Long term trend and short-term dynamics of a willow grouse population

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Abstract

Willow ptarmigan *Lagopus lagopus* and rock ptarmigan *Lagopus mutus*,are abundant in Arctic and tundra regions, but negative trends in their distribution have recently been reported. Rapid climate change has been identified as the cause of this decline. Willow ptarmigan is adapted to harsh winter conditions, and winters with less snow could increase vulnerability when the ground is snow-free. In this study, we used a hierarchical state-space model to analyze 139 km line transects in mid-Sweden over 46 years. We assessed long-term trends in the adult population and estimated the effects of breeding success and climate on short-term changes. Contrary to our expectations, the adult population did not exhibit a negative trend. Breeding success was significantly positive for adult population change, but late spring had a significant negative effect on population change. The number of snow-free days in spring and autumn increased during the study; however, neither variable had a negative effect on adult population change. The adult willow ptarmigan followed a pattern of a stationary population under the influence of both stochastic and density-dependent factors, and changes in adults showed a negative density dependence. Our study area is in the southern range of the tundra, and we suggest that the stable dynamics of the adult population can be explained by a diverse predator assemblage that makes it impossible for the population to escape a top-down regulation.

Keywords: Lagopus lagopus trend population dynamics

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Introduction

Long-term ecological data are important for separating long-term trends and stochastic fluctuations in ecosystem processes (Lindenmayer et al., 2012; Magurran et al., 2010). Analysis of long-term data such as harvest statistics and population counts has provided valuable insights into population dynamics such as periodic fluctuations, demographic time lags, and trophic interactions (Hilborn and Mangel, 1997; Keith, 1963; Royama, 1992). Rapid climate change has been identified as the cause of the decline of several bird species in northern regions (Smith et al., 2020). Two species, willow ptarmigan *Lagopus lagopus* and rock ptarmigan *Lagopus mutus*, are abundant in the Arctic and tundra regions of the northern hemisphere (Storch, 2007). The widely distributed willow ptarmigan is a popular game species, a distribution that extends to moorlands and subarctic forests below the tundra. The need for harvest regulations has been addressed in earlier studies (Aanes et al., 2002; Pedersen et al., 2004; Smith and Willebrand, 1999), and national schemes of line transects with pointing dogs and using distance sampling (Thomas et al., 2010) to estimates densities in Scandinavia have been developed the last 15 - 25 years (Eriksson et al., 2006; Helle et al., 2016; Nilsen et al., 2024).

Willow ptarmigan is adapted to harsh winter conditions when its plumage turns white and snow makes it possible to burrow and be protected from cold weather and predation (Andreev, 1991). However, the ongoing changes in climate expected to result in winters with less snow, which could increase the vulnerability of the white willow ptarmigan on snow-free ground to birds of prey (Melin et al., 2020). In accordance, a recent review of the long-term population trends of willow ptarmigan identified negative trends in parts of its distribution (Fuglei et al., 2020).

The dynamics of willow ptarmigan are characterized by the following demographic features; females begin breeding in their first year, breeding success exhibits large variation between years but is not related to adult abundance (Hörnell-Willebrand et al., 2006). Nest loss and chick mortality have mostly been attributed to predation (Breisjøberget et al., 2018; Steen et al., 1988). It has previously been shown that air temperature after snowmelt is important for the timing of spring, with warmer conditions contributing to earlier phenology in all vegetation communities (Kelsey et al., 2021). Earlier onset of spring with early appearance of new vegetation could positively affect nutritional status and breeding conditions (Brittas, 1988; Erikstad and Andersen, 1983; Marcström and Höglund, 1980).

The recent development of hierarchical state-space models in a Bayesian framework has improved the possibility of analyzing time series of wildlife count data and identifying variables that are important for population change (Bowler et al., 2020; Kéry and Royle, 2016). Such models can also make valuable short-term predictions and support management decisions (Frost et al., 2022; Henden et al., 2020). The aim of this study was to assess the dynamics of the adult segment of the willow ptarmigan population during 46 years in the Lövhögen area, Sweden. One important question was whether we could detect any significant decline in the adult population. Furthermore, we evaluated the relationship between variation in breeding success and short-term adult population changes. Similarly, we estimated the effects of late frost in May and the frequency of snow-free days in spring and autumn on annual changes in the adult population.

