each student was given a number between 0 and 59 that represented the number of minutes after each full hour. At the designated times the student stopped and registered the habitat in the acre surrounding him/herself. Habitat at random locations was used as a measure of distribution of habitat types in the study areas.

Successional stages following logging were divided into classes. Because of differences in listing the age classes from earlier years to recent, some age classes had to be merged. See Table 1 for description.

Table 1 Age classes in the forest based on height of the trees dominating 1 acre. Age class 1 and 2 (1 & 2) and Age class 5 and 6 (5 & 6) have been merged.

Age class	Description	
1	Clearcuts with no trees	1 & 2 – Clearcuts with no trees and coniferous trees from 0-0.5 meters
2	Clearcuts with coniferous trees from 0-0.5 meters	
3	Stands with an average tree height of 0.5-3 meters	
4	Stands with an average tree height of 3-10 meters	
5	Stands with an average tree height of 10-20 meters	5 & 6 - Stands with an average tree height of 10-20 meters and > 20 meters
6	Stands with an average tree height of > 20 meters	

2.3.2 Forest Grouse Data

To be able to estimate the abundance of forest grouse species, the total number of all forest grouse and the species separately were divided by total number of hours walked each year. Reproduction was calculated by dividing the number of juveniles (see Materials and Methods section; 2.3.1.1 Species Registration) by total number of capercaillie and black grouse per study area and year, giving us a measure of annual reproduction in percentage.

For Sjøliseterberget data includes all years from 1975-2016, but data for chicks of capercaillie and black grouse separately in 2005 and 2006 is missing. The combined data for chicks is not missing these years. For Hobøl data includes years from 1987-2016, but all data from 2002 is missing in addition to data for chicks in 2005 and 2006.

2.3.3 Habitat Data

The first year with random registrations was 1991. Some years are lacking random registrations; 1997, 2000, 2001, 2002 and 2005-2010 for Hobøl, and 1992, 2001, 2005 and 2006 for Sjøliseterberget. In Sjøliseterberget it was registered an average of 100.5 random habitat registrations each year with a minimum of 34 and a maximum of 173. In Hobøl it was registered an average of 78.4 random habitat registrations each year with a minimum of 28 and a maximum of 170. In analyses of habitat in relation to abundance of forest grouse, only the years that contained both species registration and habitat registration were counted.

2.3.4 Vole Data

Occurrence of voles was registered in Varaldskogen in Hedmark county (60°10'N, 12°30'E) from 1979- 2016. This is not far away from our study area in Sjøliseterberget, and it can therefore be a good estimate of the density of small rodents in the area. Data is based on the average number of

field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*) per 100 trap nights (P.Wegge-unpublished data). Due to lack of data of vole abundance close to Hobøl, the same data were also used for analyses in this area.

Small rodents are usually trapped in the autumn. However, there is generally a good correlation between densities of rodents in spring and autumn (Kausrud et al. 2008), therefore autumn data is also a good indicator of the abundance of rodents in the breeding season of forest grouse.

2.3.5 Red Fox Data

Hunting statistics for red fox (*Vulpes Vulpes*) is collected by Statistics Norway (Statistics Norway 2016). It is statistics from the total number of red foxes shot in Hedmark and Østfold county, and serve as estimates of density of red foxes. The year of hunting is from April to April, and most of the hunting occurs in late winter.

The first Norwegian case of sarcoptic mange was diagnosed in 1976, and by 1986 it had spread to the country (Smedshaug et al. 1999). The hunting statistics for our areas indicates a strong decrease in fox population from 1983-1994 in Hedmark and Østfold. These years are therefore defined as the years with most sarcoptic mange. Years before and after are defined as years with no effect of this, even though there are reasons to believe that the mange affected both the red fox population and the hunting pressure in long time after this period.

2.3.6 Weather Data

2.3.6.1 Local Weather

Precipitation and temperature have been measured each month from April to August since 1975. Both temperature and precipitation are monthly averages. The values are gathered from met.no and yr.no and are taken from active measuring stations in Hedmark and Østfold.

2.3.6.2 North Atlantic Oscillation Index

In addition to these locale climate variables, I also included seasonal North Atlantic oscillation (NAO) index. The NAO is a weather phenomenon in the North Atlantic Ocean where there is an alternation in atmospheric mass between the subtropical atmospheric high-pressure centre over the Azores, and the atmospheric subpolar low-pressure centre over Iceland (Hurrell 2002; Stenseth et al. 2002). The NAO index is used to describe the condition of these fluctuations and is often described as “high” and “low”, where a high value gives low-pressure over Iceland relative to the Azores.

The index is calculated by this formula:

$$\frac{\text{SLP in The Azores} - \text{SLP in Iceland}}{\text{standard deviation}} \quad \text{mean}$$

where SLP is the sea level pressure (Hurrell 2002)

NAO is known to have ecological effects on birds and survival of chicks (Forchhammer & Post 2000; Kvasnes et al. 2014; Stenseth et al. 2002). The focus in this thesis is chick survival. May is the month of incubation for the grouse, and the eggs often hatch the first or second week of June (Ludwig et al. 2006; Storch 1994). The rest of June is the chicks first weeks of life and they are sensitive to the weather (Slagsvold & Grasaas 1979). Cause of the importance of these months for the chicks' survival, I chose to run a seasonal NAO index for May, June and July (NAO_{MJJ}). Seasonal NAO-index for obtained for all years, except from year 2016 due to lacking data.

The NAO time series were obtained from the Climate Analysis Section, available at <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>

2.4 Statistical Analyses

Multivariate linear and logistic regression is a simpler analytical framework than multivariate time series analysis. Time series analyses is needed when there is strong temporal correlation in data. As a first step, I ran autocorrelation analysis (ACF) on all variables separately (See Appendix A) to check for temporal correlation in the time series. Since most results indicated no autocorrelation, meaning that the time sequence of data was not important, I could proceed with linear regression and logistic regression. All statistical analyses were done using R version 3.1.1 (R Core Team 2014).

2.4.1 Temporal trends in forest grouse reproduction

To examine whether the population size of capercaillie and black grouse have declined or inclined during the last decades, I made a linear regression model with population size as response variable and year as a continuous predictor variable. Since several studies have showed that breeding success might be the most important factor determining the forest grouse abundance (Helminen & Riistantutkimuslaitos 1963; Rajala 1974), I examined if the population size correlated with reproduction. Because reproduction correlated positively with the total counts (See Appendix B; $r > 0.377$ for Hobøl and $r > 0.310$ for Sjøliseterberget), I proceeded with analyses of reproduction only, to facilitate a mechanistic understanding of forest grouse population dynamics. To investigate if there were long-term trends (constant increase or decrease) in reproduction I made a linear

regression model with reproduction as response variable and year as a continuous predictor variable. The analysis was performed on each species and study area separately because of a longer observation period in Sjøliseterberget than Hobøl.

2.4.2 Habitat Selection and Temporal Trends in Logging in Sjøliseterberget and Hobøl

To investigate if capercaillie prefer old forest while black grouse prefer younger successions in the study areas, I performed chi square test statistics. The test checked whether the proportion of used habitat was different from the percentage of available habitat from the random registrations, meaning that the forest grouse chose some forest age classes and avoided other. In this analyse one observation was counted, independent of number of grouse, as one registration in the specific age class, rather than counting number of forest grouse in each observation. This is due to the numbers of forest grouse in a group not being independent, since the brood most often stays together and/or with the hen.

To test if the percentage of old forest have changed over time, I used linear regression with age class 4 and 5 & 6 (Table 1) separately as a function of age. These age classes contain medium old and old forest. A change in these classes over time could mean a change in forest composition and succession stages. The random registrations in age class 4 and 5 & 6 were divided by all random registrations the same year. The result was presented as annual percentage of age classes falling into class 4 and 5 & 6 separately.

To examine the forest grouse's preferences for forest age had changed during the time of study, I used logistic regression, where used (1) and random point (0) were set as a response variable and forest age class (two levels; young and old) and year and their interaction was used as fixed effects. The young age class was defined as 1, 2, 3 and 4 and old forest as class 5 & 6 (Table 1). Year was analysed both as a continuous and factor variable (divided into two categories - early and late years). The period 1991 to 2000 was defined as early years and 2003-2016 as late years.

2.4.2 Causes of Annual Variation in Forest Grouse Reproduction

The weather hypothesis and the alternative prey hypothesis were tested with relevant variables both through model selection and as single predictor variables after predictions in Introduction section. All analyses were performed with reproduction combining data from all species, included unknown (see Materials and Methods section; 2.3.1.1 Species Registration). The reason for this, was to get a higher sample size and due to uncertain reproduction estimates for each area each year.

The candidate predictor variables considered were differentiated vole population, differentiated red fox population, temperature in June, precipitation in June and NAO_{MJJ} . Candidate predictor variables

were checked for co-linearity, by performing a correlation test using the `cor`-function in R (R Core Team 2014). All correlation coefficients were below the critical threshold value of 0.5 (Lewis 2009) (see Appendix D; Table D1 and D2 for correlation coefficients). I performed a stepwise regression with forward model selection based on AICc (Akaike information criterion corrected) because of the quite low sample size. The AIC criteria evaluates how much the model improves when introducing an effect at the expense of degrees of freedom (Anderson et al. 1998). In the forward selection procedure, the first variable included was the one with highest F value (and lowest p-value) in univariate analysis. The second variable included was the most significant variable after accounting for the effect of the first variable etc. This procedure continued until none of the new added predictor variable were significant. Due to a relatively low sample size we a priori set a limit of maximum 3 predictor variables. Analyses for each species and each site was run separately. Since no tested predictor variables seemed important for explaining variation in reproduction of forest grouse in Hobøl (p always > 0.05), I continued with further analyses only in Sjøliseterberget.

To test the alternative prey hypothesis, I used linear regression and made time delayed variables. I tested if increases and decreases in the vole population (differentiated time series) in year t correlated with a change in the fox hunting bag (our proxy of density) of red foxes (differentiated time series) the year after ($t+1$). The vole population was set as predictor variable, while fox population were the response variable. Further, I tested if a change in red fox density (differentiated) in year $t+1$ was negatively correlated with forest grouse reproduction the same year ($t+1$). Reproduction of forest grouse was set as response variable and fox population was set as predictor variable. I additionally tested if the vole population had direct positive effect on reproduction of forest grouse in year t , and if there was a negative effect the year after ($t+1$). Due to lack of significance (p always > 0.05) between vole population and reproduction, I moved on to examine if covariation between voles and forest grouse reproduction was dependent of a high fox population. The time series were divided into two parts; during the sarcoptic mange and before/after. In Sjøliseterberget the sarcoptic mange was defined to year 1983-1994, while 1975-1982 and 1995-2016 were defined as years without the mange. In these latter analyses reproduction of forest grouse was set as response variable and vole population as predictor variable.

