Large-scale spatiotemporal variation in vital rates and population dynamics of an alpine bird

Chloé R. Nater[1,*], James A. Martin[2], Erlend B. Nilsen[1,3]

[1] *Department for Terrestrial Biodiversity, Norwegian Institute for Nature Research (NINA), Trondheim, Norway*

[2] *Warnell School of Forestry & Natural Resources, University of Georgia, Athens, USA*

[3] *Faculty of Biosciences and Aquaculture (FBA), Nord University, Steinkjer, Norway*

*corresponding author: chloe.nater@nina.no

Abstract

Quantifying temporal and spatial variation in animal population size and demography is a central theme in ecological research and important for directing management and policy. However, this requires field sampling at large spatial extents and over long periods of time, which is not only prohibitively costly but often politically untenable. Participatory monitoring programs (also called citizen science programmes) can alleviate these constraints by recruiting stakeholders and the public to increase the spatial and temporal resolution of sampling effort and hence resulting data. While the majority of participatory monitoring programs are limited by opportunistic sampling designs, we are starting to see the emergence of structures citizen science programs that employ trained volunteers to collect data according to standardized protocols. Simultaneously, there is much ongoing development of statistical models that are increasingly more powerful and able to make more efficient use of field data. Integrated population models (IPMs), for example, are able to use multiple streams of data from different field monitoring programmes and/or multiple aspects of single datasets to estimate population sizes and key vital rates. Here, we developed a multi-area version of a recently developed integrated distance sampling model (IDSM) and applied it to data from a large-scale participatory monitoring program – the

"Hønsefuglportalen" – to study spatio-temporal variation in population dynamics of willow ptarmigan (*Lagopus lagopus*) in Norway. We constructed an open and reproducible workflow for exploring temporal, spatial (latitudinal, longitudinal, altitudinal), and residual variation in recruitment, survival, and population density, as well as relationships between vital rates and relevant covariates and signals of density dependence. Recruitment rates varied more across space than over time, while the opposite was the case for survival. Slower life history patterns (higher survival, lower recruitment) appeared to be more common at higher latitudes and altitudes, portending differential effects of climate change on ptarmigan across their range. While there was variation in the magnitude of the effect small rodent occupancy had on recruitment, the relationships were predominantly positive and thus consistent with the alternative prey hypothesis. Notably, the accurate estimation of covariate effect was only made possible by integrating data from several monitoring areas for analysis. Our study highlights the potential of participatory monitoring and integrated modelling approaches for estimating and understanding spatio-temporal patterns in species abundance and demographic rates, and showcases how corresponding workflows can be set up in a reproducible and semi-automated way that increases their usefulness for informing management and regular reporting towards national and international biodiversity frameworks.

Introduction

There is growing demand for biodiversity indicators from international unions, national governments, local management bodies, and corporate and industry actors. Indicators should ideally represent a wide range of biodiversity's states and functions (e.g. Essential Biodiversity Variables, Pereira et al. 2013; Jetz et al. 2019), yet the development of suitable indicators for certain attributes, such as species abundance and demography, has been more difficult than for others (Schmeller et al. 2018; Waldock et al. 2022). This is at least partially due to challenging requirements regarding spatial scales of useful biodiversity indicators. On one hand, indicators need to be representative at large geographic scales, for example, in the context of countries' reporting towards biodiversity targets (e.g. Feld et al. 2009). On the other hand, indicators also ideally have good spatial resolution, as the scales relevant for local-level management and planning are often much smaller (Stevenson et al. 2021). This latter requirement is particularly crucial for infrastructure development strategies and for species management and conservation, both of which tend to require knowledge on species abundance and population dynamics (i.e. demographic rates) that is relevant for county- or municipality-level decision making (Christie et al. 2020). Another reason why abundance and population indicators ideally come with good spatial resolution is that there can be substantial amounts of variation in population dynamics and life history of species across space (e.g. Robinson, Morrison, and Baillie 2014; Horswill et al. 2019). This variation needs to be accounted for to develop successful and sustainable strategies for area use, harvest management, and species and biodiversity conservation (Williams, Nichols, and Conroy 2002).

While large-scale, spatially-explicit indicators for species abundance and populations are clearly needed, development and practical implementation are greatly limited due to the reliance of such indicators on the availability of data from large-scale, long-term monitoring programmes (Proença et al. 2017). Consequently, many countries have been working on setting up, maintaining, and improving such monitoring programmes over the last decades. Many now well-established programmes focus on breeding birds and butterflies, and examples include the North American Breeding Bird Survey (https://www.pwrc.usgs.gov/bbs/), the PanEuropean Common Bird Monitoring Scheme (https://pecbms.info/), the UK Butterfly Monitoring Scheme (https://ukbms.org/), the Game and Wildlife Conservation Trust Partridge Count Scheme (Aebischer and Ewald 2010), and the Swiss Biodiversity Monitoring (https://www.biodiversitymonitoring.ch/).

There is a natural trade-off between quality and quantity of data that can be collected in any monitoring programme: collecting high quality data in a structured manner is costly, requires trained specialists, and hinges on a sufficient degree of top-down control of the programme. This often limits the amount of data that can be collected, while participatory monitoring, i.e. the collection of ecological data by members of the public (also called citizen or community science, Fraisl et al. 2022), allows to greatly reduce costs and extend spatial and taxonomic scales of monitoring at the expense of data quality and risk of bias (Johnston, Matechou, and Dennis 2023). Consequently, many large-scale monitoring programmes are often limited to presence(-absence) or very simple count observations, making them suitable for the development of indicators of species distributions and perhaps population trends, but usually not of abundance, population dynamics, and demographic rates (Dickinson, Zuckerberg, and Bonter 2010; Johnston, Matechou, and Dennis 2023). The exception here are monitoring programmes that succeed in making use of a large number of volunteers that have been trained to collect data and record metadata in a structured manner and according to a carefully designed protocol. For example, in the United States hunters participate in the collection of bands and wings from harvested American Woodcock (*Scopolax minor)* to estimate survival and age ratios (Zimmerman et al. 2010). At the European level, the recently established initiative "European Observatory of Wildlife" is offering common field- and analyses protocols and aims to establish a network of "observation points" for monitoring wildlife populations at the European level (https://wildlifeobservatory.org/). In Norway there is a monitoring programme for terrestrial game bird species called "Hønsefuglportalen" (= "game bird portal", https://honsefugl.nina.no/Innsyn/en). It is a line transect survey programme carried out annually in >120 localities across the country (>2000 transects) by trained volunteers using pointing dogs. The programme has a well developed protocol for recording bird observations, auxiliary data, and relevant metadata and established routines for quality control and annual releases of publicly available data via the Global Biodiversity Information Facility (GBIF). As such, it is particularly well suited to become part of a workflow for producing and updating abundance and population indicators on an annual basis.

The line transect data from "Hønsefuglportalen" has been used previously for estimating abundance trends of willow ptarmigan (*Lagopus lagopus*) across Norway (e.g. Bowler et al. 2020; Nilsen and Rød-Eriksen 2020), and to test a range of relevant ecological hypotheses (Bowler et al. 2020; Breisjøberget, Odden, Wegge, et al. 2018). However, large-scale estimation of demographic rates underlying abundance trends has thus far remained as untapped potential of the dataset. Nilsen and Nater (2024) recently developed a novel integrated distance sampling model (IDSM) which successfully uses the age of individuals detected along line transects data coupled with radio-telemetry data to jointly estimate abundance, survival, and recruitment across years. In this study, we adapt and extend the model of Nilsen and Nater (2024) to run not just on a single site but on all areas with publicly available line transect data from "Hønsefuglportalen" simultaneously. Unlike several previous studies applying integrated models for population dynamics to multiple (sub-) populations separately and comparing results (e.g. Robinson, Morrison, and Baillie 2014; Nater et al. 2023), we opt for an approach explicitly integrating across space, thus allowing for sharing of information across locations and – in effect – space-for-time substitution (e.g. Horswill et al. 2019; Morrison et al. 2022). We then apply the resulting multi-area IDSM to "Hønsefuglportalen" data on willow ptarmigan to estimate population size, age-structure, survival, recruitment, and impacts of small rodent occupancy across 41 reporting districts and 15 years (2007-2021) for this culturally important small-game species. We further embed the modelling workflow in a reproducible, semi-automated pipeline that will greatly facilitate the repeated calculation of abundance and population indicators at different spatial scales as new data are added every year.

Methods

Study species

The willow ptarmigan is a tetraoid bird with a circumpolar distribution, mainly inhabiting sub-alpine and arctic ecosystems (see e.g. Fuglei et al. 2020). While the species is currently listed as Least Concern (LC) both in the global and Norwegian Red List of Species, it has undergone rather dramatic declines in abundance in Norway since the turn of the 20th century (Hjeljord and Loe 2022). The main reason for the long-term decline in abundance remain unresolved, but the willow ptarmigan are considered sentinel species that are sensitive to both climate change and land use changes (John-André Henden et al. 2017; Storch 2007). Moreover, being one of only a handful of bird species that spend the winter in mountain ecosystems in Scandinavia, they are important components of the ecosystem as prey species for resident predators, such as the gyrfalcon (Franke et al. 2020). The willow ptarmigan has a relatively fast pace of life (Sandercock, Martin, and Hannon 2005; Steen H. and Erikstad 1996), and can display substantial spatio-temporal variation in demographic rates (Bowler et al. 2020). Their population dynamics are characterized by large inter-annual fluctuations in abundance (Hjeljord and Loe 2022), and previous research has tied these fluctuations to rodent cycle through shared predators (Hagen 1952; Bowler et al. 2020). This tight relationship between the breeding success of ground nesting birds and the rodent cycle is known as the Alternative Prey Hypothesis (APH) and has been a central part of research on Fennoscandian grouse population dynamics for many decades (Elton 1942; Hagen 1952; Linden 1988; J. B. Steen et al. 1988). In addition, spring weather conditions and phenology is known to have considerable effects on breeding success and recruitment rates (Eriksen et al. 2023; J. B. Steen et al. 1988). Across their distributional range, willow ptarmigan are an iconic species with a high cultural value, partly linked to their popularity as game species. The latter means that information about spatio-temporal variation in demographic rates and population dynamics is particularly important in order to design sustainable harvest strategies (Eriksen et al. 2023). In addition, being a sentinel species, the willow ptarmigan is well suited as an indicator species for ecosystem status; in Norway it is included in both the main national biodiversity (Nature Index for Norway, Jakobsson and

Pedersen 2020, https://www.naturindeks.no/Indicators/lirype) and ecosystem condition (Assessment of the Ecological Condition, Framstad et al. 2022) assessments.