Material and methods

Study Area

The study area, Lövhögen 80 km^2, is located in the southern part of (62'N, 13'E) of the Swedish tundra, where the landscape is gradually transformed into continuous boreal conifer forest. The altitude varies between 750 and 1 000 m.a.s.l. and is dominated by birch forest and open tundra (Brittas, 1988). The tree line was about 800 m.a.s.l., and about 20% is wooded mainly with mountain birch *Betula pubescens var. tortuosa*. There are local stands of spruce *Picea abies* and pine *Pinus silvestris* above the tree line and a few scattered willow *Salix spp.* thickets. Almost one-third of the area is peatland, characterised by sedge *Carex spp.*, cloudberry *Rubus chamaemorus* and cotton grass *Eriophorum vaginatum* and *E. angustifolium*. About half of the study area is heathland, dominated by dwarf shrubs such as heather *Calluna vulgaris*, bilberry *Vaccinium myrtillus*, crowberry *Empetrum hermafroditum* and dwarf-birch *Betula nana*. The climate is continental, with temperatures averaging -10 C° in January and snow cover for about 6 months in winter. The corresponding figure for July is +14 C°. There are few lakes, but frequent small creeks drain the area into larger streams. The study area is privately owned by a single landowner, and the harvest of willow grouse is highly restricted (Aanes et al., 2002).

Data

Line transect counts

A permanent line transect count using pointing dogs was established in 1963 to estimate the abundance of adult willow ptarmigan. A total of 18 lines, 600 m apart, with a total distance of 139 km covering the entire study area. The start and end points of each line were marked with permanent poles. These lines have remained unchanged since counts began. In 1963, it was concluded that the perpendicular distance to the observed willow ptarmigan was necessary to estimate the probability of detection. It was assumed that the effective strip width was twice the average detection distance within 200 m of the line. Unfortunately, the distances between 1963 and 1975 were destroyed in a fire that burned down the Boda research station, but the estimated adult densities for that period are still available. The distances were also lost in four later years (1979, 1980, 1985 and 1986). The number of adult observations varied between 73 and 206, with a median of 129 during the study period. The counts are completed within a week, and most members of the team have remained for many years.

The counts were initially made in late June (Period A) but were postponed to late July or early August from 2004 (Period B) when the area was included in the national monitoring program for willow ptarmigan in the mountain region (Eriksson et al., 2006). The application *Distance Sampling* (Thomas et al., 2010) is used to estimate abundance. In the period A late June, the perpendicular distance to all detected adults were registered and sex was determined by plumage and/or behavior. It was not possible to determine the sex of all adults, and the observed ratio of males to females was used to estimate the sex ratio of undetermined adults. In this period, females are usually incubating, and the number of adjusted adult males was assumed to correspond to a pair of two adults. In period B early August, it was possible to observe both adult and brood size in the field.

Brood size

Between 1963 and 1994, brood size was estimated from the age ratio in the harvest, but unfortunately no harvest data were available for the period 1995-2003. It has previously been shown that the age ratio does not change from mid-August to harvest in early September under the harvest regime in the study area(Marcström and Höglund, 1980). From 2004, when counts were made in early August, we used the number of observed chicks per two adults as the average brood size. We used the standardized brood size in the analysis and regressed brood size on vole abundance to obtain data points for missing values, 1995 - 2003, because Jags cannot handle missing data for explanatory variables. The regression that estimated the missing values was included in the JAGS model (see Appendix B).

Vole numbers

Voles were snap-trapped during the same time as the transect counts, which accumulated between 200 and 600 trap nights each year. The logarithm-transformed number of voles per 100 trap night was used as a vole index (Hörnfeldt, 1978), data were standardized for each period and then combined. Three years lacked observations (1976, 1977 and 1990), and the first two years were replaced by the median of the complete time series. The third year was replaced by the average of 1989 and 1991.