To investigate whether reproduction was affected by weather, I examined if a high summer temperature gave a direct positive effect on reproduction of forest grouse, and if a high precipitation gave the opposite effect; low reproduction. I also tested if NAO_{MJJ} gave a positive effect on reproduction. In linear models, reproduction was set as response variable for all analyses and temperature in June, precipitation in June and NAO_{MJJ} was set as predictor variables.

3 Results

A total of 1123 capercaillie, 952 black grouse and an overall of 2998 forest grouse were registered in Sjøliseterberget during the time of study (1975-2016). In Hobøl 615 capercaillie, 392 black grouse and a total of 1311 forest grouse were registered (1987-2016). The number of random habitat registrations conducted, were 1646 in Sjøliseterberget and 980 in Hobøl from year 1991-2016. Both species fluctuated in population size as seen in Figure 3; Sjøliseterberget (Figure 3A) and Hobøl (Figure 3B). Despite the short-term fluctuations, there were no long-term decline or increase for capercaillie (estimate= -0.00607, SE= 0.0196, p= 0.758; Fig 3A) or black grouse (estimate= 0.00670, SE= 0.0211, p= 0.752; Fig 3A) in Sjøliseterberget. Lack of a long-term trend was also the case in capercaillie (estimate= -0.0554, SE= 0.0288, p= 0.0653; Fig 3B) and black grouse (estimate= -0.0298, SE= 0.0225, p= 0.195; Fig 3B) in Hobøl.

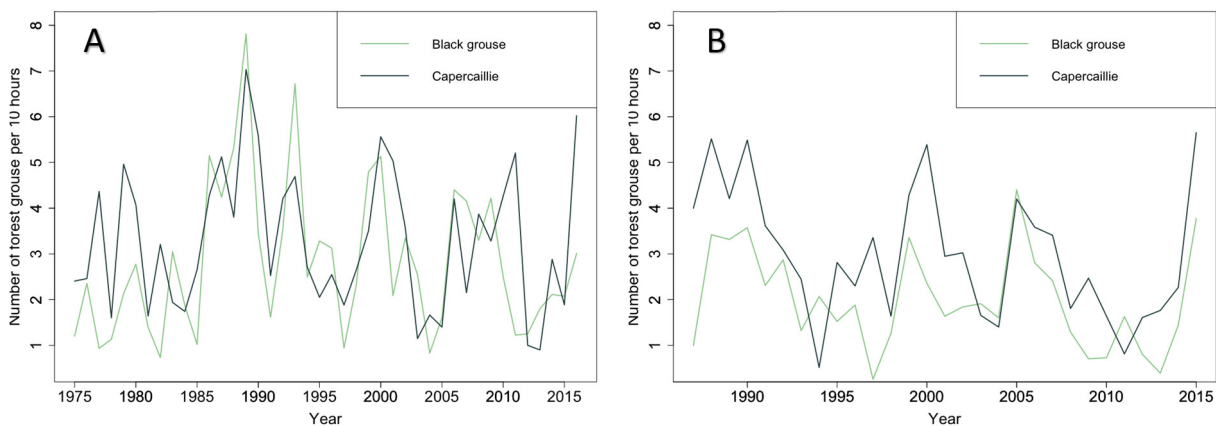


Figure 3 Number of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) observed per 10 hours in **A**) Sjøliseterberget from year 1975-2016 and **B**) Hobøl from year 1987-2016. Results are conducted from a line transect method.

3.1 Temporal Trends in Forest Grouse Reproduction

The total population of forest grouse was significantly correlated with reproduction ($r > 0.377$ for Hobøl and $r > 0.310$ for Sjøliseterberget; both $p < 0.05$; see Appendix B). Since this vital rate can tell us more about the mechanisms of population dynamics, I proceeded with reproduction instead of total number of forest grouse per 10 hours. I investigated if reproductive success differed between the two study areas over time. The reproduction for capercaillie in Sjøliseterberget showed a significant decline of about 55,4 % from the beginning of the study to the end (estimate=-0.00263, SE=0.00100, $p=0.0123$; Figure 4A). This contrasts with Hobøl (Figure 4B), where the reproduction has been more stable over the years (estimate=-0.00139, SE=0.00240, $p=0.566$). For black grouse in Sjøliseterberget the reproduction was unchanged (estimate=-0.000212, SE=0.00139, $p=0.88$; Figure 4C), while black grouse the reproduction declined 70.5 % in Hobøl (estimate=-0.00442, SE=0.00191, $p=0.0291$; Figure

4D). My prediction (P1) is thus only partially supported, due to declining reproduction in only populations.

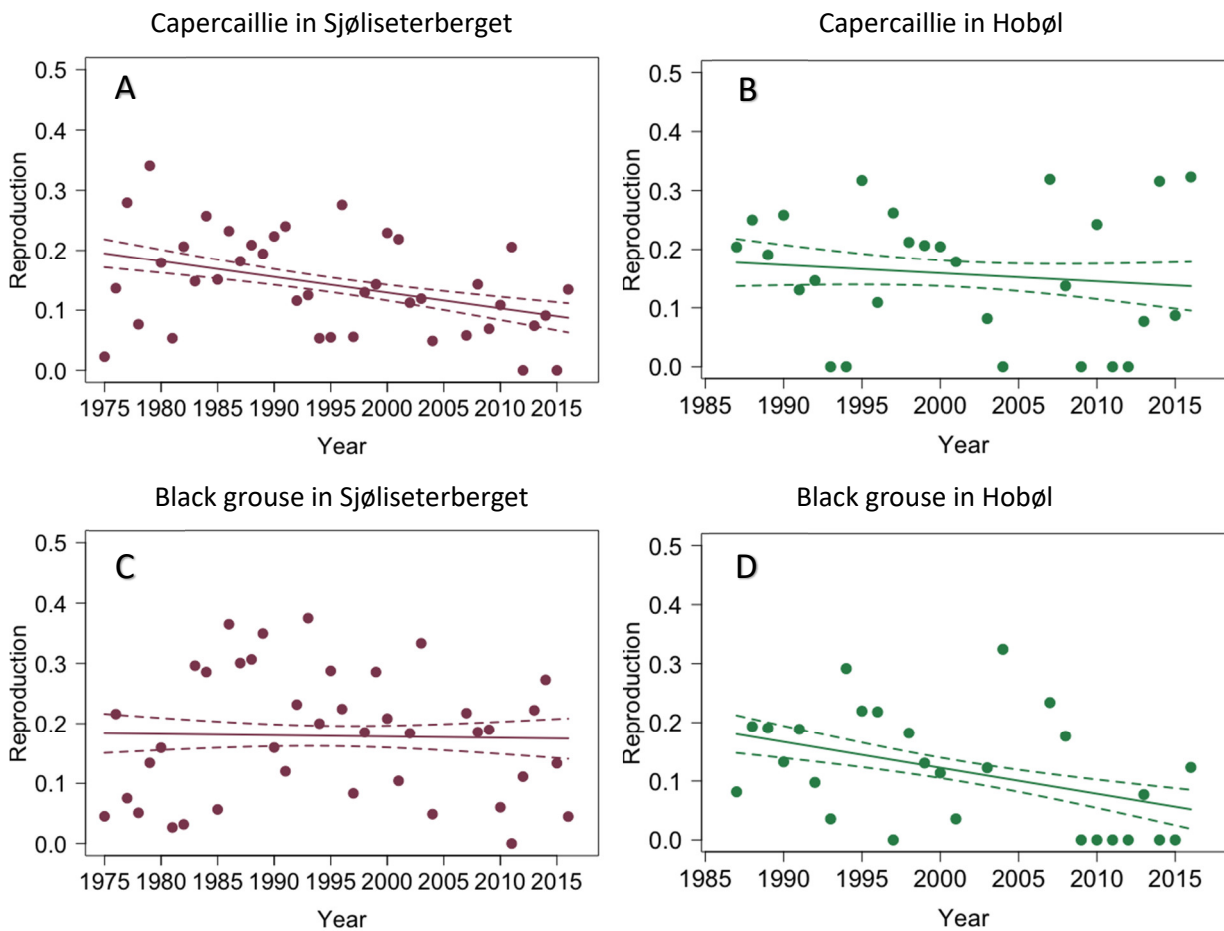


Figure 4 Trends in reproduction over time in capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) in Sjøliseterberget and Hobøl. Points are annual estimates of reproduction. Solid lines are slopes from a linear regression and stippled lines are associated standard. **A)** Reproduction of capercaillie in Sjøliseterberget. **B)** Reproduction of capercaillie in Hobøl. **C)** Reproduction of black grouse in Sjøliseterberget. **D)** Reproduction of black grouse in Hobøl.

3.2 Habitat Selection and Temporal Trends in Logging in Sjøliseterberget and Hobøl

One of the possible causes of declining population could be an alteration in habitat choice, I therefore proceeded with tests regarding their habitat preferences and change in habitat offer.

3.2.1 Habitat Preferences

The distribution of the forest age classes was quite similar in the two study areas (Figure 5). It was least of age class 1 & 2 and 3 and it went gradually up to age class 5 & 6. Capercaillie showed preferences for some age classes and choose to avoid others in Sjøliseterberget ($\chi^2=52.7$, $df=3$, $p<0.001$). Age class 5 & 6 was used the most with 10.5 % more than expected (Figure 5A). Age class 4 was also preferred and used 4.6 % more than expected. Further, age class 1 & 2 and 3 were avoided

and used respectively 10.6 % and 4.5 % less than expected. For capercaillie in Hobøl preference was also highly significant with $p < 0.001$ ($\chi^2 = 24.87$, $df = 3$; Figure 5B). The capercaillie in Hobøl had an even stronger preference for old forest (age class 5 & 6) than in Sjøliseterberget, and used this class 13.9 % more than expected. This was the only preferred forest age class. Class 1 & 2, 3 and 4 was used 5.7 %, 3.0 %, 5.2 % less than expected. Although black grouse in Sjøliseterberget tended to use age class 4 9.2 % more than expected, there was just a tendency for selection suggesting that forest age classes are used proportional to availability ($\chi^2 = 6.68$, $df = 3$, $p = 0.0829$; Figure 5C). The black grouse in Hobøl selected forest age classes almost similar to the one in Sjøliseterberget, but with significant result ($\chi^2 = 12.19$, $df = 3$, $p = 0.00676$; Figure 5D). It showed preference for both age class 4 which was used 10.04 % more than expected. Age class 5 & 6 was much used, but not preferred and 7.13 % less used than offered. Age class 1 & 2 was 6.01 % less used than expected.