Data collection, management, and preparation

Line transect sampling

The line transect survey data were collected through a structured participatory monitoring program called “Hønsefuglportalen” (https://honsefugl.nina.no/Innsyn/en). In the first three weeks of August each year, trained volunteer fieldworkers collect observations of willow ptarmigan and other grouse species (rock ptarmigan *Lagopus muta*, black grouse *Lyrurus tetrix*, and capercaillie *Tetrao urogallus*) along predefined line transects. To increase the detection probability, fieldworkers use pointing dogs to locate the birds. A survey team typically consist of at least two people (one dog handler and one person responsible for following the transect line) and one dog. Often, more than one dog is used for a survey, but only one dog should be used at a time. The transect lines vary in length, but are typically between 1 and 8 km (range: 0.3-16.2 km, median: 3 km). When birds are observed, the exact location of observation is reported, along with its perpendicular distance from the transect line, as well as the age and sex of the birds. An observation typically includes 1 - 12 birds (mean = 5.6), with groups > 1 typically representing one brood (female and or male with young-of-the-year chicks). When the surveys are conducted in August, the chicks of the year are able to fly but can be distinguished from older birds as they are still of smaller body size. Since 2019, most of the data has been collected using a mobile app tailored to the monitoring program, where the field workers can register and get access to the transect lines allocated to them by the local organizers. Prior to 2019, data were collected on a dedicated fieldwork form, and entered manually in a web portal afterwards. After field data has been registered, it undergoes several steps of quality control carried out by local stakeholders and personnel from the Norwegian Institute for Nature Research (NINA). Surveys are carried out on both public and private land. After an initial embargo period, all data from public land are published and made freely available as a sampling-event data set on GBIF (https://www.gbif.org/sampling-event-data). The published datasets contain both metadata about the transect surveys (survey date, line transect length and location, study area ID, etc.) and bird observation data (species, number of birds of different categories (adult males, adult females, juveniles, and birds of unknown category), perpendicular distance to transect line, exact location, and time of observation). Formally, the data from public land is published as three distinct data sets, one for each of the main public land administrators (Statskog, FeFo and Fjellstyrene, respectively).

Notably, the program is not designed as a centralized national monitoring programme, but rather a collection of local and regional survey programs. All involved survey areas use a common field protocol and data collection model. In addition, the local study designs are reviewed by staff at NINA, and common recommendations for study design are provided. However, because participation by stakeholders is voluntary, the spatial distribution of transects and sampling effort is not homogeneous across space. In general, sampling effort is higher in South-Eastern and Central Norway, intermediate in Northern Norway, and low in Western and Southern Norway.

In this study we used all publicly available data for the period 2007-2021, which included a total of 2225 transects in 41 different reporting districts spanning 9 counties and 50 municipalities. Transects on which no willow ptarmigan were observed during the study period (i.e. species absence likely due to low habitat suitability) were not included. After this initial filtering, a total of 2077 transects were included in the analyses.

Radio-telemetry study in Lierne

The model of Nilsen and Nater (2024) integrated line transect data with radio-telemetry data from from an ongoing field study of marked willow ptarmigans in Lierne municipality in Central Norway. From 2015 to 2019, around 50 birds were captured in winter (late February or early March) each year and fitted with VHF collars. The marked birds were then monitored on a regular basis until they either i) died, ii) their transmitter's battery stopped working, or iii) we lost contact with the bird for other reasons. For most of the year, the birds were monitored at least once a month by radio triangulation. Most of the fieldwork was conducted from the ground, but to avoid data gaps, the birds were also triangulated from helicopters in May, September, and November. During the breeding and chick-rearing season (May to July) birds were monitored more often, and during December and January we obtained fewer observations due to challenging field work conditions. A proportion of the birds were harvest annually in the regular recreational harvest, and birds that were harvested were reported as shot to the field personnel. In addition, as the collars had mortality switch, we were also able to locate and retrieve a high proportion of birds that died for natural causes, resulting in a known-fate mark-recapture dataset. The radio-telemetry study is described in detail in Israelsen et al. (2020) and in Arnekleiv et al. (2022).

In this study we used data from years 2015 - 2020, and the total sample size across these years was 139 birds for the Aug-Jan period and 258 birds for the Feb-Jul period.

Rodent occupancy data

As part of the line transect sampling (see above), observers are also requested to report whether they have seen any small rodents while surveying a transect. For each transect survey, this information is recorded as 1's (small rodents spotted at least once) and 0's (no small rodents spotted). We aggregated this data into area- and year-specific rodent occupancy covariates by averaging the 0 and 1 reports for all transect surveys within a given area and year and subsequently z-standardizing values. We note that while we refer to the covariate as "rodent occupancy" throughout the manuscript, it can be interpreted as an index for rodent abundance.

National-scale integrated model

Integrated distance sampling model (IDSM) for willow ptarmigan

Nilsen and Nater (2024) recently developed an integrated distance sampling model (IDSM) which jointly analyses line transect and radio-telemetry data and applied it to willow ptarmigan in the Western part of Lierne municipality in Norway. The model consists of a population model with two age classes (juveniles and adults) and four data likelihoods: 1) likelihood for observation distances from transect lines for estimating detection probability; 2) likelihood for age-specific counts on transect surveys for estimating numbers of juveniles and adults present; 3) likelihood for juvenile to adult ratios observed at the locality level to provide estimate recruitment rate (as juveniles/adult); and 4) likelihood for known-fate telemetry data to estimate seasonal and annual survival. Below, we describe our new extension of this model to include data from several areas as opposed to just one. For more detailed information on the single-site model, including tests of model performance, see Nilsen and Nater (2024).

Multi-area model extension

For applying the ptarmigan IDSM across all 41 reporting districts we included an area index in all model parameters (Figure 1) and enabled sharing of information among areas by explicitly modelling spatial variation alongside shared temporal and residual variation in vital rates and detection parameters.

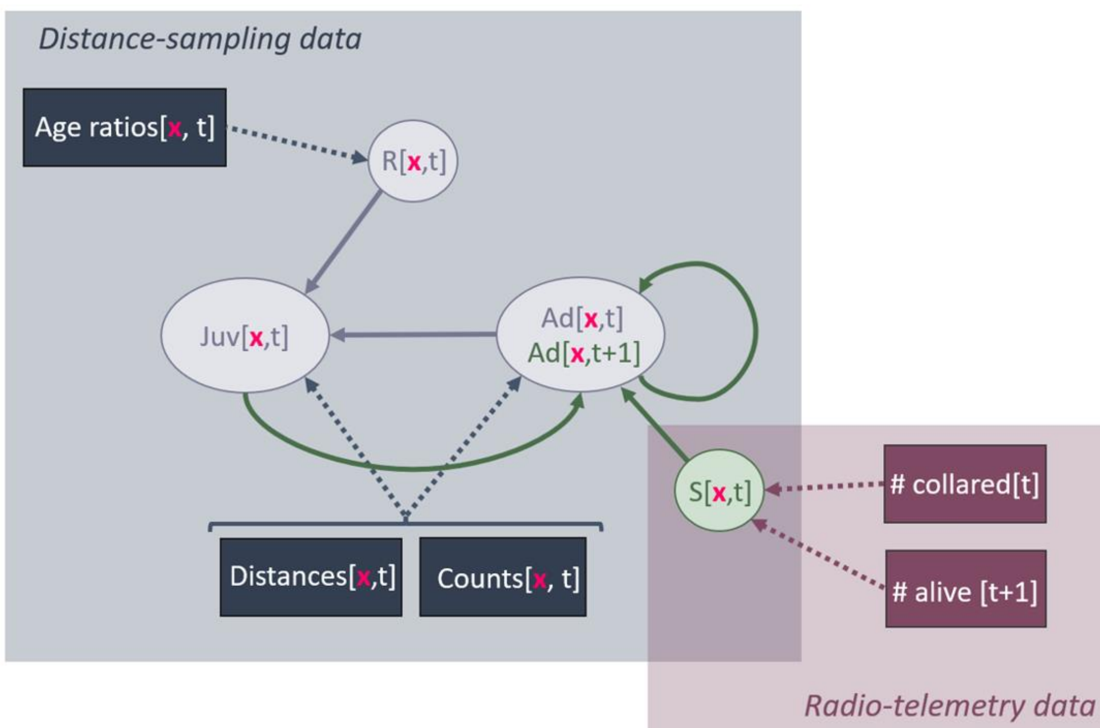


Figure 1: Simplified graphical representation of the ptarmigan life cycle with two age classes and the data sources included in the integrated distance sampling model. The pink "x"'s indicate the added dimension for area. Juv[x,t] = juveniles in area x year t. Ad[x,t] = adults in area x in year t. R[x,t] = recruitment rate in area x in year t. S[x,t] = survival probability from year t to t+1 in area x. Note that the additional site (=transect) dimension, "j", is omitted for the sake of illustration.

The spatially-explicit formulation of the two age-class population model can be written as:

$$\begin{aligned} D_{juv,x,j,t+1} &= D_{ad,x,j,t+1} * R_{x,t+1} \\ D_{ad,x,j,t+1} &= S_{x,t} * \left(D_{juv,x,j,t} + D_{ad,x,j,t}\right) \end{aligned}$$

Here, $D_{juv,j,x,t}$ and $D_{ad,j,x,t}$ are the densities of juvenile and adult ptarmigan in survey site (= transect) j of area x in year t, respectively. Both juveniles and adult survive from year t to $t+1$ with an area- (x) and year- (t) specific survival probability $S_{x,t}$, and survivors produce the next generation of juveniles according to an area- and year-specific recruitment rate ($R_{x,t}$).

The initial densities, $D_{juv,x,j,1}$ and $D_{ad,x,j,1}$ are modelled for each site (= transect) as random realizations of log normal distributions with area-specific log means (μ_x^{D1}) and log standard deviations (σ_x^{D1}). Survival ($S_{x,t}$) and recruitment ($R_{x,t}$), on the other hand, are assumed to be the same for all sites j within a given area x and were modelled as:

$$\begin{aligned} logit\left(S_{x,t}\right) &= logit(\mu^S) + \varepsilon_x^{X.S} + \varepsilon_t^{T.S} + \varepsilon_{x,t}^{R.S} \\ log\left(R_{x,t}\right) &= log(\mu^R) + \beta_x * rodentOcc_{x,t} + \varepsilon_x^{X.R} + \varepsilon_t^{T.R} + \varepsilon_{x,t}^{R.R} \end{aligned}$$

The global means ,μ, and the normally distributed spatial random effects, ε^X, represent the equivalent of what is elsewhere referred to as "hyper-parameter distributions" for sharing information on demographic rates across areas (e.g. Horswill et al. 2019, 2021). We also used this same approach for defining the area-specific effects (β_x) of local yearly rodent occupancy ($rodentOcc_{x,t}$) on recruitment. In addition to spatial variation in survival and recruitment, we also included large-scale temporal variation through random year effects that were shared by across all areas (ε_t^T) and otherwise unaccounted for variation through year- and area-specific residual random effects ($\varepsilon_{x,t}^R$). Spatial, temporal, and residual random effects were modelled as normally distributed with globally defined (= shared) standard deviations.

The three likelihoods for data resulting from the line transect sampling (observation distances, age-specific counts, and juvenile to adult ratios, see above) were also formulated as spatially explicit, with year- and area-specific distance sampling detection parameters modelled in the same way as survival and recruitment (except the effect of rodent occupancy, Figure 1). For the known-fate telemetry data (and the seasonal decomposition of survival estimated from it), on the other hand, we did not add an additional area dimension as this data was only available for on study area (the Lierne area).