Metrological data

Data on snow depth was obtained from the Swedish Meteorological and Hydrological Institute for the Särna station (61.70, 13.13), 437 m.a.s.l. The station is about 28 km southwest of Lövhögen. Data were not available for May in 2000 due to the renovation of the station; therefore, we used the average number of observations for each time and day in May for 1999 and 2001 in the analysis.

The number of snow-free days was extracted for April and May (spring) and October and November (autumn). The number of snow-free days was standardized and included as a covariate of adult change. We extracted the ambient temperatures for all days in May at 03:00 h during the study. The last day with a temperature less than -2.2C° (Schwartz et al., 2006) was used as the index of annual variation phenology. The days were standardized and included a covariate of late spring for adult change.

Analysis

Distance data were prepared for analysis using a cutoff 200 m and a bin width of 20 m. This resulted in 10 distance intervals, where each observation was categorized into a specific distance interval (1-10). During the 48 years in which distances were available we included 3531 distances less than 200 m, corresponding to an area of approximately 55 km^2.

We developed a hierarchical state-space model in JAGS (Plummer et al., 2003) following (Henden et al., 2020; Kéry and Royle, 2016). See appendix. The detection probability was computed in a multinomial model of cell probabilities, assuming a half-normal detection function. The distances for all lines and years were pooled to estimate the detection probability, and no covariates were added to the detection equation. The process model comprises two parts. The first part calculates the initial density in the first year to estimate the observation error. The second part models the population dynamics of subsequent years using a Gompertz model to estimate annual process variation. See appendix B.

We used Markov Chain Monte Carlo (MCMC) methods to estimate the posterior distribution of parameters and adult density estimates. The model was run for 100 000 iterations with a burn-in of 25 000. The thinning was set to 2, and three chains were used to evaluate convergence. The package MCMCvis (Youngflesh, 2018) was used to evaluate the trace plots and posterior distribution of the model parameters. All parameters had an R-hat value less than 1.01. Parameter estimates are presented with a 95% credible interval (Cr. I), and the plot of the estimated time series of adult densities show the 80% highest posterior density. All analyses and graphics were performed in R (R Core Team, 2024) and the JagsUI package was used as an interface to JAGS from R (Su and Masanao Yajima, 2021).

We used the autocorrelation function in the stats package to explore regular fluctuations in the time series of estimated adult densities, breeding success, and vole numbers. The correlation values at different time lags were considered significant when exceeding the 95% confidence interval (C.I.).

Results

Breeding success and vole index

There was a positive relationship between standardized brood size and vole index the same year, slope= 0.376 (95% Cr. I. 0.093 - 0.665). In period A, the standardized chick production showed a strong positive correlation (0.608) four years apart. In the period B, the correlation at lag four was still positive but not significant (0.288). Similarly, the standardised vole data showed a statistically significant positive correlation four years apart (0.302).

Changes in snow-free days and last frost in May

The number of snow-free days in spring and autumn tended to increase during the study but showed large annual variation. The number of snow-free days in spring and autumn was highly correlated (0.693, t=6.51, P<0.001). See figure 1. Due to the high correlation we run the model separately for each variable, in both cases the parameter was positive and significant. We decided to keep snow-free days in autumn in the final model becasue we already had a variable for spring climate. The pattern of late frost in May was initially late, then became warmer from 1981 until 2005 when springs again became late again. The values of last frost was not correlated with snow-free days in spring or autumn, and none of the these indices showed any autocorrelation.

Detectability, observation, and process error

The average probability of detecting willow ptarmigan within the $\pm$200 m strip around the line transect was 0.437 (95% Cr. I. 0.424 - 0.451). This corresponds to an effective strip width of 87.4 m, which is substantially longer than the 63.8 m of the average distance previously used as the effective strip width in period A. The standard deviation of the observation error was larger than the process error, 0.450 (95% Cr. I. 0.021 - 0.963) vs. 0.208 (95% Cr. I. 0.155 - 0.275), but the difference was not statistically significant due to the large uncertainty in the observation error.