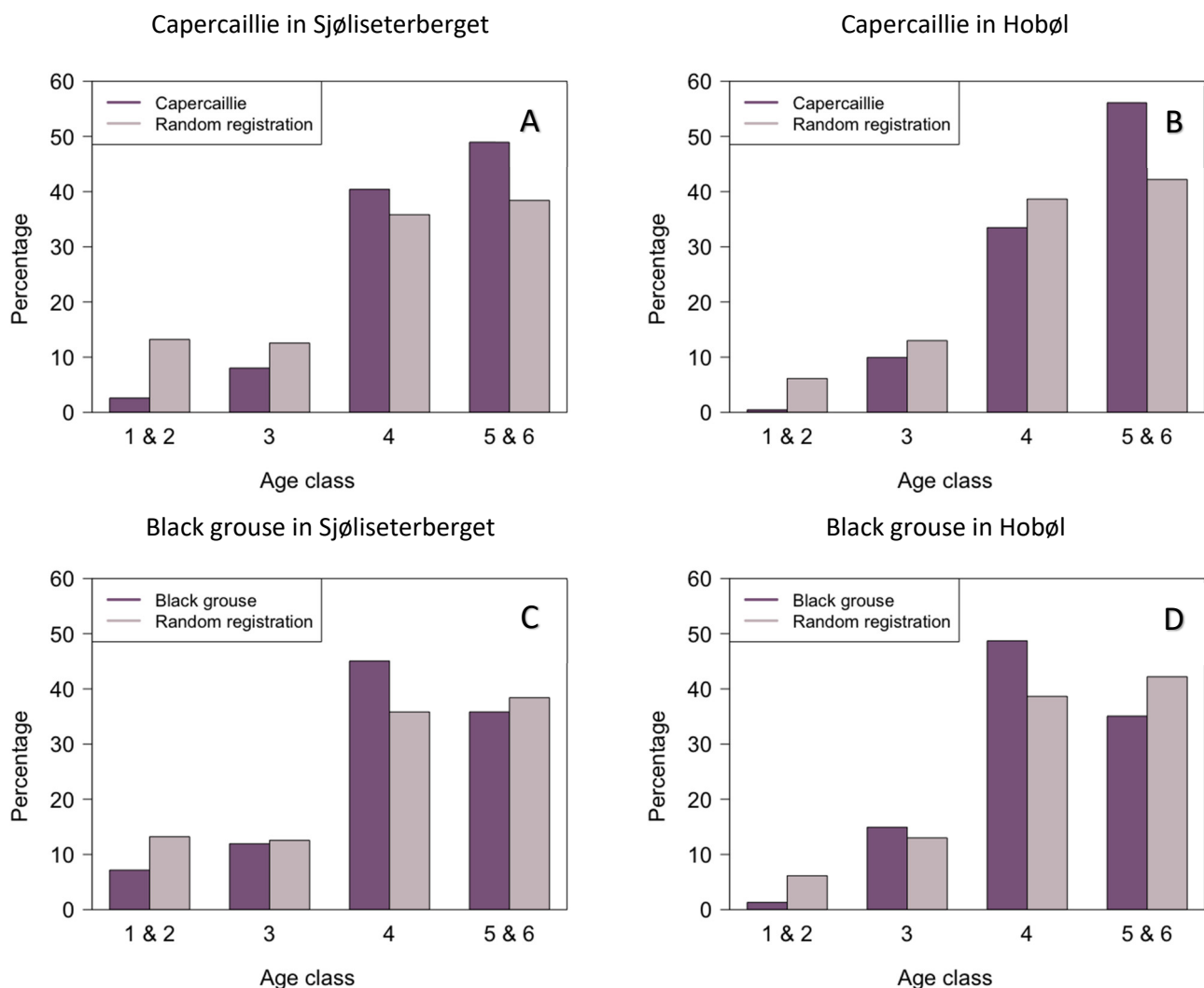


Figure 5: Distribution of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) in different age classes relative to random registrations, where **A**) is capercaillie in Sjøliseterberget, **B**) is capercaillie in Hobøl, **C**) is black grouse in Sjøliseterberget, **D**) is black grouse in Hobøl. The dark purple bar shows the percentage of forest grouse species in the specific age class and the light purple bar shows the percentage of age class registered randomly.

3.2.2 Temporal Trends in logging

Based on habitat description on random sites, where the proportion of old forest (class 5&6) in Sjøliseterberget (estimate= 0.00326, SE=0.00227, p=0.165; Figure 6A) and Hobøl (estimate= - 0.00104, SE= 0.00277, p= 0.713; Figure 6B), and the proportion of medium old forest (class 4) in Sjøliseterberget (estimate= 0.00320, SE= 0.00204, p=0.133; Figure 6C) and Hobøl (estimate=0.00313, SE=0.00292, p=0.303; Figure 6D), the trend in forest age structure was absent (p always > 0.133). In contrast to my prediction (P2), the key habitat of black grouse, and especially capercaillie have not seemed to decline. (In all classes the change over time was limited with a maximum change of 8 %)

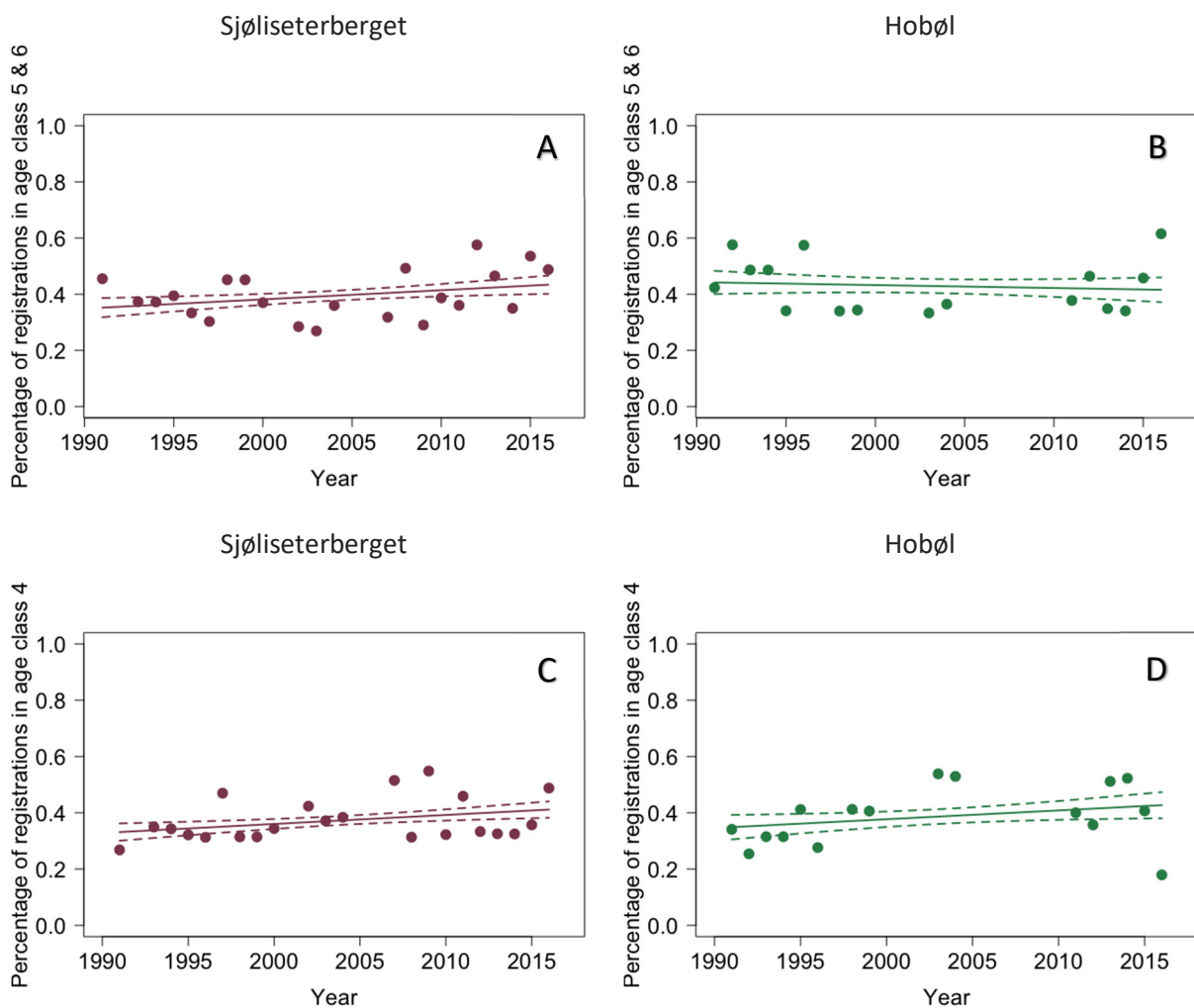


Figure 6 Percentage of registrations of a specific age class each year in Sjøliseterberget (purple) and Hobøl (green) from 1991-2016. Points are annual percentage of registrations of the specific age class in the different areas. Solid lines are slopes from a linear regression and stippled lines are associated standard errors. **A)** Percentage of registrations in age class 5&6 (old forest) in Sjøliseterberget. **B)** Percentage of registrations in age class 5&6 (old forest) in Hobøl. **C)** Percentage of registrations in age class 4 (medium old forest) in Sjøliseterberget. **D)** Percentage of registrations in age class 4 (medium old forest) in Hobøl.

3.2.3 Temporal Trends in Habitat Selection

Change in habitat preference over time was examined with logistic regression. The interaction between period of time (early and late years) and use of specific age classes (old and young) were never significant (p always > 0.28 ; Table 2), meaning there were no change in choice of habitat over time, in contrast to my prediction (P2b). Due to no change in habitat and no change in habitat choice my prediction (P2) is rejected.