Model implementation

We implemented our multi-area IDSM in a Bayesian framework using NIMBLE version 1.0.1 (Valpine et al. 2017) in R version 4.3.1 (R Core Team 2023). For the likelihood for line transect observation distances we used a custom half-normal distribution developed by Michael Scroggie in the "nimbleDistance" package (https://github.com/scrogster/nimbleDistance). We used non-informative uniform priors for all parameters, but used biologically sensible boundaries where possible. We simulated complete sets of initial values for all model nodes prior to model running and using pre-defined seeds to ensure reproducibility. Using NIMBLE's standard samplers, we then ran 5 MCMC chains of 150k iterations each. We discarded the first 75k samples of each chain as burn-in, and thinned the remainder by a factor 25, resulting in a final joint posterior containing a total of 5 x 3k = 15k samples (note that high thinning rates were necessary to constrain memory load of the joint posterior, which included 314568 monitored parameters).

Post-hoc variance decomposition

Following model fitting, we calculated posterior distributions for the proportions of variance in survival probabilities, recruitment rates, and detection decay explained by 1) spatial variation (var_{area}), 2) temporal variation (var_{year}), 3) residual variation ($var_{residual}$), and 4) variation in rodent occupancy (var_{rodent}). To obtain the proportion variance explained by each of the component, we divided it by the sum of all the components ($var_{area} + var_{year} + var_{residual} + var_{rodent}$). The spatial, temporal, and residual variance components were defined as the square of the estimated corresponding random effects standard deviation from the model while var_{rodent} was calculated as the variance of all area- and year-specific $\beta_x * rodentOcc_{x,t}$ products. This approach for variance decomposition is equivalent to that used by Nater et al. (2018) and inspired by Nakagawa and Schielzeth (2013).

Reproducible workflow with “targets”

Reproducibility and ease of repeating analyses was a key focus when developing the multi-area IDSM. To that end, we set up the workflow as a “targets pipeline”, implemented through the R package “targets” (Landau 2021). The pipeline contains a variety of options for controlling modelling decisions in the workflow such as the year range of data to consider, the level of spatial aggregation (i.e. reporting district vs. survey locality), whether to model time variation in survival and/or effects of rodent occupancy, whether to run MCMC chains sequentially or in parallel, etc. A visual representation of the pipeline is also displayed in Figure 2 and for more details on pipeline implementation and options, we refer the reader to the GitHub repository: https://github.com/ErlendNilsen/OpenPop_Integrated_DistSamp.

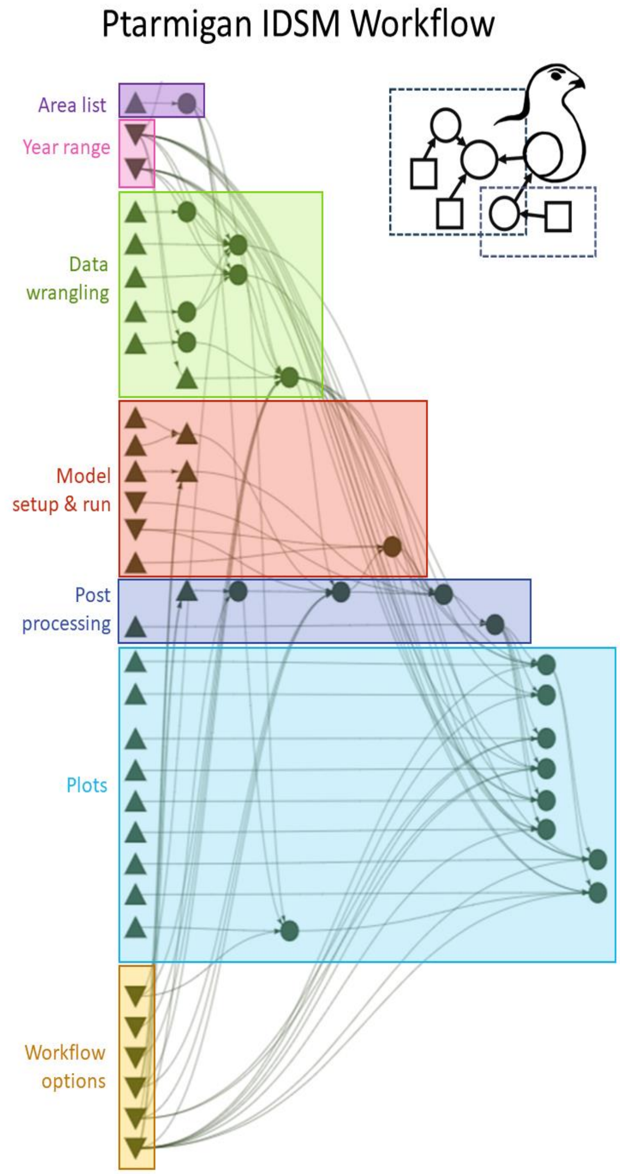


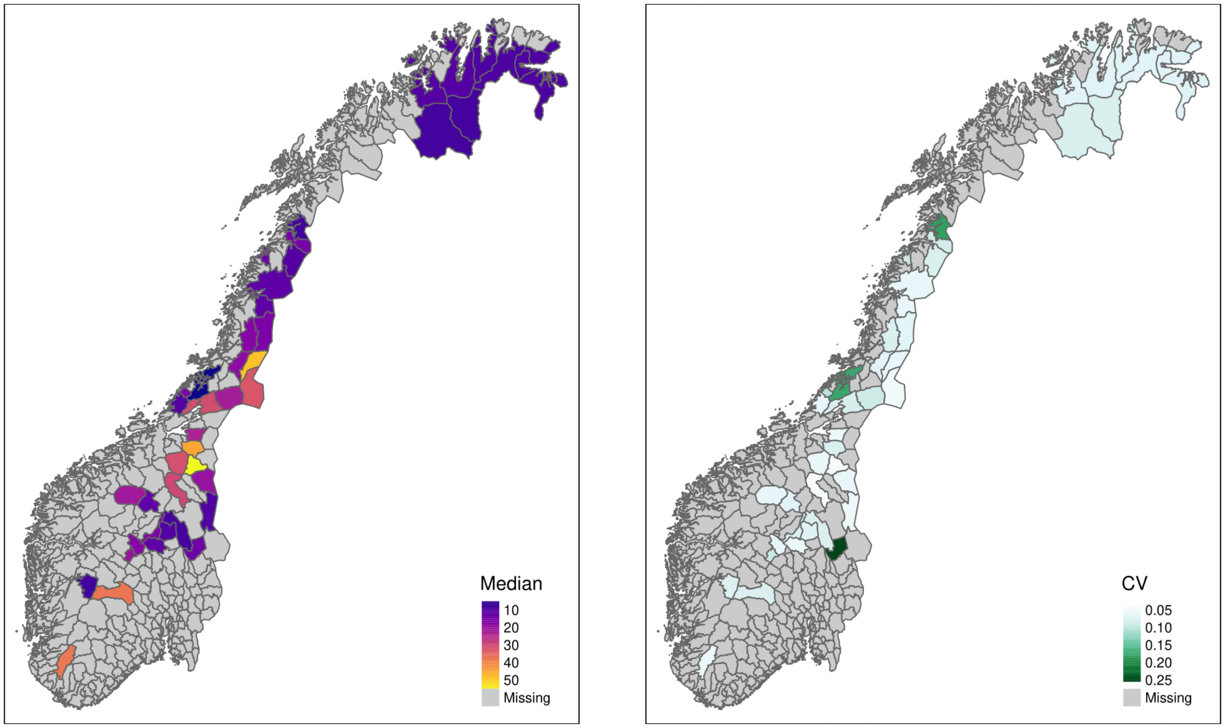
Figure 2: Graphical representation of the “targets pipeline” for the multi-area modelling setup. Upward facing triangles are functions, downward facing triangles are general options/arguments, circles are objects and outputs (=“targets”) created as part of the workflow.

Results

All numerical results in the following are presented as median [95% credible interval] unless otherwise indicated. Posterior summaries (median, 95% credible interval, mean, standard deviation, coefficient of variation) for all main parameters are also provided in the supplementary file "PosteriorSummaries_byAreas.csv". Supplementary figures (SFs) are provided as .pdf files with captions in "SuppFigures_Captions.txt"; all files are deposited on OSF (https://osf.io/7326r/).

Population density

Only during the most recent four years (2018-2021) has data been collected regularly for all reporting areas included in the analyses. During this period, estimated population densities varied between 2.205 [1.551, 3.097] birds/km^2 in the area "Statskog og Klinga utm." close to the coast in central Norway to 55.85 [51.699, 60.003] birds/km^2 in "Ålen og Haltdalen Fjellstyre" further south near the Swedish border. In general, recent population density appeared to be lowest in the northern Norway and highest in the eastern part of central Norway (Figure 3 (a)). Uncertainty in density estimates was relatively consistent, with a few areas (including the one with the lowest estimated density, "Statskog og Klinga utm.") sticking out by having substantially less precise estimates (Figure 3 (b)). Populations fluctuated substantially over time in any given area (SF "TimeSeries_popDens1.pdf") and some years seemed to be indicative of relatively high (e.g. 2011, 2014, 2018) or low (e.g. 2012, 2015) densities across a substantial number of areas.

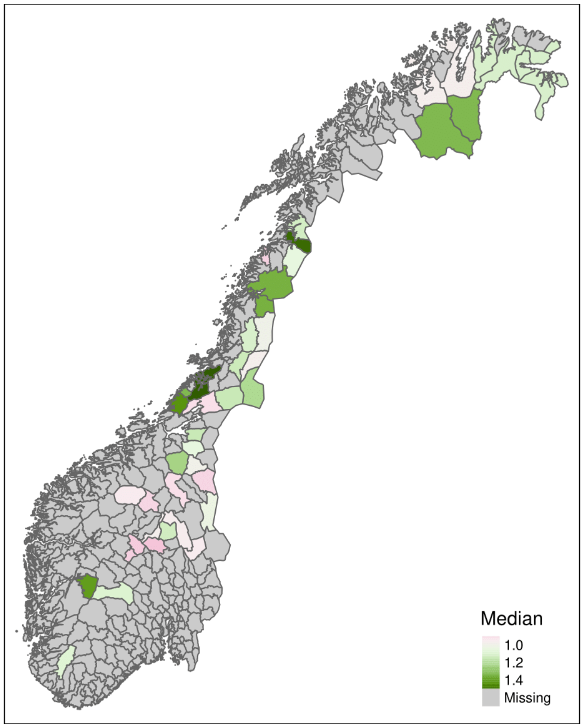


(a) Median density estimates *(b) Uncertainty in density estimates*

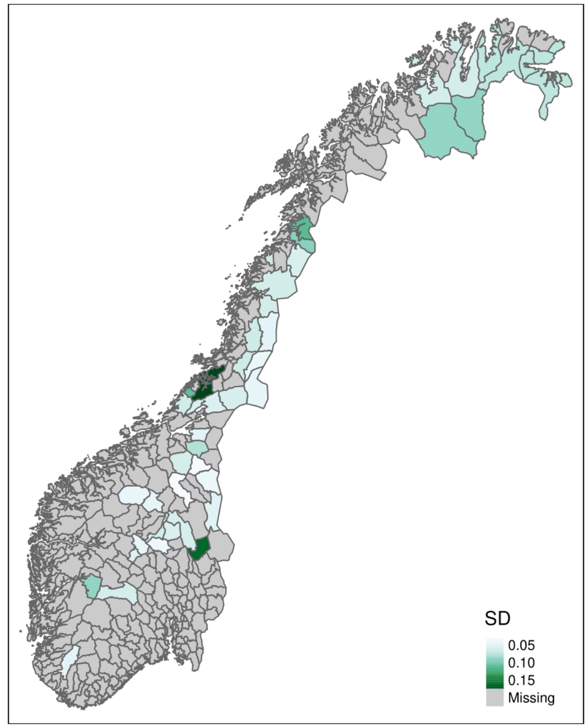
Figure 3: Median (a) and coefficient of variation (standard deviation / mean) (b) of posterior estimates of average ptarmigan density in the four most recent years (2018-2021) across 41 reporting areas (summarised at the municipality level) in Norway. Darker colors indicate higher median values and higher uncertainty.