Trend, stability and density dependent feedback

There was no trend in the population of adults, and the trend parameter was not significantly different from zero (0.005, 95% Cr. I. -0.008 - 0.019). The average of adults during 1976 - 2023

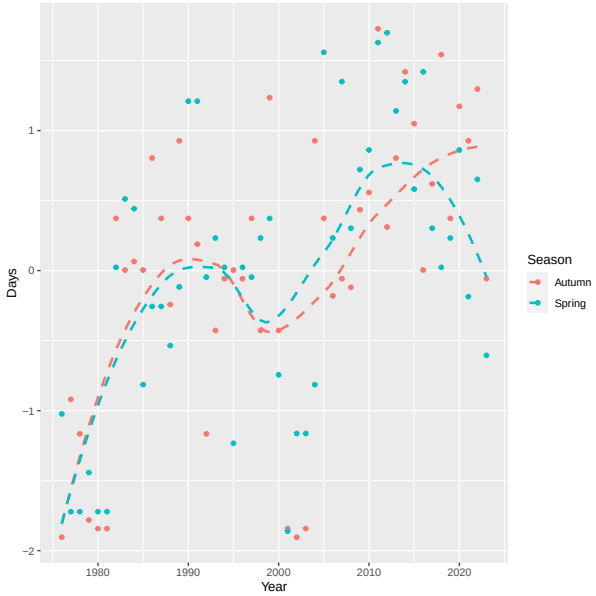

Figure 1 – Standardized values for snow free days in spring (April and May), and autumn (October and November)

Table 1 – Summary of posterior parameter distributions of the model used to estimate population development. The last column list the parameter names of the model presented in appendix B.

Parameter	Mean	SD	2.5%	50%	97.5%	Model
Density Dep	0.019	0.185	-0.354	0.035	0.361	btDD
Pop. Trend	0.005	0.006	-0.006	0.005	0.018	btTREND
Brood Size	0.114	0.052	0.012	0.115	0.215	btCHICK
Late Frost	-0.096	0.044	-0.185	-0.095	-0.011	btFrost
Snow Spring	0.065	0.050	-0.035	0.066	0.163	btSPsnow
Snow Autumn	0.052	0.048	-0.040	0.052	0.149	btAUsnow
Intercept[1]	1.746	0.313	1.192	1.702	2.411	beta0[1]
Intercept[2]	1.293	0.336	0.736	1.249	2.051	beta0[2]

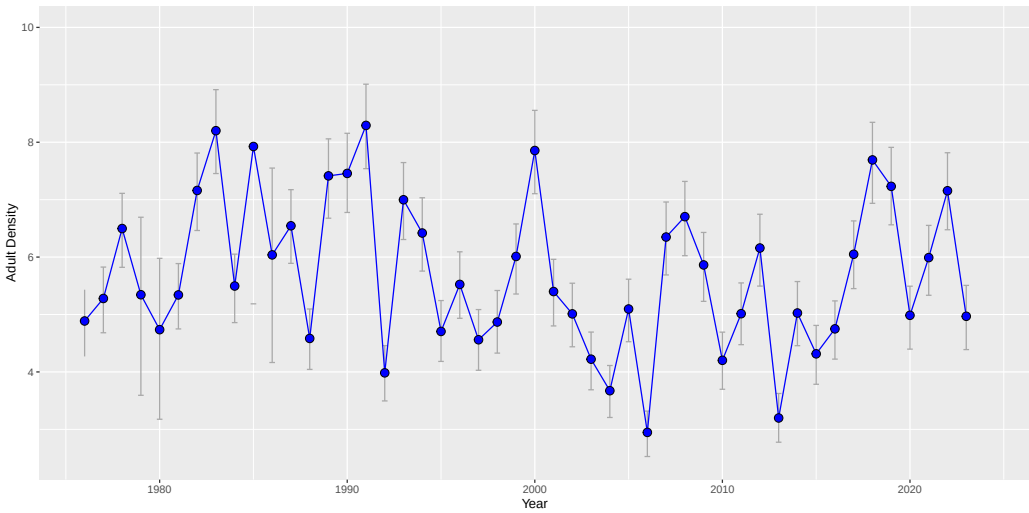

Figure 2 – Estimated adult population sizes during 1976 - 2023. The vertical lines show the 80% highest posterior density intervals

was 5.72 (95% C.I. 5.34 - 6.10), and peaks and lows occurred irregularly. See figure 2. The annual changes in adults showed a negative density dependence; the parameter was significantly lower than 1, -0.003 (95% Cr. I. -0.401 - 0.381). See also table 1 and figure 3.