Table 2 Result from the logistic regression showing change in preference over time. Age classes were divided into two groups; young forest (age class 1 & 2, 3 and 4) and old forest (5 & 6). Year was analysed both as a continuous and factor variable (divided into two categories - early and late years). The period 1991 to 2000 was defined as early years and 2003-2016 as late years.

Variable	Estimate	SE	<i>t</i>	<i>P</i>
a) Capercaillie in Sjøliseterberget				
Intercept	-1.77	0.102		
Age class, old	0.481	0.147	3.27	0.00107
Year, late years	0.407	0.162	2.51	0.0122
Age class, old : year, late years	-0.114	0.240	-0.477	0.634
b) Capercaillie in Hobøl				
Intercept	-1.54	0.127		
Age class, old	0.767	0.170	4.53	<0.001
Year, late years	-0.143	0.210	-0.678	0.498
Age class, old : year, late years	-0.315	0.294	-1.073	0.283
c) Black grouse in Sjøliseterberget				
Intercept	-1.75	0.102		
Age class, old	-0.130	0.169	-0.767	0.443
Year, late years	-0.0100	0.180	-0.056	0.956
Age class, old : year, late years	0.0957	0.297	0.322	0.748
d) Black grouse in Hobøl				
Intercept	-1.55	0.127		
Age class, old	-0.227	0.210	-1.081	0.280
Year, late years	-0.284	0.220	-1.289	0.197
Age class, old : year, late years	0.140	0.358	0.390	0.696

3.3 Factors Explaining Annual Variation in Forest Grouse Reproduction

From the stepwise regression process considering both predictor variables linked to weather and predation in the same model (Table 3), the best model explaining annual variation in reproduction in Sjøliseterberget included effects of annual change in red fox population between years in Hedmark and temperature in June (Table 4). In this model, an increased fox population gave a lower reproduction in forest grouse, while an increased temperature in June had a positive effect on reproduction. In Hobøl the best model explaining annual variation in reproduction was annual change in vole population between years (marginally better than the intercept model; Table 5). An

increase in vole population from one year to another indicated an increase in reproduction, but only as a non-significant trend (Table 6).

Table 3 Model selection for linear models for annual variation in reproduction in Sjøliseterberget. Model selection criteria are based on AIC values and the best model has the lowest AIC and highest rank. Models are ranked after the step-wise inclusion of new variables.

A) Model structure	k	AICc	deltaAICc	AICc weight	Rank
1) Precipitation June	3	-37.6	10.0	0.00450	7
2) Intercept	2	-39.7	7.93	0.0128	6
3) Vole population(diff)	3	-40.1	6.55	0.0256	5
4) NAO _{MJJ}	3	-41.2	6.43	0.0273	4
5) Temperature June	3	-41.6	6.00	0.0337	3
6) Fox population (diff)	3	-45.4	2.27	0.218	2
7) Fox population (diff) + Temperature june	4	-47.6	0.00	0.678	1

Table 4 Test statistics for the most supported model in Sjøliseterberget. Overall model results: $R^2=0.293$, $p=0.00276$

B) Summary statistics Source	Effect	SE	F	P
Intercept	0.0545			
Fox population (diff)	-0.107	0.0359	9.39	0.00425
Temperature June	0.0300	0.0138	4.70	0.0373

Table 5 Model selection for linear models of annual variation in reproduction in Hobøl. Model selection criteria are based on AIC values and the best model has the lowest AIC and highest rank. Models are ranked after the step-wise inclusion of new variables.

Model structure	k	AICc	deltaAICc	AICc weight	Rank
1) Fox population (diff)	3	-14.1	3.06	0.0768	6
2) Temperature June	3	-14.4	2.75	0.0894	5
3) Precipitation June	3	-14.4	2.71	0.0912	4
4) NAO _{MJJ}	3	-14.7	2.37	0.108	3
5) Intercept	2	-16.7	0.471	0.280	2
6) Vole population(diff)	3	-17.1	0.00	0.354	1

Table 6 Test statistics for the most supported model in Hobøl. Overall model results: $R^2=0.116$, $p=0.0965$

B) Summary statistics Source	Effect	SE	F	P
Intercept	0.366			
Vole population(diff)	0.00556	0.00321	3.00	0.0965

3.3.1 Alternative Prey Hypothesis

Small rodents in this study, field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*), peaked every fourth year (significant lagged autocorrelation; see Appendix A3; Figure A3c). The vole population density estimate varied from 0 to 32 voles, with an average of approximately 9 voles per 100 trap nights (see Appendix C; Figure C1 for graphical approach). Number of shot red foxes ranged

from 1500 to 9600 with an average 3700 per year (see Appendix C; Figure C2A for graphical approach). To examine if predation was dependent on alternative prey, I first tested if the vole population size had a positive effect on the fox population (Figure 7) as predicted (P3a). In accordance with my prediction, there was a significant positive effect of vole population on fox population (Figure 7), were an increase in vole population gave an increase in fox population in year $t+1$ (estimate=0.0154, SE=0.00614, $p=0.0171$)

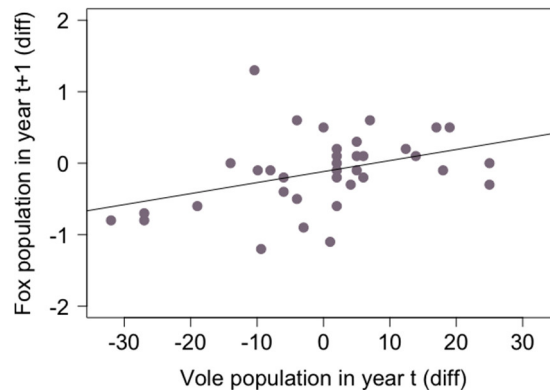


Figure 7 The effect of change in vole population measured in number trapped per 100 trap nights, at Varaldskogen in year t on change in red fox population (*Vulpes vulpes*) the year after ($t+1$) from year 1979-2016. The fox population is estimated by the annual harvest bag in Hedmark county. The vole species include field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*).

In years with increased fox population in year $t+1$, when the vole population have crashed, there was a negative effect of fox population on reproduction of forest grouse in Sjøliseterberget the same year $t+1$ (P3b) (estimate=-0.108, SE=0.0372, $p=0.00596$; Figure 8).

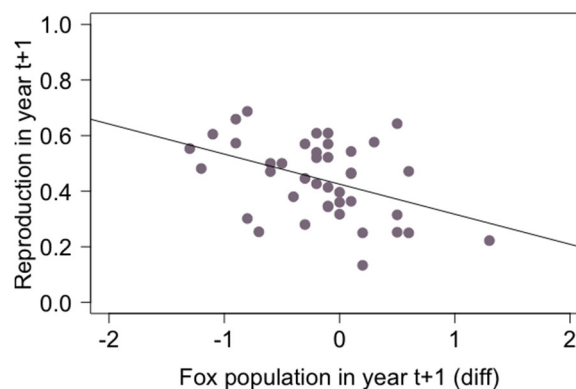


Figure 8 The effect of increase and decline in red fox population (*Vulpes vulpes*) in year $t+1$ on reproduction of forest grouse the same year ($t+1$) in Sjøliseterberget from year 1976-2016.

In order to facilitate interpretation of predation on forest grouse being dependent on alternative prey, I also examined if incline and decline in vole population had effect on reproduction the same year (Figure 9A) and the year after (Figure 9B). I found a near-significant positive relationship the same year (estimate=0.00323, SE=0.00164, $p=0.0567$), but no sign of the expected negative effect the year after (estimate=-0.0000818, SE=0.00175, $p=0.963$).

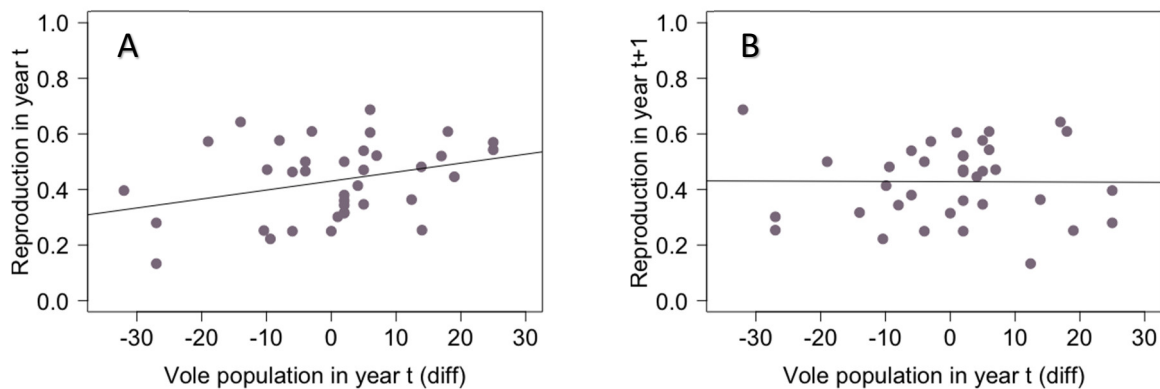


Figure 9 The effect of incline and decline in vole population, including field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*) at Varaldskogen in year t on **A**) reproduction of forest grouse the same year t and **B**) reproduction of forest grouse the year after ($t+1$) Sjøliseterberget from year 1976-2016.

Due to lack of significant effects during the whole time period of my study, I moved on to investigating vole population in time periods during the sarcoptic mange and in periods without it. My prediction (P4a) of no covariation between vole population and reproduction during the sarcoptic mange (Figure 10A and B) was confirmed, showing that without an increase in fox population, an increase in vole population does not positively affect the reproduction the same year t (estimate=0.00223, SE=0.00216, $p=0.326$) or the year after ($t+1$) (estimate=-0.00301, SE=0.00200, $p=0.164$). I also predicted that vole population and reproduction of forest grouse would covary in periods without the sarcoptic mange (P4b), because then there would be an effect of fox population. This was rejected (Figure 10C and D), meaning that an increased vole population had no effect on reproduction the same year t (estimate=0.00372, SE=0.00197, $p=0.0716$) or the year after ($t+1$) (estimate=0.00158, SE=0.00222, $p=0.484$). My prediction (P4) was thus given little support, showing that covariation between voles and forest grouse reproduction was never occurring irrespective of the size of the fox population.