Population growth rate

Average population growth rates over the last four years (2018-2021) ranged from moderate declines (0.718 [0.639, 0.923] in the "Kongsvoll" area) to > 50% increase (1.553 [1.262, 1.961] in the "Statskog og Klinga utm." area). In the majority of reporting areas (24 out of 41), populations of willow ptarmigan have been increasing over the period 2018-2021 (Figure 4). Some areas – predominantly in central Norway – also had declining populations, but many of those declines followed upon periods of increase between the start of data collection in 2007 and sometime between 2016 and 2018 (SF "TimeSeries_popDens1.pdf").



(a) Median population growth rate estimates



(b) Uncertainty in population growth rate estimates

Figure 4: Median (a) and standard deviation (b) of posterior estimates of average annual population growth rate over the four most recent years (2018-2021) across 41 reporting areas (summarised at the municipality level) in Norway. In a), pinkish colors indicate declining populations while greenish colors indicate growing populations (white = stable populations). In b) darker colors indicate higher uncertainty.

The highest recent population growth rates were estimated for areas with relatively low recent population densities across latitudes but we did not find evidence for a strong association between population growth rates and population densities overall (Figure 5 A).

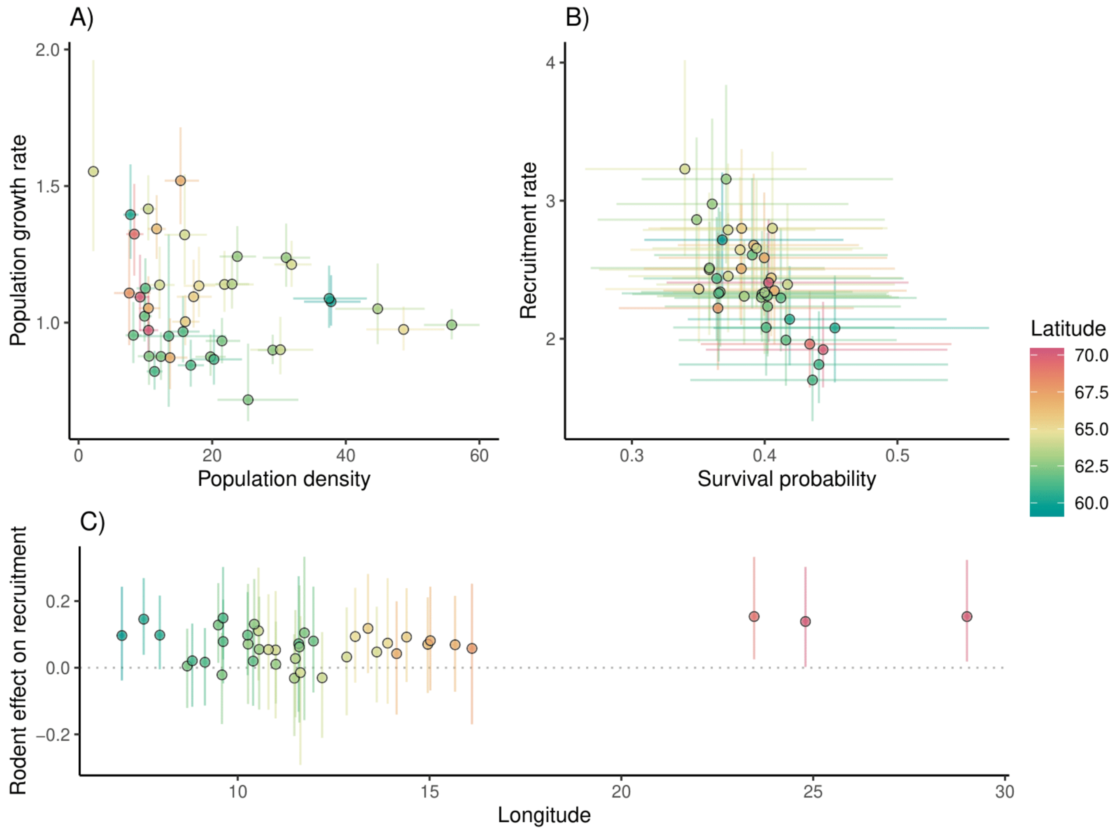
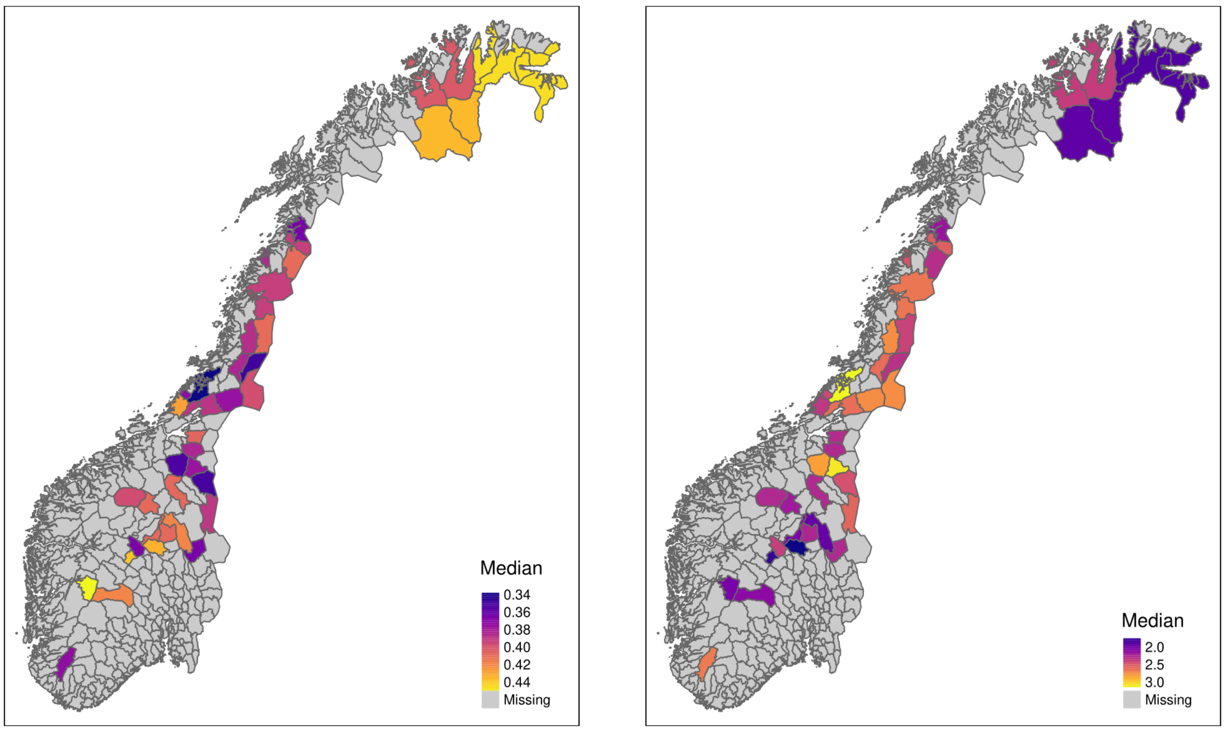


Figure 5: Posterior summaries (points = posterior medians, lines = 95% credible intervals) of area-specific population growth rate vs. population density over the four most recent years (2018-2021, A), recruitment rate vs. survival probability (B) and rodent effect on recruitment along a longitudinal gradient (C). Color indicates latitude of the midpoint of each area.

Survival probabilities and recruitment rates

Annual survival probabilities ranged from 0.34 [0.265, 0.431] (area “Statskog og Klinga utm.”) to 0.453 [0.362, 0.569] (area “Eidfjord Fjellstyre”) across reporting areas in Norway, with the highest values occurring in the far north and in the mountains in the south (Figure 6 (a)). The global average survival probability across all areas and years (μ^S) was estimated at 0.4 [0.347, 0.459]. Spatial variation in survival (random effect SD = 0.169 [0.079, 0.28]) was relatively low compared to temporal (0.548 [0.291, 1.042]) and residual (0.636 [0.577, 0.703]) variation.

Recruitment rates varied between 1.701 [1.404, 2.02] (area “Gausdal Fjellstyre”) and 3.229 [2.6, 4.018] (area “Statskog og Klinga utm.”) and displayed a spatial pattern opposite to that of annual survival, i.e., lower recruitment rates co-occurring with higher survival rates and vice-versa (Figure 6 (b); Figure 5 B). Across all areas and years, average recruitment rate was 2.383 [2.155, 2.835]. Unlike for survival, the model predicted similar magnitudes of spatial and temporal variation (random effect SDs of 0.167 [0.126, 0.233] and 0.121 [0.069, 0.205], respectively), and about twice as much residual variation (0.331 [0.307, 0.356]).



(a) Median survival probabilities

(b) Median recruitment rates

Figure 6: Posterior medians of average annual survival probabilities (a) and recruitment rates (b) across 41 reporting areas (summarised at the municipality level) in Norway. Darker colors indicate higher median values. Measures for corresponding uncertainty in estimates are visualized in SFs "Avg_pSurv_Map.pdf" and "Avg_rRep_Map.pdf" for survival and recruitment, respectively.

The MCMC chains for many of the area-specific average survival probabilities and recruitment rates, as well as for the global averages for both vital rates, were mixing rather poorly. Despite that, mixing was good and resulting posteriors well defined for the area-and year-specific estimates of survival and recruitment (SF “PostDens_tS_tR.pdf”). There was substantial variation in both vital rates across time (SFs “TimeSeries_pSurv.pdf” and “TimeSeries_rRep.pdf”). In a substantial number of areas, the years 2011, 2014, and 2018 not only supported high population densities (see above) but were also characterized by both high recruitment and low subsequent survival. The overall low density years 2012 and 2015, conversely, often featured lower recruitment and, in some cases, higher survival. Notably, there were also years with very little spatial synchrony, i.e. very different relative yearly survival probabilities and recruitment rates (e.g. 2010 and 2020 for survival and 2013, 2016, and 2017 for recruitment).