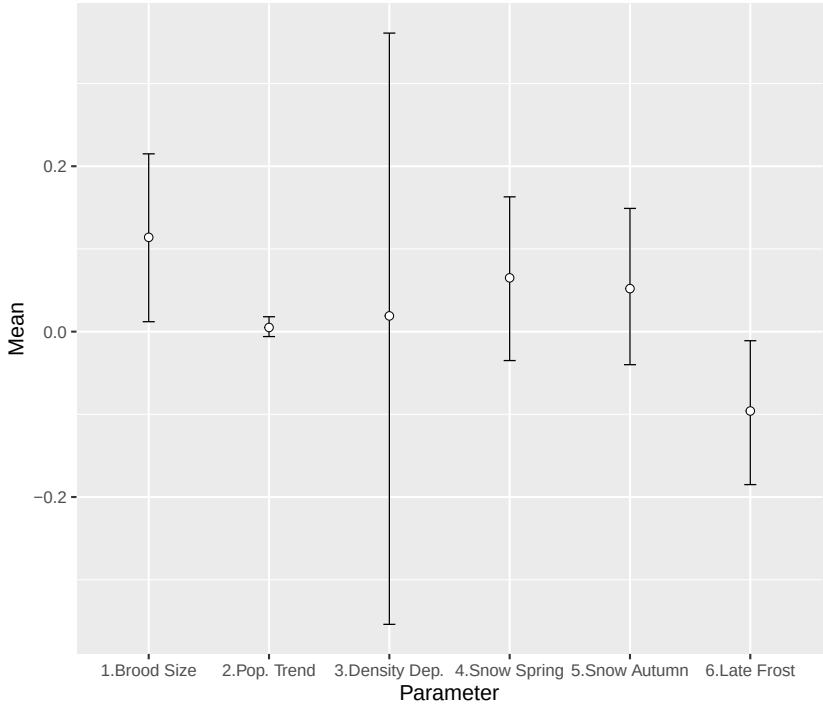

Figure 3 – Parameter values and 95% credible intervals for the explanatory variables of annual change in the adult population of willow ptarmigan.

Effect of chick production, and climate variables

Average brood size had a statistically significant positive effect on adult population change, the parameter for standardized brood size was 0.114 (95% Cr. I. 0.012 - 0.215). Springs with late frost showed a statistically significant negative effect on adult population change, the parameter was -0.096 (95% Cr. I. -0.185 - -0.011). Brood size and cold springs were weakly correlated (-0.328, t = -2.07, p = 0.045). Neither the number of snow-free days in spring or autumn showed any significant effect on adult population change. See table 1 and figure 3

Discussion

Contrary to our expectations, and as reported for willow ptarmigan populations elsewhere (Fuglei et al., 2020; Melin et al., 2020), the adult population in our study did not show a negative trend. Neither was any decline detected in a nine-year study of the willow ptarmigan population in an area at the same latitude about 100 km west of our study (Breisjøberget et al., 2018). Furthermore, Hjeljord and Loe (2022) did not find any relationship between climate and the decline in catch per unit effort of willow ptarmigan over 142 years in Norway. The number of snow-free days in spring and autumn increased during the study, but neither variable had a negative effect on adult population change. The expected increase in vulnerability of white colored prey to predators when snow is absent might be less than assumed, and few studies have investigated how survival is affected when snow is lacking. Lack of snow could increase vigilance and alter habitat selection as part of antipredator strategies (Broom and Ruxton, 2005). In addition, the relative abundance of predator and prey species may affect the behaviour of the prey, white mountain hares (*Lepus timidus*) did not seek snow patches in areas with low densities and diversity of generalist predators in Scotland (Zimova et al., 2024). The hypothesis that willow ptarmigan in winter plumage suffer substantially higher predation on snow free ground will require data

on individual survival and mortality cause, when actual snow cover also can be measured in the field.