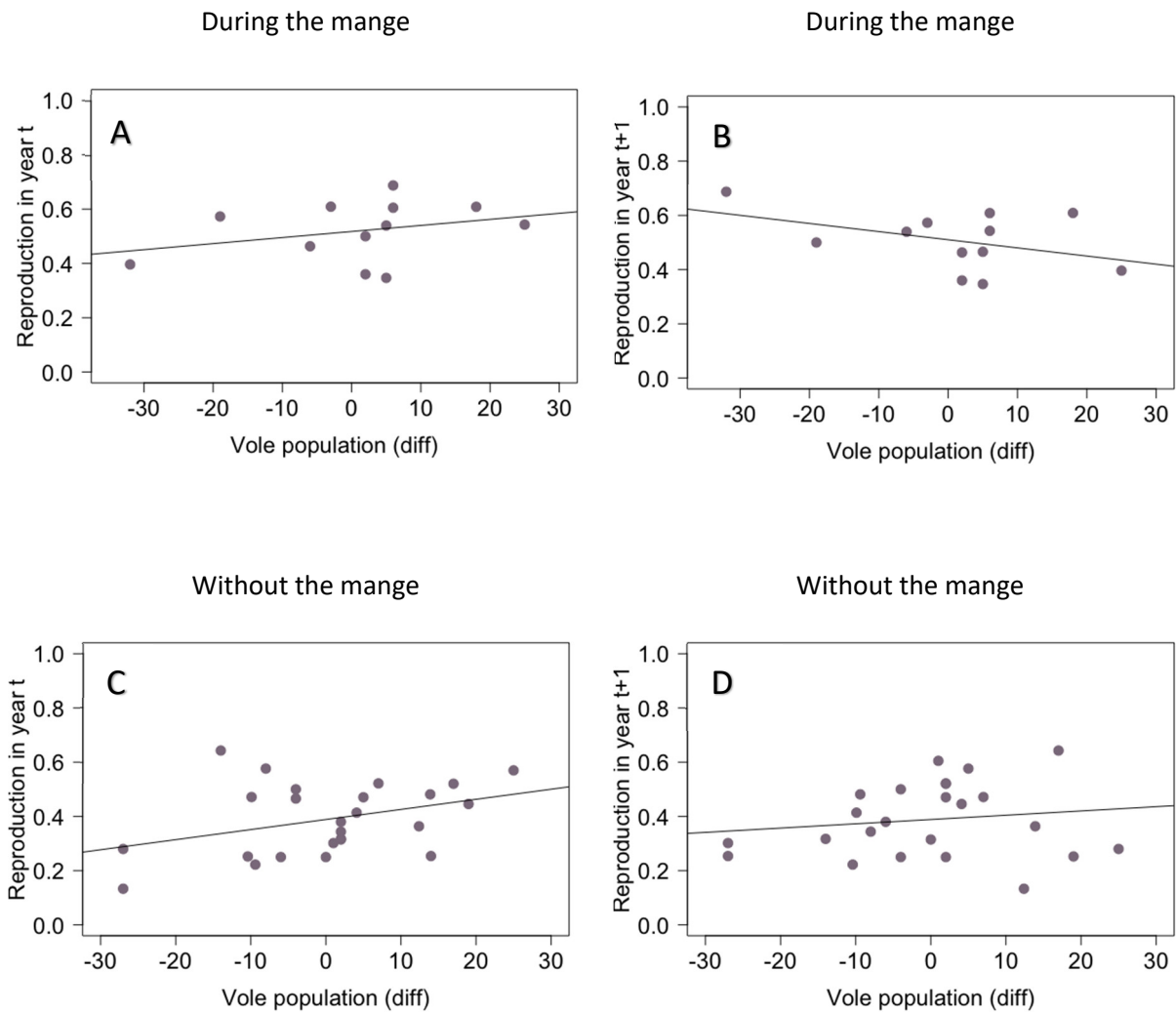


Figure 9 The effect of differentiated vole population in year t and $t+1$ on reproduction of forest grouse in Sjøliseterberget during (A and B) and periods without (C and D) the sarcoptic mange. The sarcoptic mange was set to year 1983-1994, and years before and after was years accounted with a higher fox population density. **A)** year t without mange. **B)** year $t+1$ without mange **C)** year t with mange **D)** year $t+1$ without the mange

3.3.2 Weather hypothesis

The hypotheses of weather included both local temperature and precipitation and seasonal NAO-index. The temperature in June in Sjøliseterberget varied from 9.6°C to 14.9°C, with an average of 12.4°C from 1975-2016. As predicted (P5a), temperature in June had a direct positive effect on reproduction in Sjøliseterberget (estimate=0.0310, SE=0.0151, p=0.0466; Figure 10).

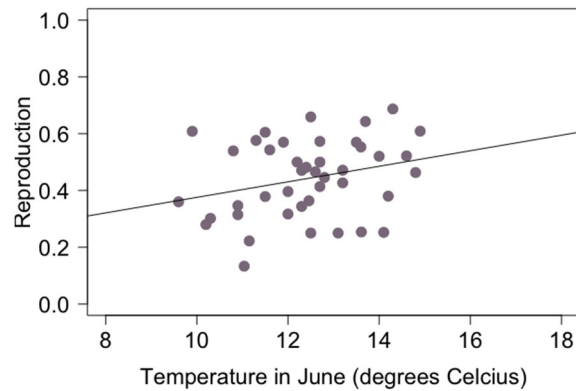


Figure 10 The effect of average temperature in June on reproduction of forest grouse in Sjøliseterberget from 1975-2016.

Precipitation in June in Sjøliseterberget ranged from 8.4 mm to 162.9 mm, with an average 72.2 mm from 1975-2016. Contradicting to my predictions (P5b), the precipitation in the summer had no effect on reproduction (estimate=0.000455, SE=0.000659, $p=0.494$; Figure 11) in Sjøliseterberget.

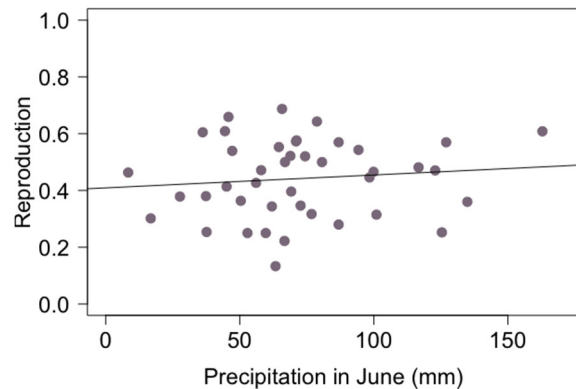


Figure 11 The effect of precipitation (mm.) in June on reproduction of forest grouse in Sjøliseterberget from 1975-2016.

The seasonal NAO-index for May, June and July varied from -3.7 to 2.9 with an average of 0.435. The NAO_{MJJ} had an impact on reproduction (estimate=0.0337, SE=0.0156, $p=0.0368$) in Sjøliseterberget, where a higher value of NAO_{MJJ} gave a higher reproduction (Figure 12) and my prediction (P5c) was therefore confirmed.

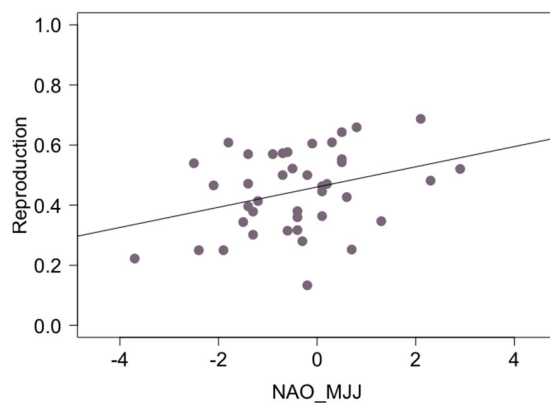


Figure 12 The effect of Seasonal NAO for May, June and July on reproduction of forest grouse in Sjøliseterberget.

Due to precipitation giving no significant effect on reproduction of forest grouse, my prediction (P5) of weather affecting reproduction is only partially approved.

4 Discussion

This study demonstrates that reproduction of some forest grouse populations has declined over the past 4 decades, despite limited change in key habitat. While capercaillie has declined in Sjøliseterberget, which is part of the large, continuous forests at Finnskogen, black grouse have declined in Hobøl which has extensive agriculture close to the forests. Drivers of forest grouse dynamics were explored, where annual change in fox population and temperature in June were the most important factors explaining variation in reproduction in Sjøliseterberget. At the same time, no factors explained the variation in reproduction in Hobøl significantly, possibly due to a lower sample size.

This thesis supports the alternative prey hypothesis considering a large vole population increased the fox population the next year, and this fox population decreased reproduction of forest grouse. Regardless of this two-step link between voles and forest grouse, no significant covariation between vole abundance and forest grouse reproduction was detected, even in periods with a high fox population. Further, this study partially confirms the weather hypothesis showing that local temperature and seasonal NAO-index for the summer, increased reproduction of forest grouse, but there was no indication of effects of precipitation. Together, these analyses provide better understanding of annual drivers causing short-term fluctuations in forest grouse reproduction, as well as negative long-term trends in population dynamics.

4.1 Population Size and Dynamics

Even though the populations of capercaillie and black grouse showed short-term fluctuations, they did not show a long-term decline in Sjøliseterberget and Hobøl. This contrasts with findings of Gregersen & Gregersen (2009), who used hunting bag statistics as an estimate of forest grouse density in all counties of Norway. From 1971-2007 they found a total decline of approximately 35 % for capercaillie and 20 % for black grouse. However, they found the border-counties to Sweden to have the least declines and this includes Hedmark county where Sjøliseterberget is located. Studies have also shown that the density of forest grouse in Europe has fallen dramatically (Ludwig 2007; Storch 2000), where the suggested reasons have been exploitation, predation, human disturbance and climate change. Despite no drastic change in population size, this study verifies that forest grouse reproduction have partially declined (Kurki et al. 2000). In Sjøliseterberget, reproduction of capercaillie had a significant decline from 1975-2016, while reproduction of black grouse declined significantly in Hobøl in 1987-2016, and thus my prediction (P1) is partially confirmed. In line with my results of declining forest grouse populations, an extensive review of Jahren et. al. (2016) reported

declining reproductive output in capercaillie and black grouse over a time period of 80 years in both Fennoscandia and other parts of Europe. Findings showed that despite adult survival trends being positive, the decline in net reproductive output made larger total population declines.