Effects of rodent occupancy

The model predicted a positive global effect of rodent occupancy on recruitment rate (average slope on the log scale = 0.067 [-0.004, 0.124]). Nonetheless, spatial variation in the rodent effect was substantial (random effect SD = 0.093 [0.031, 0.153]). This resulted in negative (median) effects in 4 areas, positive (median) effects in 37 areas, and a range of effect sizes from -0.031 [-0.205, 0.1] (area “Selbu Fjellstyre”) to 0.154 [0.025, 0.332] (area “Indre Finnmark”, Figure 5 C, SF “Rep_betaR.R.pdf”). The largest positive rodent effects were estimated for areas in the very North of Norway, as well as in the mountaineous regions in the central and southwestern parts of the country (SF “betaR_Map.pdf”). Effects with negative posterior medians were located mostly at intermediate latitudes, but we note that all of these had posterior distributions featuring substantial overlap with 0 (Figure 5 C).

Detection parameters

Detection decay parameters, which determine detection probability in distance sampling surveys, varied across areas from between 69.461 [61.075, 79.231] in “Namskogan Fjellstyre” to 125.03 [109.715, 142.31] in “Engerdal Fjellstyre, resulting in detection probabilities over the transect sites ranging from 0.435 [0.383, 0.497] to 0.784 [0.688, 0.892], respectively (truncation distance = 200 m) . The global average detection decay was 95.668 [86.858, 105.263] (detection probability = 0.6 [0.544, 0.66]), and in general, higher values were more common in the Southern half of the country than the Northern half (SF"Avg_detect_Map.pdf"). Variation in detection over time was modest (SF "TimeSeries_pDetect.pdf"), and among-year variation in detection decay (random effect log SD = 0.144 [0.097, 0.234]) was almost identical in magnitude to spatial (0.143 [0.109, 0.19]) and residual (0.142 [0.124, 0.16]) variation.

Variance decomposition

The relative importance of different components for explaining parameter variation differed among recruitment rate, survival probability, and detection decay (Figure 7). The largest portion of variation in recruitment was attributed to residual variation (65.3 [53.2, 76] %), followed by spatial (16.7 [9.8, 28.5] %) and temporal (8.8 [2.9, 22.3] %) variation. Rodent occupancy, which contains both a spatial and a temporal dimension, explained 7.8 [2.3, 13.6] % of the total variation. For survival, there was large uncertainty in the estimated proportions of variance explained by different components. The model predicted similar potential contributions from temporal (40.5 [16.6, 71.2] %) and residual (54.7 [26.7, 80.7] %) variation and suggested that spatial variation was only responsible for 3.6 [0.9, 9.6] % of the total variance. Total variance in detection decay was attributed evenly to spatial, temporal, and residual variation at 32.8 [18, 49.6] %, 33.6 [17.5, 58.6] %, and 31.9 [19.5, 45.3] %, respectively.

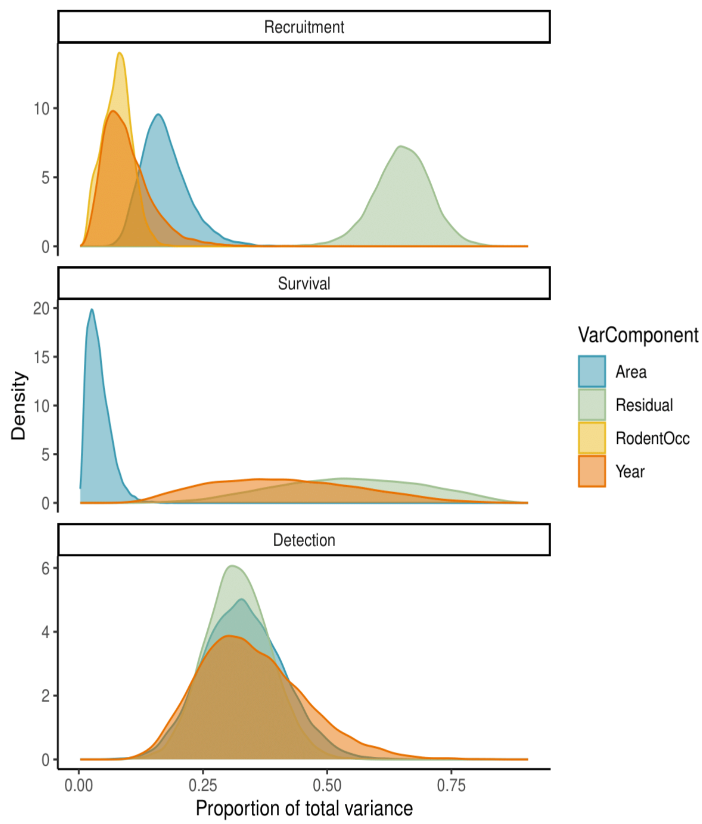


Figure 7: Posterior distributions for the proportions of parameter variance explained by spatial (blue), temporal (orange), and residual (green) variation, as well as by effects of rodent occupancy (yellow).

Discussion

Building on the work of Nilsen and Nater (2024), we applied a novel integrated population model to data collected through a national-scale participatory monitoring programme to estimate spatial and temporal variation in demography of a culturally important game bird species, the willow ptarmigan. While our study was exploratory in nature, it recovered patterns consistent with ecological and life-history theory including trade-offs between survival and recruitment, and a tendency towards slower life histories at higher latitudes and altitudes. Space-for-time substitution also provided the statistical power necessary for the analysis to provide evidence for the alternative prey hypothesis, i.e. ptarmigans benefiting from high abundance of alternative rodent prey for their predators. Taken together, the results highlight the potential of integrating demographic data across large spatial scales in the contexts of both informing management and creating biodiversity indicators for higher-level reporting.

Abundance and vital rates across space and time

The wide spatial distribution of the line transect monitoring afforded us the opportunity to explore variation in population density and vital rates across a relatively large spatial extent.

Ptarmigan densities across the 41 reporting districts included in our analyses varied from around 2 birds/km^2 to 55 birds/km^2, with the lowest densities occurring far north in the country, as well as on the west coast and in the mountains in central Norway Figure 3 (a). The same spatial pattern was also evident at the level of the demographic rates: consistent with basic life history theory (Stearns 1992), average recruitment rates were inversely related to average survival probabilities Figure 5, and the slower life histories (higher survival and lower recruitment) were more common in the northern and mountaineous parts of the country. This aligns with previous studies reporting relatively slower bird life histories in alpine / high altitude areas (e.g. Sandercock, Martin, and Hannon 2005; Bears, Martin, and White 2009; Wilson and Martin 2011; Alice Boyle, Sandercock, and Martin 2016). In Norway, the northern and mountainous areas are characterized by more extreme climatic conditions, boasting cold temperatures and short growing seasons. Resulting reduced primary production limits food availability and as ptarmigan are income breeders that use food resources acquired from nesting areas to supply energy and nutrients for egg production and incubation (Sandercock, Martin, and Hannon 2005), lower carrying capacity in such areas is to be expected.

We found increasing population trends over recent years in over half of the reporting districts, but population declines were also evident in some areas, particularly in the mountains in central Norway Figure 4 (a). Predominantly increasing population trends are consistent with a recent national-scale analysis by Nilsen and Rød-Eriksen (2020) which found an overall increase in the Norwegian ptarmigan population between 2009 and 2020. While we may speculate that recent population trends could be linked to changes in harvest regulations and/or climatic conditions, considering the whole time-series (2007-2021) illustrated that population densities in all areas were subject to substantial variation across years, featuring periods of stability, increase, and decrease (SF "TimeSeries_PopDens1.pdf"). In most areas, there were also strong year-by-year fluctuations in population density on top of longer-term trends. Some of the resulting "high density years" were highly synchronized across large spatial scales, such as the years 2011, 2013, and 2018. Taking a closer look, we find that these are years that are characterized by high recruitment (SF "TimeSeries_rRep.pdf"), followed by a low survival the year after (SF "TimeSeries_pSurv.pdf"). This often resulted in steep population declines towards the following year. The fact that these same years also match up with observed peaks in rodent abundance in many areas, together with the largely positive effects of rodent occupancy on recruitment estimated by our model (Figure 5 C), provides evidence for the Alternative Prey Hypothesis [APH; Hagen (1952)]. The APH stipulates that high abundance of alternative prey (rodents, in this case) for common predators leads to population growth, and is well-supported throughout the literature for a range of taxa (e.g., Hagen 1952; Kjellander and Nordström 2003; Reif et al. 2001), including willow ptarmigan (Bowler et al. 2020). While Nyström et al. (2006) suggested that gyrfalcons, which are specialized ptarmigan predators, do not respond to rodent populations or switch to alternative prey when ptarmigan populations are low, generalist predators, such as red foxes, are likely to shift from preying on ptarmigans to rodents when the latter become abundant (e.g. Breisjøberget, Odden, Wegge, et al. 2018; Bowler et al. 2020). Taking a spatial perspective, the highest latitude and highest altitude areas stood out once more, sporting the strongest effects of rodent occupancy (SF "betaR_Map.pdf"). This could be related to warmer areas generally having larger predator guilds, and consequently more generalists that are able to maintain relatively stable populations irrespective of small rodent abundance (Bowler et al. 2020).

Notably, the conclusive estimation of overall positive effects of rodent occupancy on recruitment in our model was only possible thanks to the integration and sharing of data across multiple areas. When Nilsen and Nater (2024) fit the IDSM to data from only a single area, they were unable to obtain a reliable estimate for the rodent effect due to limited statistical power. Consequently, the space-for-time substitution that comes with extending the model across multiple area allows estimation of covariate effects that otherwise cannot be estimated, and opens up for future possibilities for studying effects of not just rodents, but also other environmental drivers on ptarmigan population dynamics. Doing so may also help with better understanding the mechanisms underlying the large portion of demographic rate variation that could only be attributed to random variation so far. This is the case especially for the relatively large residual variation Figure 7 but also relevant for constant spatial and shared temporal variation. In previous work based on both marked (Eriksen et al. 2023) and unmarked birds (Bowler et al. 2020; J. A. Henden et al. 2020; Novoa et al. 2016), spring conditions has come out as an important predictor of ptarmigan recruitment rates. In general, warmer and earlier springs seem to favour earlier breeding, larger clutch sizes (Eriksen et al. 2023), and resulting higher recruitment rates measured in the late summer and early fall. Bowler et al. (2020) further reported that the strength of this relationship was not consistent in time and space, but was generally stronger in colder areas, similar to what we found for the effect of rodent occupancy here. In practice, measures representing spring conditions, such as the cover of ericaceous shrubs (a proxy for food availability) or spatially-explicit spring green up dates derived from remote-sensing data, thus constitute relevant candidate covariates for future work alongside temperature.

Another important determinant of vital rate variation is density dependence, in particular for exploited species like willow ptarmigan (Andrewartha and Birch 1954; Sandercock et al. 2011; Aanes et al. 2002; Willebrand and Hörnell 2001). Negative density dependence has been found in several gallinaceous birds such as northern bobwhites *Colinus virginianus* (McConnell et al. 2018), *Perdix perdix* (Bro et al. 2003), and wild turkeys *Meleagris gallopavo* (McGhee and Berkson 2007)). For willow ptarmigan, evidence for density-dependent population regulation has been mixed. Myrberget (1988), for example, observed no change in productivity despite a 50% decrease in abundance, while Pedersen et al. (2004) reported strong negative density-dependence over winter and posited that dispersal may be the vital rate that responded to changes in density most strongly. Similarly, J. A. Henden et al. (2020) reported negative density dependence when using a Gompertz-model to examine how density and a range of environmental covariates affected willow ptarmigan population dynamics in the northernmost parts of Norway. While we did not explicitly model density dependence in this study, our results can provide some preliminary insights into potential density feedbacks from both a spatial (cross-population) and a temporal (within-population) angle. Comparing average population densities and growth rate across areas did not provide evidence for strong density dependence, but there was a tendency towards the highest population growth rates appearing areas with relatively low density, and relatively low growth rates in high-density areas Figure 5. When considering density dependence across years within select areas, however, we found that higher density years were associated with higher recruitment the same year, but followed by lower apparent survival probabilities and, consequently, lower population growth rates (as determined by post-hoc Pearson correlation coefficients, supplementary file "DD_corrCoef.csv"). While this seems to support the notion of negative density-dependence, testing for this post-hoc gives results that are confounded with sampling correlation (Freckleton et al. 2006). Hence, formally modelling density-dependence, possibly using different forms and time-lags, could prove to be a promising extension of our modelling framework in the future.