Despite large annual variations, the average onset of spring begin earlier in our study area (Jin et al., 2019). Callaghan et al. (2022) noted that Arctic vegetation has not changed significantly despite a rapid warming climate, and herbivores, including domestic reindeer (*Rangifer tarandus*), respond to changes in plant composition through increased browsing, which could mitigate the effects of climate warming (Lindén et al., 2021; Olofsson et al., 2009). It is not clear how fast plant communities respond to a warmer climate (Bjorkman et al., 2015; Morison et al., 2023), and a time lag between a warmer climate and vegetation change would delay a negative effect on willow ptarmigan.

Our results showed that breeding success was significantly positive for adult population change. There are several factors that can contribute to the apparent stochastic variation in breeding success, but *per capita* breeding success is not affected by changes adult density (Hörnell-Willebrand et al., 2006). We found a but significant positive relationship between the vole index and breeding success, and changes in the predation rate on nests and young varies inversely when alternative prey such as voles fluctuates (Breisjøberget et al., 2018; Hörnfeldt, 1991; Steen et al., 1988). It is interesting to note that the outbreak of sarcoptic mange and the dramatic decline in red fox (*Vulpes vulpes*) during late 1970's in Sweden (Willebrand et al., 2022) did not affect the willow ptarmigan population in our study area as was observed in small game populations elsewhere (Lindström et al., 1994; Small et al., 1993). A possible explanation is that small sized predators as stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*) increased numerically as suggested for the American mink (*Neovison vison*) (Carlsson et al., 2010), and compensated for reduced red fox predation.

We found that late springs had a significant negative effect on adult population change. Late springs are associated with delayed egg laying (Wiebe and Martin, 1995) and the onset of spring cause variation in hatching date, which in our study area was on average 12 days (17 - 29 June) (Marcström and Höglund, 1980). Spring phenology and emerging vegetation is important for many wildlife herbivores, and the maternal hypothesis states that female body condition during egg laying and incubation affect survival of chicks and subsequent recruitment (Blomqvist et al., 1997; Coslovsky and Richner, 2011). In our study area, Brittas (1988) showed that the digestibility of spring food in willow ptarmigan crops was positively correlated with female body condition during egg laying and subsequent breeding success. We believe the negative effect of late frost in May on adult population change can be explained by reduced body condition that affect also the vulnerability to predation in addition to breeding success.

In this study, the fluctuations of the adult willow ptarmigan followed a pattern of a stationary population under the influence of both stochastic and density dependent factors (Sæther et al., 2008). Many grouse species experience cyclic fluctuations (Kaitala et al., 1996; Moss and Watson, 2001), which in large parts of Scandinavia have been attributed to variations in recruitment. In our study, the adult population did not show any regular fluctuation pattern despite a positive effect from a periodically fluctuating breeding success. Natal dispersal and recruitment processes are not well understood in many grouse species. Large scale natal dispersal can reduce recruitment effects from local variation in breeding success (McCullough, 1996; Pulliam and Danielson, 1991; Willebrand and Hörnell, 2001), and it was suggested that the recruitment of female willow ptarmigan depends on breeding success in areas larger than several hundred

km^2 due to the distribution of natal dispersal distances (Hörnell-Willebrand et al., 2014). Predation is the dominating natural death cause of willow ptarmigan (Smith and Willebrand, 1999), and predators probably response to changes in the adult population due to varying recruitment. We found a statistically significant negative feedback between years but the parameter was associated with large variation, which probably can be explained by a varying predator response to the variation in recruitment.

While this is one of the longest existing time series on willow ptarmigan in Scandinavia, the fact that the initial years (1963-1975) that could not be included in the analysis due to lacking information about the distances display the highest adult densities in the time series leaves some uncertainty about the trend assessment. This is further increased as the timing of the yearly monitoring was change during the coarse of the study, which was addressed using a covariate in the model. Further, the climate data (snow and temperature) was retrieved from the weather station closest to the study area, which was still located at considerably lower elevation potentially representing slightly different climatic conditions relative to the study area. Despite these challenges we believe this analysis provide valuable insight from a unique long term time-series about the population dynamics of willow ptarmigan.