My finding of no long-term decline in population size despite a decrease in reproduction seems at first to be in conflict. Reasons for differences between total population size and reproduction of forest grouse, can be an increased survival of adults or migration. The latter for smaller study areas like these. My study areas may therefore be sink areas, which has been found in coastal forests in Norway (Gregersen & Gregersen 2009). These areas are habitats that are net importers of individuals (Pulliam 1988). In this context, the population are therefore dependent on immigration of forest grouse from other areas to maintain a viable population, and the death rate is thus higher than the reproduction at current state.

4.2 Habitat Selection and Temporal Trends in Logging in Sjøliseterberget and Hobøl

4.2.1 Habitat Preferences

Capercaillie in this study showed preference for certain age classes and chose to avoid others in both areas. They preferred old forest with tree stands over 10 meters, but also used medium old forest with tree height of 3-10 meters, in Sjøliseterberget the latter was also preferred. Further they avoided younger forest in both areas. The preference for older forest and avoidance of the youngest succession stages is consistent with Swenson and Angelstams' (1993) conclusions, but differed as they reported on preference being limited to the oldest forest ≥ 90 years old. Capercaillie in both areas of this study showed preference for forest with tree stands down to 10 meters, which is practically forest down to 40 years old. Seiskari (1962) differentially predicted that female capercaillie would prefer tree stands between 40-80 years old and male capercaillie would prefer those over 40 years (Seiskari 1962) in the winter, and despite the difference in season the results of this study is consistent with his findings.

Black grouse in Hobøl showed a strong preference for young and medium old forest with tree stands from 0.5-10 meters. In Sjøliseterberget black grouse did not show strong preferences, even though the distribution of forest age classes was quite similar. Again, my results partially agree with studies of Swenson and Angelstam (1993), as they both show black grouse's preference for younger forest. On the other hand, they differed on findings showing black grouse preferences for the earliest succession stages with forest <20 years. Their result therefore included clearcuts and very young forest. In contrast, I found that black grouse did not prefer tree stands below 0.5 meters and clearcuts. However, young to medium old forest with tree stands from 0.5-10 meters was preferred

in Hobøl and are forest below <20 years, so the difference might be due to difference in splitting and defining forest age classes. Another factor that might have influenced the difference between my result and Swenson and Angelstam (1993) are types of forestry. Despite their examination of both natural and managed forest, the forestry practices may have been different, such as thinning, clearcut and replanting practices. There is also a greater proportion of young forest in an intensively managed forest, but my findings clearly show that the forest which is defined as very young in this study, composed less than 14 % in Sjøliseterberget and below 7 % in Hobøl (age class 1 & 2). For black grouse, which prefer younger forest than capercaillie, the biotope conditions can have changed in a direction where the young forest has gotten too dense, resulting in less ground vegetation. On the contrary, Seiskari (1962) predicted black grouse to prefer tree stands between 20-60 years old, which is more in line with my results (age class 3-6). Since habitat use depend on availability (Myrsterud & Ims 1998), the different selection patterns may be caused by differences in availability of old-growth forest.

4.2.2 Temporal Trends in Logging and Habitat Selection

In disagreement with my prediction (P2), key habitats of capercaillie and black grouse in the study areas have not changed, meaning that there were no significant trends in logging over time in neither old forest (age class 5 & 6) nor medium old forest (age class 4), or change in habitat selection. Old forest in this study is tree stands down to 10 meters (40-50 years), whereas medium old forest contains forest down to 3 meters (10-40 years). This indicates that the age structure of the forest has been quite stable during the time of study in both areas. This was somewhat surprising, since vegetation types with older deciduous succession and coniferous forest are cut first, as they are the most productive forest and therefore greatly affected by modern forestry (Framstad et al. 2002; Rolstad et al. 2002). However, definition of old forest in this study covers a large age span with all forest over 40 years old. Even though forest over 80 years old can still have declined, this will not be easily detectable in this combined forest age class. Lack of significant decline in long-term trend of forest age classes, can also be explained by the fact that the forest industry has changed over the past decades, trying to take both timber management and biodiversity considerations into account (Spence 2001). Today, ecological sustainable forestry is achieved in varying extent in Fennoscandia (Jahren et al. 2016), and the importance of habitat diversity for chick production in forest grouse is now recognized (Lande et al. 2014). My study therefore contrasts previous studies which show that modern forestry have modified the habitat preferred by forest grouse, causing declining populations (Gregersen & Gregersen 2009; Kurki et al. 2000).

The interesting finding of difference between capercaillie declining in Sjøliseterberget and black grouse in Hobøl, might be due to the two study areas difference in landscape composition. In Hobøl a

large proportion of the land contains settlements and agricultural land, while the forest at Sjøliseterberget is part of a larger, continuous forest. There might thus be differences in forest composition that my analyses were not able to identify, and other factors behind the decline may have interacted with forestry regardless. Aspects of forestry such as decreased patch size, patch connectivity or mosaic-like variability may be more important than decline in forest age (Helle et al. 1987; Lindén et al. 2000). Logging may also disturb dispersal and reduce the amount of suitable food and cover for juveniles (Hannon & Martin 2006), and also a large-scale forest drainage can have negative effects of grouse productivity (Ludwig et al. 2008). Anyhow, recent findings have shown that the habitat structure in Fennoscandia today, do not limit chick production under present-day densities (Sirkiä et al. 2010). The habitat requirements for both capercaillie and black grouse are in the later years also found to not be as strict as previously thought (Lande et al. 2014). My study therefore shows that when the age structure is stable some forest grouse populations are still declining. The difference in declining populations thus remains unexplained.

4.3 Factors Explaining Annual Variation in Forest Grouse Reproduction

From the stepwise regression process the best model included effects of difference in fox population and temperature in June in Sjøliseterberget. In this model, difference in fox population explained most of the variance in reproduction of forest grouse, but both variables were highly significant. This together reinforces the assumption of both weather and predation being important to reproduction of forest grouse as earlier findings have shown (Marcstrom et al. 1988; Slagsvold & Grasaas 1979; Summers et al. 2004).

In Hobøl the result was profoundly different and no effects of neither temperature in June, precipitation in June, NAO_{MJJ} , differentiated vole population or differentiated fox population of the reproduction was reported. This large dissimilarity between Sjøliseterberget and Hobøl is most likely to be caused by differences in length of the time series giving Hobøl a much lower sample size, and the different predictor variables in Hobøl are thus not explaining variation in reproduction. Hobøl was therefore excluded from further discussion.

4.3.1 Alternative Prey Hypothesis

An increase in the red fox population had a negative effect on reproduction of forest grouse (P3). A two-step link was established between voles and forest grouse, whereas the first link was between an increased vole population causing an increase in the red fox population the next year, as predicted (P3a). Coinciding with my results, previous studies have shown that since *Microtus* voles are preferred prey by red fox (Henttonen 1989), their abundance increases the red fox population in

a 3-4 year periodic pattern (Angelstam et al. 1985; Englund 1980; Kaikusalo 1982). Since peak vole abundance only lasts one year, the fox population the next year usually coincides with low vole abundance and foxes will switch to an alternative prey (Angelstam et al. 1985). The next link was, as predicted (P3b), established between the red fox population, the year after a vole population peak, and forest grouse reproduction the same year. The red fox had a large negative effect on reproduction of forest grouse. This is in line with the alternative prey hypothesis (Hagen 1952; Lack 1954). It is not necessarily the red fox that actively search for grouse eggs and chicks in these cases (Angelstam 1992; Rolstad & Wegge 1989), since grouse eggs usually are difficult to find and are not occurring in densities high enough to serve as a reliable food source for red foxes (Storaas & Wegge 1985). They rather find the nest randomly (Angelstam 1992; Rolstad & Wegge 1989), as they move larger distances in cases of low vole numbers.

In contrast to my prediction (P4), covariation between voles and forest grouse was not dependent of a high fox population, meaning that there was no covariation in periods before and after the mange (P4b). My findings contradict with Wegge & Storaas (1990), who found that during the low phase and the prepeak year of the rodent cycle, nest loss was mainly determined by the resident number of predators and led by their behavioural response to the prey base. This transfer effect from voles to forest grouse, has also been found in both natural studies with fox population during and after the mange (Lindström et al. 1994), and experimental studies with removal of red fox (Marcstrom et al. 1988). Both the latter studies report that the grouse populations had a positive response showing an increase in breeding success as a result of the low abundance of red foxes. The reasons why this effect was not found, can be due to a too low sample size, inaccuracy in vole population estimates, or the fact that reproduction of forest grouse is combined data of both capercaillie and black grouse. There is still a general perception that the time of breakdown of the rodent cycle matters to the grouse reproduction (Angelstam et al. 1985), but almost all reports on population fluctuations of rodents have been confined to autumn populations. Wegge & Storaas (1990) on the contrary, showed that in some cases, the crash years of voles can happen in the middle of the summer making the predation of eggs and small chicks lower compared to years where the breakdown happens in spring or early summer. In years when the vole population collapse in the middle of the summer, the autumn catch will not reflect the vole population during the time of egg and chick predation. In other words, the vole population estimate can have been inaccurate due to trapping voles only in a very limited time of the year. Further, the forest grouse species combined reproduction estimate, can also affect the outcome. Nest losses have been found to be inversely related to autumn abundance of rodents in capercaillie, but the same study did not find this effect in black grouse (Wegge & Storaas

1990). The combined data can therefore contribute to a lack of significant effect as a result of different responses to rodent abundance.

Despite lack in results connecting vole population directly to forest grouse reproduction, even in period with a high fox population, the strong two-step link between voles and red fox, and red fox and forest grouse together confirms the alternative prey hypothesis.