Implications for management and monitoring

Management decisions made at the resolution of large geopolitical boundaries (e.g., Norway) run a high risk of being inadequate when there is substantial spatial variation in demographic processes and population dynamics, as is the case for willow ptarmigan. In Norway, willow ptarmigan – and small game in general – is managed at the local and/or regional scale, with rather limited national regulation beyond updating the length of the hunting season every fourth year. In effect, management system, regulation type (quota type, season length, number of licences, bag limit etc.), and quota size are governed by the local or regional stakeholders (Eriksen, Moa, and Nilsen 2018; Breisjøberget, Odden, Storaas, et al. 2018). Thus, while national estimates (abundance and/or temporal trend in abundance) might be important for red listing decisions and for setting the maximum hunting season length, remaining decisions about harvest management are taken locally. The results from our study highlight a large degree of spatio-temporal variation in both ptarmigan densities and demographic rates, suggesting that it is indeed suitable for management decisions to be spatially refined and ideally informed by up-to-date knowledge about recent "local" population processes. Accessible and easily repeatable modelling workflows, such as the one we have developed in this study, can thus become a valuable source of information for local decision-makers.

Our results also provided some insights into the value, and possibly opportunities for improving the monitoring programme. First and foremost, our study demonstrates the tremendous potential lying in coordinating structured monitoring that employs common sampling protocol, training programmes, and data processing pipelines. These were indeed the prerequisites that allowed us to easily and efficiently integrate data collected across the entire country in a joint analysis, and draw inference on fine-scale spatio-temporal variation in demography and population dynamics at across a large area. While overall less variable across space and time than vital rates, differences in detection probabilities were nonetheless evident (SFs "Avg_detect_Map.pdf" and "TimeSeries_pDetect.pdf") and may help with mapping out potential for improvement in the monitoring programme. Particularly, we found generally lower detection probabilities in the northern half of Norway. This may be related to habitat features, as the transects in the North might be to a larger extent located in birch forests and rugged terrain, which may hamper detectability. Additionally, the slower life histories in the northern areas are reflected as generally smaller bird clusters as well, and smaller clusters have previously been shown to have a lower detectability than larger ones (e.g. Bowler et al. 2020, see also next section). Our modelling framework can be easily adapted for studying the impact of these and other variables on detectability (see below). Additionally, our results could motivate taking a closer look at monitoring challenges and potential improvements in the northern part of the country in particular. Ultimately, increased detection probability would contribute to obtaining more precise estimates of both population density and demographic rates, which – in turn – would be of great value in particular in areas with relatively low population densities, low number of transects, and less years of data.

Model limitations and outlook

The primary focus of this work was placed on developing an effective pipeline for integrating data and modelling population dynamics across a large number of areas. Consequently, many additional opportunities for improving and refining the modelling framework itself remain. First, the precision and accuracy of model estimates might be increased through better accounting for heterogeneity and potential biases in detection of birds during the line transect surveys. In an earlier study analyzing data from the same monitoring programme, Bowler et al. (2020), found that detection probability was not independent of the size of group birds were part of, resulting in birds in larger groups being more likely to be detected, especially at larger distances. When birds are observed in larger groups, it is also not unlikely that human observers may miscount, i.e. that there is some observation error in the number reported. This could be incorporated by including an additional layer of hierarchy to the observation process (see e.g., Hamilton et al. 2018), and possibly further extended to also account for error in judging the observation distance (e.g., Marques 2004). Another potential source of bias in our IDSM is related to failure to correctly assign the age class of observed birds. Nilsen and Nater (2024) showed that incorrect age assessment can bias (relative) estimates of survival and recruitment, and while they only found a weak bias in their case study on a single area, the problem may be larger in a multi-area setting that may contain areas with different proportions of misclassified observations. If misclassification happened at random, mixture models could be used to determine the likely age class of individuals to whom no age class was assigned during observations (McCrea, Morgan, and Cole 2013). In our case, we might suspect that an observed is more likely to classify an adult bird as juvenile rather than the other way around, and more likely to assign "unknown" age class to juveniles than adults. One reason for this is that observers look for specific signs to classifying a bird as adult (e.g. size, male sound), and might default to juvenile or unknown if the signs are not clearly detected. Future studies should investigate to what degree available information on e.g. group composition could be used for this, and what kind of auxiliary data would need to be collected to reliably model misclassification error.

The second (and perhaps most attractive) aspect of our modelling framework in the context of future work is its spatio-temporal hierarchical structure. While we included spatial, temporal, and residual variation in our framework here, we treated them as independent. Alternatively, spatial (and temporal) correlations among parameters can be modelled explicitly, something that is commonly done e.g. in modern species distribution models (e.g. Pacifici et al. 2017; Guélat and Kéry 2018). For demographic models, this has rarely been implemented so far, not least due to the fact that few demographic models have sufficient spatial resolution (Schaub and Kéry 2021). The ptarmigan IDSM presented in this study, however, does have sufficient resolution and our results do indeed support that there is spatial clustering in both overall and time-dependent demographic parameters (e.g. Figure 6, SFs "Avg_pSurv_Map.pdf" & "Avg_rRep_Map.pdf"). Furthermore, we did find that mixing of several of the global and area-specific intercept parameters in the current model was suboptimal, suggesting that there may be much to gain from additional structuring, as well as from development of more efficient MCMC sampling strategies for the resulting extended model. One promising framework for approaching this are conditionally autoregressive models (CARs, Ver Hoef et al. 2018). Such models have been used repeatedly for modelling spatial autocorrelation in species occupancy and demographic rates (e.g. Saracco et al. 2010, 2012; Guélat and Kéry 2018) and are straightforward to implement using NIMBLE (Lawson 2020). One possible challenge with using CAR models to explicitly model spatial correlations within our ptarmigan IDSM is that CAR models rely on "neighborhood" relationships between discrete areas and many "neighbors" are missing in our ptarmigan data (e.g. Figure 3). While estimation of latent parameters in missing areas may possible (Perry de Valpine, personal communication; Schaub and Kéry (2021) chapter 19), this also provides an opportunity for inclusion of additional data. The line transect survey data included in this study constitutes just the publicly available part of the data collected through "Hønsefuglportalen" but the programme also includes additional surveys on private land. Extending to data from private land would provide better coverage especially in south-eastern and southern parts of Norway, which includes areas where only very limited amounts of data are collected on public land. Exploring to what degree additional data from Hønsefuglportalen could be included in future studies employing an extended IDSM with additional spatial structuring is therefore a worthwhile endeavor.

Finally, including further data beyond the line transect surveys may be relevant in the future, and in particular in the context of informing and improving management of ptarmigan hunting. In the present study, we have used auxiliary radio-telemetry data to supplement information on survival, but since this data was available for only one out of 41 areas, its influence was likely small. Nonetheless, this illustrates a way for how smaller datasets from single or subsets of areas can be integrated into a large-scale modelling framework. Other relevant data could be included using the same approach, for example data from ongoing nesting success monitoring, data from past studies of marked birds (Sandercock et al. 2011), and data from other monitoring programs for breeding birds based on point counts (see e.g. the Norwegian Breeding Bird Monitoring: https://hekkefuglovervakingen.nina.no/). The most relevant source of data to be included into the IDSM framework in the near future, however, is harvest data. Such data might be available with different spatial and temporal resolutions. First, at the municipality level there are data with national coverage collected annually by Statistics Norway (https://www.ssb.no/). Second, many public land owners have data with much higher temporal (daily) and spatial (harvest area) resolution, including both harvest bags and harvest effort (number of hunters per area per day). As the IDSM framework is, in essence, an IPM, harvest can be modelled through partitioning of survival into cause-specific mortality in the process model and inclusion of relevant harvest data likelihoods (e.g., Gamelon et al. 2021; Nater et al. 2021). While harvest effects on willow ptarmigan have been studied previously, much uncertainty remains (Sandercock et al. 2011; Aanes et al. 2002; Pedersen et al. 2004; Willebrand and Hörnell 2001). For example, little is known about how harvest pressure and density feedbacks interact on different temporal and spatial scales (Kvasnes et al. 2015), despite this knowledge being crucial for preventing over-exploitation and ensuring sustainable harvest (Williams, Nichols, and Conroy 2002; Breisjøberget, Odden, Storaas, et al. 2018). Additionally, harvest effects often interact with other (emergent) factors such as climate change and habitat degradation, making predictive models that account for harvest alongside other mechanisms invaluable for informing policy changes (Gamelon, Sandercock, and Sæther 2019).

Reproducible workflows for a sustainable future

Producing a transparent and reproducible workflow for the analysis presented here was a central objective in this study. We have done this by setting up "targets" pipeline (Landau 2021), which allows (re-)running the complete workflow from downloading the publicly available data to visualizing the results produced by the IDSM Figure 2. Modern applied ecology needs research to be published not just as scientific papers, but as reproducible and well documented workflows (Lewis, Vander Wal, and Fifield 2018). This is particularly crucial for research that is (to be) closely tied to management and/or used to create biodiversity indicators that are to be reported nationally or internationally, or to be used by industrial partners (Powers and Hampton 2019). This is both because of the enhanced transparency and credibility provided by openly available reproducible workflows and because of their cost-effectiveness, which allows for more sustainable use of funding in the mid- to long-term. Finally, open and reproducible workflows facilitate collaboration and inclusion of stakeholders in the research process, paving the path for the translational science that is required for society to tackle the the biodiversity crisis (Rubert-Nason et al. 2021). It is our hope that this study can serve as an example of where to start.

Author contributions

Chloé R. Nater: Conceptualization, Methodology, Software, Formal analysis, Writing - Original Draft, Writing - Review and editing, Visualization.

James A. Martin: Conceptualization, Writing - Original Draft, Writing - review and editing.

Erlend B. Nilsen: Conceptualization, Methodology, Data curation, Writing - Original Draft, Writing - Review and editing, Project administration, Funding acquisition

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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 in relation to the content of the article.

Data and code availability

The raw data from the line transect surveys is deposited on GBIF and can be accessed freely via the Living Norway Data Portal (https://data.livingnorway.no/). The work presented above is based on versions 1.7, 1.8, and 1.12 for the datasets from Fjellstyrene (Nilsen, Vang, Kjønsberg, and J. 2022), Statskog (Nilsen, Vang, and I. 2022), and FeFo (Nilsen, Vang, Kjønsberg, and E. 2022), respectively.