The structure of trophic levels becomes simpler in the north compared to further south (Callaghan et al., 2004b) where of the tundra becomes fragmented and is surrounded by continuous boreal forests. At lower latitudes, animal diversity increase including a wide range of predators, generalists and specialists, and prey species (Callaghan et al., 2004a). Trophic interactions and time lags influence patterns of population dynamics, and it is known that vole populations show declining densities and amplitudes along a geographical gradient from north to south (Erlinge, 1987; Turchin and Hanski, 1997). Our study area is in the southern range of the tundra and we suggest that the stable dynamics of the adult population is explained by a diverse predator assemblage that make it impossible for the population to escape a top-down regulation. Further north, this may well be relaxed, and an increase in amplitude and density would be expected. We encourage an increased research cooperation that use the excellent and extensive line transect counts in Scandinavia to further investigating similarities and differences in fluctuation patterns along a latitudinal gradient and under different management policies.

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Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest related to the content of the article.

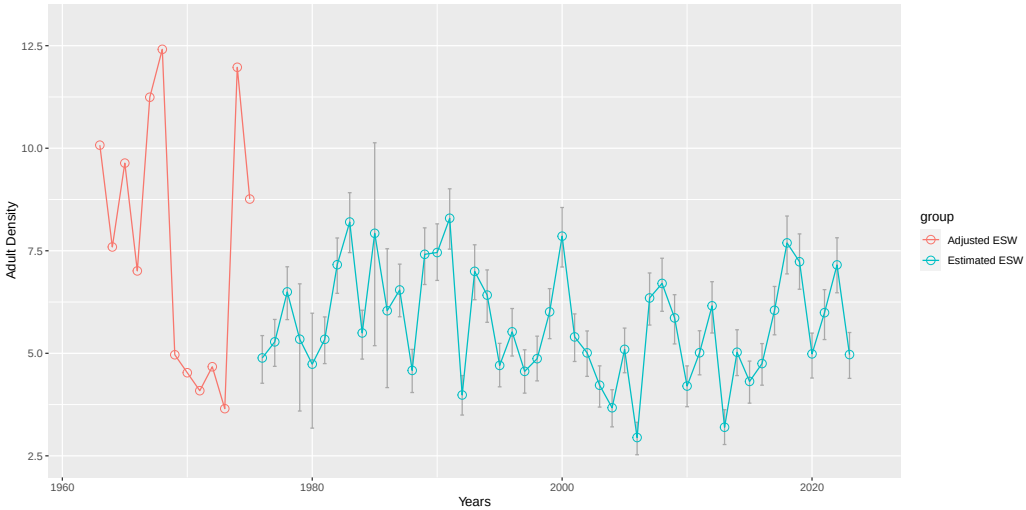

Figure 4 – The recalculated density in the period 1963 - 1975 based on the ratio of the effective strip widths in this study and the old estmate based on the average distances of observed birds.

Appendix A. Estimating adult abundance 1963 - 1975

Appendix B. Data, script, code, and supplementary information availability

Data are available online : needs to be fixed!