4.3.2 Weather Hypothesis

Some aspects of weather influenced the reproduction of forest grouse. As predicted (P5a), an increased temperature in June gave a significant increase in reproduction of forest grouse. On the other hand, my prediction of declining reproduction due to increased precipitation received little support (P5b). My analyses are therefore only partially consistent with findings of Marcström (1960), who studied capercaillie in captivity. Marcströms' study showed that chicks had lower nutrient uptake, lower growth rate and lower survival rate in cold and wet summers, compared to dry and warm summers. This has its natural explanation since chicks are precocial and start to forage on their own after they have been hatched. It can therefore be critical if it is cold and wet because the chicks are almost poikilotherm after hatching, meaning that their body temperature alternate with the surrounding temperature. Another suggested reason for high temperature being beneficial to chicks, are the abundance of specific insects (Baines et al. 1996; Wegge et al. 2010). The chicks' main diet consists of insects (Wegge & Kastdalen 2008) and easily digestible plantparts low in fiber their first weeks of life and then gradually switch over to a plant-dominated diet as they grow. Weather and access to food may act in concert, both as the insects are not easily observed by a chick during colder weather, due to insects being inactive, and as the access to food is inhibited in cold and wet weather due to the chicks easily getting cold. Research has demonstrated that low numbers of insects were inversely correlated with the distance the brood moved. These studies were tested on partridges and pheasants (Green 1984; Hill 1985), but can still be highly relevant for this context. Movements over larger distances are energy inefficient and can cause a lower chick survival. The chicks are therefore dependent on being surrounded by a habitat with high insect abundance (Rolstad et al. 1988). For capercaillie and black grouse the time of hatching seems to be correlated with the maximal amount of moth larvae (Baines et al. 1996). Besides the importance of warm and dry weather in June, Moss, Oswald & Baines (2001) also found evidence for temperature in April and capercaillie productivity, and found that when temperature rose more in early April the hens reared more chicks. This is suggested to happen because an increase in temperature makes plants grow faster and more nutrients available and in turn improving the hens' health. This implies that temperature is not only important for the period when the chicks' hatches, but also for the whole nesting period.

Increased precipitation had no effect on reproduction of forest grouse, and this was somewhat surprising, and in contrast to e.g. Slagsvold & Grasaas (1979). Other findings have shown that the number of chicks reared by capercaillie was inversely related to the number of days with rain during and just after hatching, but rain had no detectable effect on breeding success of black grouse in the same study area (Moss 1986). The combined data of forest grouse in the present study might therefore cause the lack of significant result. While the capercaillie chicks' response to rainy weather is well documented, the effect of black grouse chicks has limited documentation.

The seasonal NAO-index for the spring and summer months (May, June and July) had a significant positive effect on reproduction, as predicted (P5c). A positive NAO_{MJJ} gives dry and warm weather in the summer. These are conditions that will benefit the chicks. Kvasnes et al. (2014) found that recruitment of juveniles in willow ptarmigan was more related to large-scale climate than local climate. In addition, he found this climate effect to be stronger than the effect of rodent abundance. In contrary, my model selection chose local temperature in June as more important than NAO_{MJJ} in Sjøliseterberget, but then again, I found no correlation between local weather variables and the seasonal NAO-index, like he did.

5 Conclusions

This study shows that reproduction in some of the capercaillie and black grouse populations in my two study areas have declined, which may be caused by a combination of factors. Surprisingly, there were no change in forest age structure over time, but the possibility that other factors connected to forestry can have changed the habitat cannot be excluded. Even though these study areas did not change in age structure, the reproduction of capercaillie declined in Sjøliseterberget and black grouse declined in Hobøl. Annual variation in reproduction of forest grouse was in Sjøliseterberget explained by temperature in June and difference in fox population from one year to another, while no variables seemed to explain the variation in reproduction in Hobøl. The lack of significant result in Hobøl were suggested to be due to lower sample size.

The alternative prey hypothesis was confirmed based on findings linking an increased vole population one year to an increased fox population the year after, and further this fox population to a decreased reproduction of forest grouse the same year. This enhances the suspected negative effect the fox population has on forest grouse reproduction, despite lack of direct correlation between vole population and reproduction of forest grouse. In addition to predation, weather in the summer had large impact on reproduction. The weather hypothesis was partially confirmed showing that especially increased temperature in June and seasonal NAO-index led to increase in reproduction.

We know for certain that numerous of forest grouse populations are declining in Europe. Increased awareness and knowledge about forest grouse species and about the consequences in long-term changes in key habitat, as well as short-term fluctuations caused by annual drivers are therefore important. Although many links in the argument remain to be tested, it is safe to suggest that both management of fox populations and encouraging to sustainable forestry might help the forest-dwelling species both now and in the future.

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7 Appendices

Appendix A

Autocorrelation was run of all variables to check for repeating patterns in the time series.

A1: Autocorrelation of age classes of the forest

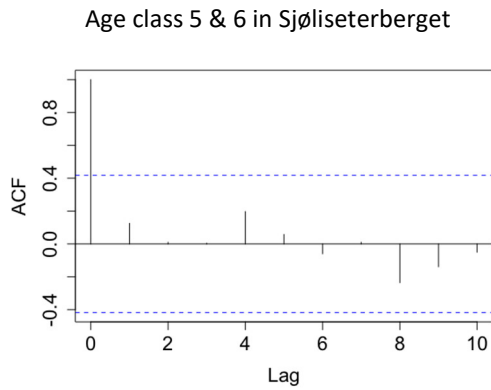


Figure A1a Autocorrelation of random registrations of age class 5 & 6 of over time in Sjøliseterberget ($r < 0.418$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

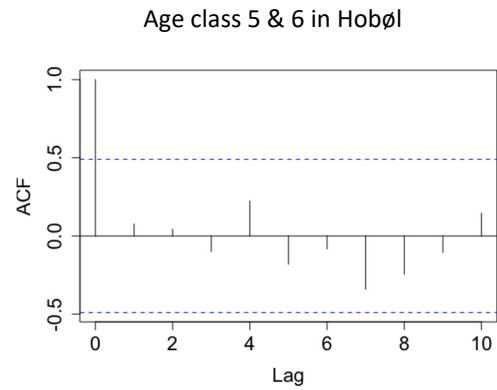


Figure A1b Autocorrelation of random registrations of age class 5 & 6 of over time in Hobøl ($r < 0.490$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.



Figure A1c Autocorrelation of random registrations of age class 4 of over time in Sjøliseterberget ($r < 0.418$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

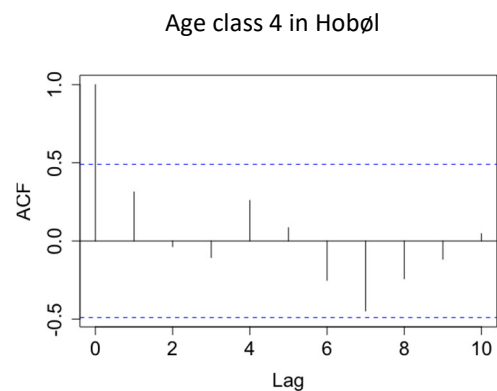


Figure A1d Autocorrelation of random registrations of age class 4 of over time in Hobøl ($r < 0.490$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

A2: Autocorrelation in reproduction of the forest grouse species



Figure A2a Autocorrelation of reproduction in Sjøliseterberget ($r < 0.302$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

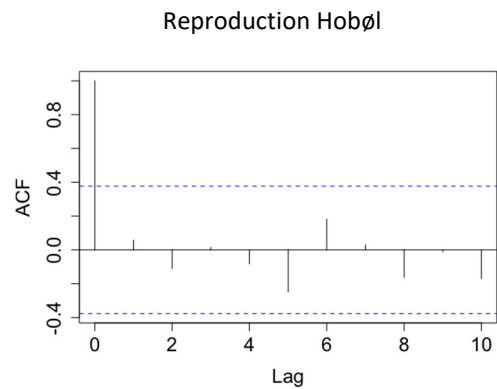


Figure A2b Autocorrelation of reproduction in Hobøl ($r < 0.377$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

A3: Autocorrelation in variables connected to annual drivers

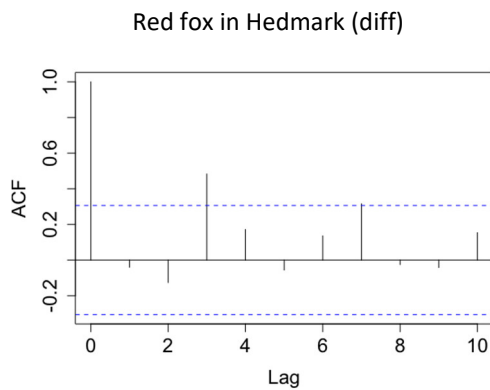


Figure A3a Autocorrelation of difference in fox population from one year to another in Hedmark (Sjøliseterberget) ($r > 0.306$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

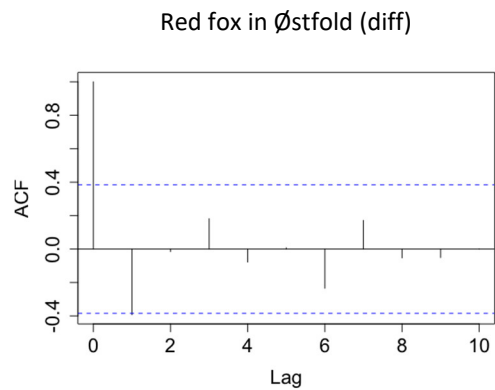


Figure A3b Autocorrelation of difference in fox population from one year to another in Østfold (Hobøl) ($r > 0.384$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

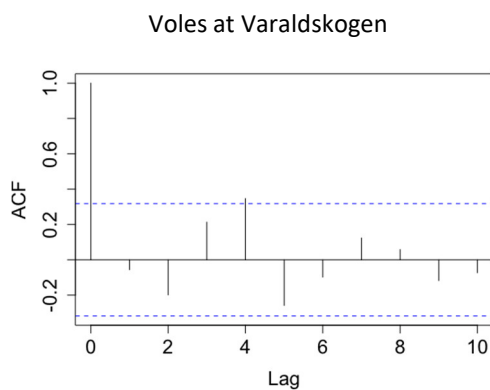


Figure A3c Autocorrelation of field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*) population at Varaldskogen. Every fourth year they had a peak in the cycle. ($r > 0.318$) Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

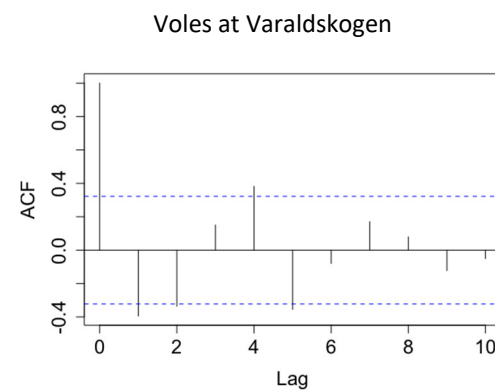


Figure A3d Autocorrelation of differentiated field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*) population at Varaldskogen. Autocorrelation of differentiated voles at Varaldskogen ($r > 0.322$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