The auxiliary radio-telemetry data, rodent occupancy data, posterior summaries, and supplementary figures are archived on OSF (Nater, Nilsen, and Martin 2024).

All code including the "targets pipeline" can be found in the project's repository on GitHub: https://github.com/ErlendNilsen/OpenPop_Integrated_DistSamp. The results presented in this paper were created using version 2.0 of the code (ChloeRNater et al. 2024).

References

Aanes, Sondre, Steinar Engen, Bernt-Erik SÆther, Tomas Willebrand, and Vidar Marcström. 2002. "Sustainable Harvesting Strategies of Willow Ptarmigan in a Fluctuating Environment." *Ecological Applications* 12 (1): 281–90.

Aebischer, Nicholas J., and Julie A. Ewald. 2010. "Grey Partridge Perdix Perdix in the UK: Recovery Status, Set-Aside and Shooting." *Ibis* 152 (3): 530–42. https://doi.org/https://doi.org/10.1111/j.1474-919X.2010.01037.x.

Alice Boyle, W, Brett K Sandercock, and Kathy Martin. 2016. "Patterns and Drivers of Intraspecific Variation in Avian Life History Along Elevational Gradients: A Meta-Analysis." *Journal of Animal Ecology* 91 (2): 469–82.

Andrewartha, Herbert George, and L. Charles Birch. 1954. *The Distribution and Abundance of Animals.* University of Chicago press.

Arnekleiv, Øyvind, Katrine Eldegard, Pål F. Moa, Lasse F. Eriksen, and Erlend B. Nilsen. 2022. "Drivers and Consequences of Partial Migration in an Alpine Bird Species." Journal Article. *Ecology and Evolution* 12 (3): e8690. https://doi.org/https://doi.org/10.1002/ece3.8690.

Bears, H, K Martin, and GC White. 2009. "Breeding in High-Elevation Habitat Results in Shift to Slower Life-History Strategy Within a Single Species." *Journal of Animal Ecology* 78 (2): 365–75.

Bowler, Diana E, Mikkel AJ Kvasnes, Hans C Pedersen, Brett K Sandercock, and Erlend B Nilsen. 2020. "Impacts of Predator-Mediated Interactions Along a Climatic Gradient on the Population Dynamics of an Alpine Bird." *Proceedings of the Royal Society B* 287 (1941): 20202653.

Breisjøberget, Jo Inge, Morten Odden, Torstein Storaas, Erlend B. Nilsen, and Mikkel A. J. Kvasnes. 2018. "Harvesting a Red-Listed Species: Determinant Factors for Willow Ptarmigan Harvest Rates, Bag Sizes, and Hunting Efforts in Norway." *European Journal of Wildlife Research* 64 (5): 54. https://doi.org/10.1007/s10344-018-1208-8.

Breisjøberget, Jo Inge, Morten Odden, Per Wegge, Barbara Zimmermann, and Harry Andreassen. 2018. "The Alternative Prey Hypothesis Revisited: Still Valid for Willow Ptarmigan Population Dynamics." *PLOS ONE* 13 (6): 1–14. https://doi.org/10.1371/journal.pone.0197289.

Bro, Elisabeth, Benoît Deldalle, Manuel Massot, François Reitz, and Slaheddine Selmi. 2003. "Density Dependence of Reproductive Success in Grey Partridge Perdix Perdix Populations in France: Management Implications." *Wildlife Biology* 9 (2): 93–102. https://doi.org/10.2981/wlb.2003.031.

ChloeRNater, ErlendNilsen, christofferhohi, Matthew Grainger, and Bernardo Brandão Niebuhr. 2024. "ErlendNilsen/OpenPop_Integrated_DistSamp: Ptarmigan IDSM v2.0." Zenodo. https://doi.org/10.5281/zenodo.10572340.

Christie, Alec P, Tatsuya Amano, Philip A Martin, Silviu O Petrovan, Gorm E Shackelford, Benno I Simmons, Rebecca K Smith, David R Williams, Claire FR Wordley, and William J Sutherland. 2020. "Poor Availability of Context-Specific Evidence Hampers Decision-Making in Conservation." *Biological Conservation* 248: 108666.

Dickinson, Janis L, Benjamin Zuckerberg, and David N Bonter. 2010. "Citizen Science as an Ecological Research Tool: Challenges and Benefits." *Annual Review of Ecology, Evolution, and Systematics* 41: 149–72.

Elton, Charles. 1942. *Voles, Mice and Lemmings: Problems in Population Dynamics*. Clarendon Press.

Eriksen, L. F., P. F. Moa, and E. B. Nilsen. 2018. "Quantifying Risk of Overharvest When Implementation Is Uncertain." Journal Article. *Journal of Applied Ecology* 55 (2): 482–93. https://doi.org/10.1111/1365-2664.12992.

Eriksen, L. F., T. H. Ringsby, H. C. Pedersen, and E. B. Nilsen. 2023. "Climatic Forcing and Individual Heterogeneity in a Resident Mountain Bird: Legacy Data Reveal Effects on Reproductive Strategies." Journal Article. *Royal Society Open Science* 10 (5): 221427. https://doi.org/doi:10.1098/rsos.221427.

Feld, Christian K, Pedro Martins da Silva, José Paulo Sousa, Francesco De Bello, Rob Bugter, Ulf Grandin, Daniel Hering, et al. 2009. “Indicators of Biodiversity and Ecosystem Services: A Synthesis Across Ecosystems and Spatial Scales.” *Oikos* 118 (12): 1862–71.

Fraisl, Dilek, Gerid Hager, Baptiste Bedessem, Margaret Gold, Pen-Yuan Hsing, Finn Danielsen, Colleen B Hitchcock, et al. 2022. “Citizen Science in Environmental and Ecological Sciences.” *Nature Reviews Methods Primers* 2 (1): 64.

Framstad, Erik, Nina E Eide, Wenche Eide, Kari Klanderud, Anders Kolstad, Joachim Töpper, and Vigdis Vandvik. 2022. “Vurdering Av økologisk Tilstand for Fjell i Norge i 2021.” *NINA Rapport* 2050.

Franke, Alastair, Knud Falk, Kevin Hawkshaw, Skip Ambrose, David L. Anderson, Peter J. Bente, Travis Booms, et al. 2020. “Status and Trends of Circumpolar Peregrine Falcon and Gyrfalcon Populations.” Journal Article. *Ambio* 49 (3): 762–83. https://doi.org/10.1007/s13280-019-01300-z.

Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. “Census Error and the Detection of Density Dependence.” Journal Article. *Journal of Animal Ecology* 75 (4): 837–51. https://doi.org/10.1111/j.1365-2656.2006.01121.x.

Fuglei, Eva, John-André Henden, Chris T. Callahan, Olivier Gilg, Jannik Hansen, Rolf A. Ims, Arkady P. Isaev, et al. 2020. “Circumpolar Status of Arctic Ptarmigan: Population Dynamics and Trends.” *Ambio* 49 (3): 749–61. https://doi.org/10.1007/s13280-019-01191-0.

Gamelon, Marlène, Chloé R Nater, Éric Baubet, Aurélien Besnard, Laura Touzot, Jean-Michel Gaillard, Jean-dominique Lebreton, and Olivier Gimenez. 2021. “Efficient Use of Harvest Data: A Size-Class-Structured Integrated Population Model for Exploited Populations.” *Ecography* 44 (9): 1296–1310.

Gamelon, Marlène, Brett K. Sandercock, and Bernt-Erik Sæther. 2019. “Does Harvesting Amplify Environmentally Induced Population Fluctuations over Time in Marine and Terrestrial Species?” *Journal of Applied Ecology* 56 (9): 2186–94. https://doi.org/10.1111/1365-2664.13466.

Guélat, Jérôme, and Marc Kéry. 2018. "Effects of Spatial Autocorrelation and Imperfect Detection on Species Distribution Models." *Methods in Ecology and Evolution* 9 (6): 1614–25.

Hagen, Yngvar. 1952. *Rovfuglene Og Viltpleien*. Gyldendal Norsk forlag.

Hamilton, Olivia NP, Sophie E Kincaid, Rochelle Constantine, Lily Kozmian-Ledward, Cameron G Walker, and Rachel M Fewster. 2018. "Accounting for Uncertainty in Duplicate Identification and Group Size Judgements in Mark–Recapture Distance Sampling." *Methods in Ecology and Evolution* 9 (2): 354–62.

Henden, J. A., R. A. Ims, N. G. Yoccoz, E. J. Asbjornsen, A. Stien, J. P. Mellard, T. Tveraa, F. Marolla, and J. U. Jepsen. 2020. "End-User Involvement to Improve Predictions and Management of Populations with Complex Dynamics and Multiple Drivers." Journal Article. *Ecol Appl* 30 (6): e02120. https://doi.org/10.1002/eap.2120.

Henden, John-André, Rolf Anker Ims, Eva Fuglei, and Åshild Ønvik Pedersen. 2017. "Changed Arctic-Alpine Food Web Interactions Under Rapid Climate Warming: Implication for Ptarmigan Research" 2017 (SP1): wlb.00240. https://doi.org/https://doi.org/10.2981/wlb.00240.

Hjeljord, Olav, and Leif Egil Loe. 2022. "The Roles of Climate and Alternative Prey in Explaining 142 Years of Declining Willow Ptarmigan Hunting Yield." *Wildlie Biology* 2022 (6): e01058. https://doi.org/https://doi.org/10.1002/wlb3.01058.

Horswill, Cat, Holly K Kindsvater, Maria José Juan-Jordá, Nicholas K Dulvy, Marc Mangel, and Jason Matthiopoulos. 2019. "Global Reconstruction of Life-History Strategies: A Case Study Using Tunas." *Journal of Applied Ecology* 56 (4): 855–65.

Horswill, Cat, Andrea Manica, Francis Daunt, Mark Newell, Sarah Wanless, Matthew Wood, and Jason Matthiopoulos. 2021. "Improving Assessments of Data-Limited Populations Using Life-History Theory." *Journal of Applied Ecology* 58 (6): 1225–36.

Israelsen, M. F., L. F. Eriksen, P. F. Moa, B. R. Hagen, and E. B. Nilsen. 2020. “Survival and Cause-Specific Mortality of Harvested Willow Ptarmigan (Lagopus Lagopus) in Central Norway.” *Ecol Evol* 10 (20): 11144–54. https://doi.org/10.1002/ece3.6754.

Jakobsson, Simon, and Bård Pedersen. 2020. “Naturindeks for Norge 2020. Tilstand Og Utvikling for Biologisk Mangfold.” *NINA Rapport* 1886.

Jetz, Walter, Melodie A McGeoch, Robert Guralnick, Simon Ferrier, Jan Beck, Mark J Costello, Miguel Fernandez, et al. 2019. “Essential Biodiversity Variables for Mapping and Monitoring Species Populations.” *Nature Ecology & Evolution* 3 (4): 539–51.

Johnston, Alison, Eleni Matechou, and Emily B Dennis. 2023. “Outstanding Challenges and Future Directions for Biodiversity Monitoring Using Citizen Science Data.” *Methods in Ecology and Evolution* 14 (1): 103–16.