Script and codes

```
# Script to run model

library(tidyverse)
library(here)
library(jagsUI)
library(MCMCvis)

data <- "../STATESPACE6/DATA"
model <- "SCRIPT"
latex <- "LATEX/figures"

# Load data for analysis
dat1 <- readRDS(here(data, "LovDatJuneFrost.rds"))
str(dat1)
dat1$chick2 <- dat1$chick

# inits
Nst_init <- dat1$y + 1
inits <- function(){list(N=Nst_init, btDD = runif(1,-0.05,0.05), beta= runif(2,1.2,2))}

ni <- 100000   ;   nb <- 50000   ;   nt <- 4   ;   nc <- 3
params <-c("pcap", "btDD", "btTREND", "sdprectau", "sdproctau", "beta0", "D", "btvole", "btCHICK", "
    btSPsnow", "btAUsnow", "btFrost")

mod_june_11A2 <- jags (dat1, inits, params, here(model, "WillowGrouseModelFinal_Breed2.jags"), n.thin=nt, n
    .chains=nc, n.burnin=nb, n.iter=ni, parallel=TRUE)

print(mod_june_11A2, dec=3)

MCMCtrace(mod_june_11A2, params <-c("pcap", "btDD", "btTREND", "sdprectau", "sdproctau", "beta0[1]","beta0
    [2]", "btvole","btCHICK", "btSPsnow", "btAUsnow", "btFrost"),    ISB = FALSE, exact = TRUE, ind = TRUE,
        Rhat = TRUE, n.eff = TRUE, pdf = TRUE)


# Model WillowGrouseModelFinal_Breed2.jags

model{
# Priors
alpha0 ~ dunif(-10,10)  # Intercept for sigma in half-.normal detection function

# Different intercept for two different counting periods, late June or early August
for(i in 1:2){
beta0[i] ~ dunif(-10, 10)
}

btCHICK ~ dunif(-10, 10)   # Parameter for the effect of brood size
btDD ~ dunif(-1,1)       # Parameter for Density dependence
btTREND ~ dunif(-10,10)    # Parameter for trend parameter (i.e. Year)
btSPsnow ~ dunif(-10,10)
btAUsnow ~ dunif(-10,10)
btFrost ~ dunif(-10,10)    # Parameter for the effect of last day of frost in May


## Precision (T=1) and process variation (T>1). Expressed as standard deviation
PrEc <- 1 / (sdprectau * sdprectau)
sdprectau ~ dunif(0, 1)
PrOc <- 1 /(sdproctau * sdproctau)
sdproctau ~ dunif(0,1)

# Priors for estimating brood size (chicks per pair)

chick.inter ~ dunif(-10, 10)  # Intercept for brood size dependent on vole
btvole    ~ dunif(-10, 10)    # Parameter for the effect of vole abundance
chick.err <-  1 / (sdchick * sdchick)
sdchick ~ dunif(0, 1)
```

```
# Parameter for precision (tau) of chick - vole model

##############################################
## Distance sampling observation model for observed (binned)
## All lines combined into one, same lines all years

# Distance data:
log(sigma) <- alpha0   # linear model detection
for(i in 1:nobs){
   dclass[i] ~ dcat(fc+ 0.01)  # 0.01 must be added if the model should converge
             }
## Likelihood
# Construct cell probabilities for nD multinomial cells
  for(g in 1:nD){    # distance classes
# Half-normal detection function
  log(p[g]) <- -midpt[g] * midpt[g] / (2 *sigma*sigma)
  pi[g] <- delta / B
  f[g] <- p[g] * pi[g]
  fc[g] <- f[g] / pcap
                 }
pcap <- sum(f[]) # Pr(capture): sum of rectangular areas


## Process model:
# Initial density model for Year 1:
      y[1] ~ dbin(pcap, N[1])
      N[1] ~ dpois( lambda[1] )
      lambda[1] <-  D[1] * area[1]
      logD[1] ~ dnorm(mu[1], PrEc) mu[1] <- beta0[1]
      D[1] <- exp(logD[1])

# Population dynamics model for subsequent years:
    for (t in 2:T){
      y[t] ~ dbin(pcap, N[t])
      N[t] ~ dpois(lambda[t])
      lambda[t] <- D[t] * area[t]
      logD[t] ~ dnorm( mu[t] , PrOc )
      mu[t] <- beta0[Period[t]] + btDD * mu[t-1]  + btTREND * (t-1) + btCHICK * chick2[t-1] + btSPsnow * No
     _Spring[t] + btAUsnow * No_Autumn[t-1] + btFrost * Frost[t-1]
      D[t] <- exp(logD[t])
                        }
# End pop dynamics subsequent years

## Model of brood size with vole index as predictor
  for(i in 1:T){
        # regression model on chick, given voles
        chick[i] ~ dnorm(chick.est[i], chick.err )
        chick.est[i] <- chick.inter + btvole * voles[i]
    }
chick2[20:28] <- chick.est[20:28]

} # End model
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References

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