Temperature in June in Sjøliseterberget

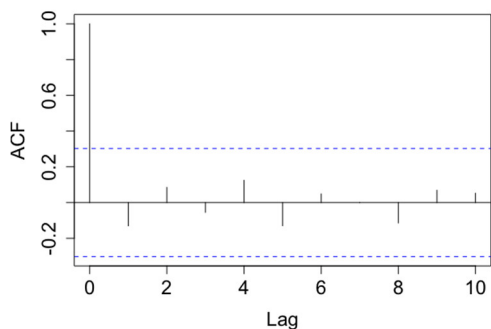


Figure A3e Autocorrelation of temperature in June in Sjøliseterberget ($r < 0.302$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

Temperature in June in Hobøl

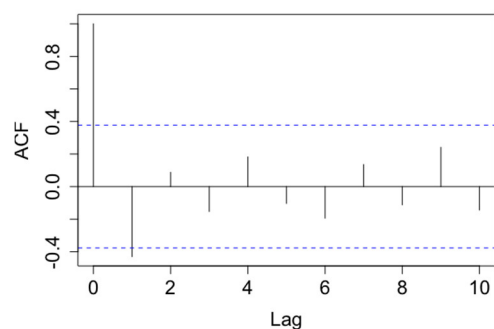


Figure A3f Autocorrelation of temperature in June in Hobøl ($r > 0.377$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

Precipitation in June in Sjøliseterberget

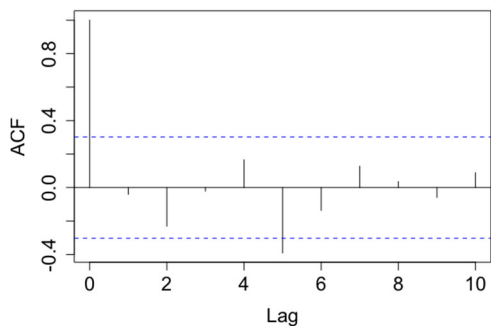


Figure A3g Autocorrelation of precipitation in June in Sjøliseterberget ($r > 0.302$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

Precipitation in June in Hobøl

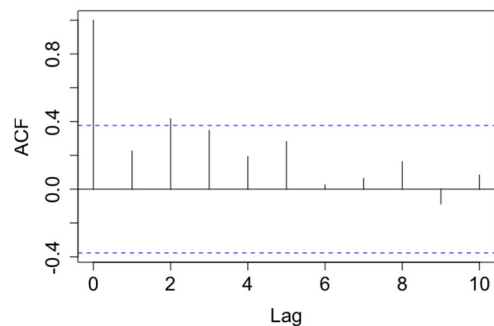


Figure A3h Autocorrelation of precipitation in June in Hobøl ($r > 0.377$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

NAO_{MJJ}

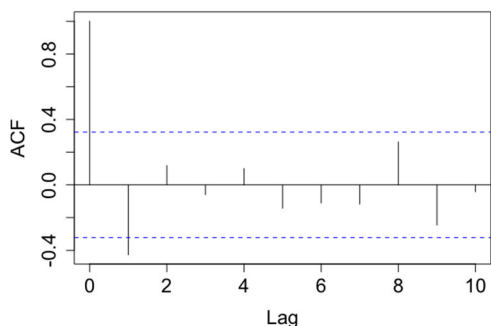


Figure A3i Autocorrelation of seasonal NAO (NAO_{MJJ}) ($r > 0.322$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

Appendix B

The correlation between annual reproduction and total number of birds per 10 hours.

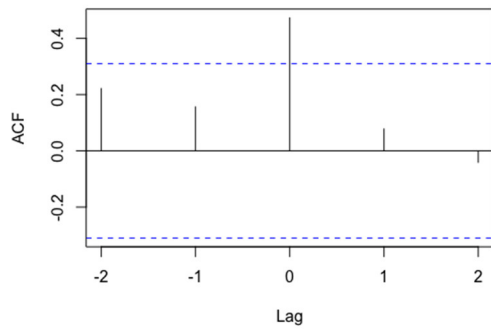


Figure B1 Correlation between reproduction and total number of capercaillie in Sjøliseterberget ($r > 0.310$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

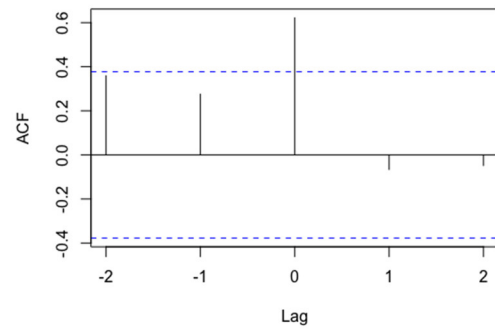


Figure B2 Correlation between reproduction and total number of capercaillie in Hobøl ($r > 0.377$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

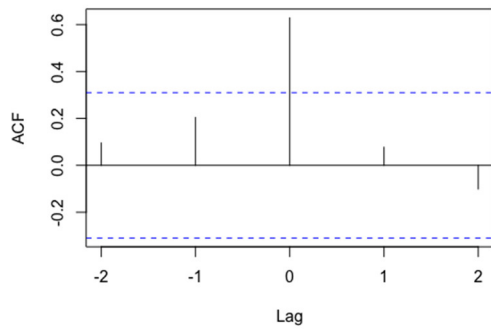


Figure B3 Correlation between reproduction and total number of black grouse in Sjøliseterberget ($r > 0.310$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

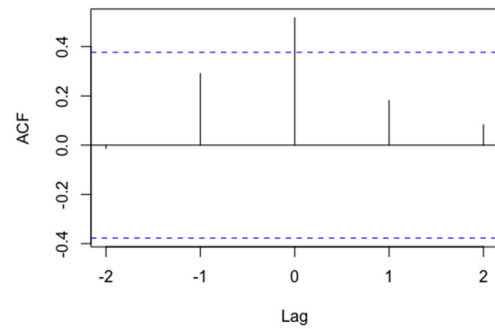


Figure B4 Correlation between reproduction and total number of black grouse in Hobøl ($r > 0.377$). Blue dotted line is the minimum correlation significant at $p=0.05$. Lags are in years.

Appendix C

Time series plots for vole population at Varaldskogen and red fox in Hedmark and Østfold county

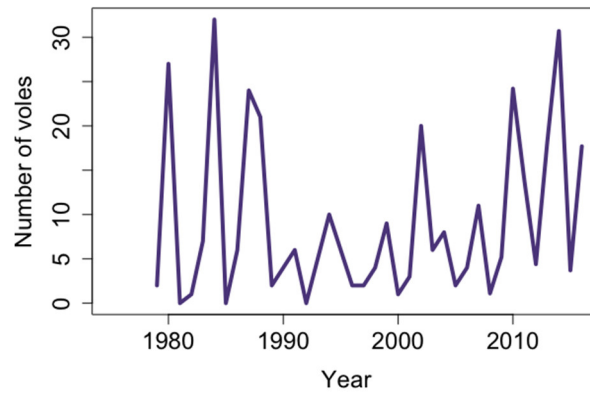


Figure C1 Synchronous vole fluctuations with field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*) at Varaldskogen from 1979. The peaks and crash years of this cycle were as following; peak years in 1980, 1984, 1987, 1991, 1994, 1999, 2002, 2007, 2010 and 2014 and crash years in 1981, 1985, 1989, 1992, 1996, 2000, 2005, 2008, 2012 and 2015. Figure shows average number of voles per 100 trap nights (P.Wegge – unpublished data)

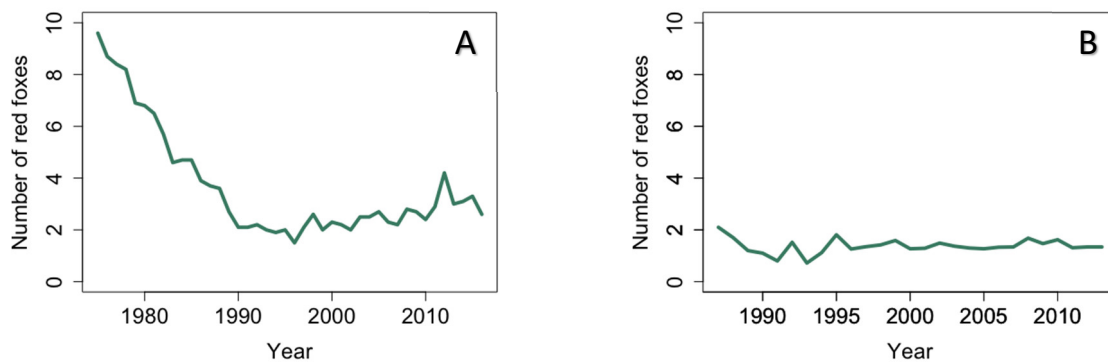


Figure C2 Hunting statistics of red fox as an estimate of red fox population densit. Data are obtained from Statistics Norway and all numbers are divided by 1000. **A)** Hedmark from 1975-2016 **B)** Østfold from 1987-2016

Appendix D

Pearson's product-moment correlation

Table D1 Correlation coefficients for the candidate predictor variables for Sjøliseterberget. All correlation coefficients were below the critical value of 0.5 and all the predictor variables could thus be included in the same model.

Variables	Precipitation in June	Temperature in June	NAO _{MJJ}	Vole population (diff)	Fox population (diff)
Precipitation in June					
Temperature in June	-0.248				
NAO _{MJJ}	0.0780	0.347			
Vole population (diff)	0.272	0.0820	0.235		
Fox population (diff)	0.0746	-0.0430	-0.459	-0.248	

Table D2 Correlation coefficients for the candidate predictor variables for Hobøl. All correlation coefficients were below the critical value of 0.5 and all the predictor variables could thus be included in the same model.

Variables	Precipitation in June	Temperature in June	NAO _{MJJ}	Vole population (diff)	Fox population (diff)
Precipitation in June					
Temperature in June	0.0751				
NAO _{MJJ}	0.156	0.209			
Vole population (diff)	-0.062	0.0396	0.264		
Fox population (diff)	0.115	0.265	0.246	0.0359	



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