Kjellander, Petter, and Jonas Nordström. 2003. “Cyclic Voles, Prey Switching in Red Fox, and Roe Deer Dynamics – a Test of the Alternative Prey Hypothesis.” *Oikos* 101 (2): 338–44. https://doi.org/10.1034/j.1600-0706.2003.11986.x.

Kvasnes, Mikkel A. J., Hans Chr. Pedersen, Håkon Solvang, Torstein Storaas, and Erlend B. Nilsen. 2015. “Spatial Distribution and Settlement Strategies in Willow Ptarmigan.” *Population Ecology* 57 (1): 151–61. https://doi.org/10.1007/s10144-014-0454-1.

Landau, William Michael. 2021. “The Targets r Package: A Dynamic Make-Like Function-Oriented Pipeline Toolkit for Reproducibility and High-Performance Computing.” *Journal of Open Source Software* 6 (57): 2959. https://doi.org/10.21105/joss.02959.

Lawson, Andrew B. 2020. “NIMBLE for Bayesian Disease Mapping.” *Spatial and Spatio-Temporal Epidemiology* 33: 100323.

Lewis, Keith P, Eric Vander Wal, and David A Fifield. 2018. “Wildlife Biology, Big Data, and Reproducible Research.” *Wildlife Society Bulletin* 42 (1): 172–79.

Linden, H. 1988. “Latitudinal Gradients in Predator-Prey Interactions, Cyclicity and Synchronism in Voles and Small Game Populations in Finland.” Journal Article. *Oikos* 52 (3): 341–49. <Go to ISI>://A1988N893200014 .

Marques, Tiago A. 2004. “Predicting and Correcting Bias Caused by Measurement Error in Line Transect Sampling Using Multiplicative Error Models.” *Biometrics* 60 (3): 757–63.

McConnell, Mark D., Adrian P. Monroe, Richard Chandler, William E. Palmer, Shane D. Wellendorf, Jr., L. Wes Burger, and James A. Martin. 2018. “Factors Influencing Northern Bobwhite Recruitment, with Implications for Population Growth.” *The Auk* 135 (4): 1087–99. https://doi.org/10.1642/AUK-18-49.1.

McCrea, Rachel S, Byron JT Morgan, and Diana J Cole. 2013. “Age-Dependent Mixture Models for Recovery Data on Animals Marked at Unknown Age.” *Journal of the Royal Statistical Society Series C: Applied Statistics* 62 (1): 101–13.

McGhee, Jay D., and James M. Berkson. 2007. “Estimation of a Nonlinear Density-Dependence Parameter for Wild Turkey.” *Journal of Wildlife Management* 71 (3): 706–12. https://doi.org/10.2193/2005-630.

Morrison, Catriona A, Simon J Butler, Jacquie A Clark, Juan Arizaga, Oriol Baltà, Jaroslav Cepák, Arantza Leal Nebot, et al. 2022. “Demographic Variation in Space and Time: Implications for Conservation Targeting.” *Royal Society Open Science* 9 (3): 211671.

Myrberget, S. 1988. “Demography of an Island Population of Willow Ptarmigan in Northern Norway.s. 379-419. I Bergerud, a. T, & Gratson, MW [Red.], Adaptive Strategies and Population Ecology of Northern Grouse.” *I. Population Studies. University of Minnesota Press. Minneapolis, Minnesota, USA*.

Nakagawa, Shinichi, and Holger Schielzeth. 2013. “A General and Simple Method for Obtaining R2 from Generalized Linear Mixed-Effects Models.” *Methods in Ecology and Evolution* 4 (2): 133–42.

Nater, Chloé R, Malcolm D Burgess, Peter Coffey, Bob Harris, Frank Lander, David Price, Mike Reed, and Robert A Robinson. 2023. “Spatial Consistency in Drivers of Population Dynamics of a Declining Migratory Bird.” *Journal of Animal Ecology* 92 (1): 97–111.

Nater, Chloé R, Nina E Eide, Åshild Ø Pedersen, Nigel G Yoccoz, and Eva Fuglei. 2021. “Contributions from Terrestrial and Marine Resources Stabilize Predator Populations in a Rapidly Changing Climate.” *Ecosphere* 12 (6): e03546.

Nater, Chloé R, Erlend B Nilsen, and James Martin. 2024. “Large-Scale Spatiotemporal Variation in Vital Rates and Population Dynamics of an Alpine Bird.” OSF. https://doi.org/10.17605/OSF.IO/7326R.

Nater, Chloé R, Atle Rustadbakken, Torbjørn Ergon, Øystein Langangen, S Jannicke Moe, Yngvild Vindenes, Leif Asbjørn Vøllestad, and Per Aass. 2018. “Individual Heterogeneity and Early Life Conditions Shape Growth in a Freshwater Top Predator.” *Ecology* 99 (5): 1011–17.

Nilsen, E. B., and C. R. Nater. 2024. “An Integrated Open Population Distance Sampling Approach for Modelling Age-Structured Populations.” *EcoEvoRxiv*. https://doi.org/10.32942/X2Q899.

Nilsen, E. B., and L. Rød-Eriksen. 2020. “Trender i Størrelsen på Den Norske Lirypebestanden i Perioden 2009-2020. Analyser Basert på Data Fra hønsefuglportalen.” *NINA Rapport* 1869.

Nilsen, E. B., R. Vang, and Breisjøberget J. I. 2022. “Tetraonid Line Transect Surveys from Norway: Data from Statskog. Version 1.8.” Norwegian Institute for Nature Research. Sampling event dataset. https://doi.org/10.15468/q2ehlk.

Nilsen, E. B., R. Vang, M. Kjønsberg, and Asbjørnsen E. 2022. “Tetraonid Line Transect Surveys from Norway: Data from Finnmarkseiendommen (FeFo). Version 1.12.” Norwegian Institute for Nature Research. Sampling event dataset. https://doi.org/10.15468/s7c8qd.

Nilsen, E. B., R. Vang, M. Kjønsberg, and Kvasnes M. A. J. 2022. "Tetraonid Line Transect Surveys from Norway: Data from Fjellstyrene. Version 1.7." Norwegian Institute for Nature Research. Sampling event dataset. https://doi.org/10.15468/975ski.

Novoa, C., G. Astruc, J. F. Desmet, and A. Besnard. 2016. "No Short-Term Effects of Climate Change on the Breeding of Rock Ptarmigan in the French Alps and Pyrenees." Journal Article. *Journal of Ornithology* 157 (3): 797–810. https://doi.org/10.1007/s10336-016-1335-5.

Nyström, J., L. Dalén, P. Hellström, J. Ekenstedt, H. Angleby, and A. Angerbjörn. 2006. "Effect of Local Prey Availability on Gyrfalcon Diet: DNA Analysis on Ptarmigan Remains at Nest Sites." *Journal of Zoology* 269 (1): 57–64. https://doi.org/https://doi.org/10.1111/j.1469-7998.2006.00050.x.

Pacifici, Krishna, Brian J Reich, David AW Miller, Beth Gardner, Glenn Stauffer, Susheela Singh, Alexa McKerrow, and Jaime A Collazo. 2017. "Integrating Multiple Data Sources in Species Distribution Modeling: A Framework for Data Fusion." *Ecology* 98 (3): 840–50.

Pedersen, HC, H Steen, L Kastdalen, H Brøseth, RA Ims, W Svendsen, and NG Yoccoz. 2004. "Weak Compensation of Harvest Despite Strong Density–Dependent Growth in Willow Ptarmigan." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271 (1537): 381–85.

Pereira, Henrique Miguel, Simon Ferrier, Michele Walters, Gary N Geller, Rob HG Jongman, Robert J Scholes, Michael William Bruford, et al. 2013. "Essential Biodiversity Variables." *Science* 339 (6117): 277–78.

Powers, Stephen M, and Stephanie E Hampton. 2019. "Open Science, Reproducibility, and Transparency in Ecology." *Ecological Applications* 29 (1): e01822.

Proença, Vânia, Laura Jane Martin, Henrique Miguel Pereira, Miguel Fernandez, Louise McRae, Jayne Belnap, Monika Böhm, et al. 2017. "Global Biodiversity Monitoring: From Data Sources to Essential Biodiversity Variables." *Biological Conservation* 213: 256–63.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Reif, Vitali, Risto Tornberg, Sven Jungell, and Erkki Korpimäki. 2001. “Diet Variation of Common Buzzards in Finland Supports the Alternative Prey Hypothesis.” *Ecography* 24 (3): 267–74. https://doi.org/10.1034/j.1600-0587.2001.240304.x.

Robinson, Robert A, Catriona A Morrison, and Stephen R Baillie. 2014. “Integrating Demographic Data: Towards a Framework for Monitoring Wildlife Populations at Large Spatial Scales.” *Methods in Ecology and Evolution* 5 (12): 1361–72.

Rubert-Nason, Kennedy, AM Aramati Casper, Matt Jurjonas, Caitlin Mandeville, Rebecca Potter, and Kirsten Schwarz. 2021. “Ecologist Engagement in Translational Science Is Imperative for Building Resilience to Global Change Threats.” *Rethinking Ecology* 6: 65–92.

Sandercock, Brett K., Kathy Martin, and Susan J Hannon. 2005. “Life History Strategies in Extreme Environments: Comparative Demography of Arctic and Alpine Ptarmigan.” *Ecology* 86 (8): 2176–86.

Sandercock, Brett K., Erlend B. Nilsen, Henrik Brøseth, and Hans C. Pedersen. 2011. “Is Hunting Mortality Additive or Compensatory to Natural Mortality? Effects of Experimental Harvest on the Survival and Cause-Specific Mortality of Willow Ptarmigan.” *Journal of Animal Ecology* 80 (1): 244–58. https://doi.org/https://doi.org/10.1111/j.1365-2656.2010.01769.x.

Saracco, James F, J Andrew Royle, David F DeSante, and Beth Gardner. 2010. “Modeling Spatial Variation in Avian Survival and Residency Probabilities.” *Ecology* 91 (7): 1885–91.

———. 2012. “Spatial Modeling of Survival and Residency and Application to the Monitoring Avian Productivity and Survivorship Program.” *Journal of Ornithology* 152: 469–76.

Schaub, Michael, and Marc Kéry. 2021. *Integrated Population Models: Theory and Ecological Applications with r and JAGS*. Academic Press.

Schmeller, Dirk S, Lauren V Weatherdon, Adeline Loyau, Alberte Bondeau, Lluis Brotons, Neil Brummitt, Ilse R Geijzendorffer, et al. 2018. "A Suite of Essential Biodiversity Variables for Detecting Critical Biodiversity Change." *Biological Reviews* 93 (1): 55–71.

Stearns, Stephen C. 1992. *The Evolution of Life Histories*. Vol. 249. Oxford university press Oxford.

Steen, H., and K. E. Erikstad. 1996. "Sensivity of Willow Grouse Lagopus Lagopus Population Dynamics to Variations in Demographic Parameters." Journal Article. *Wildlife Biology* 2: 27–35.

Steen, J. B., H. Steen, N. C. Stenseth, S. Myrberget, and V. Marcström. 1988. "Microtine Density and Weather as Predictors of Chick Production in Willow Ptarmigan, Lagopus Lagopus." Journal Article. *Oikos* 51 (3): 367–73.

Stevenson, Simone L, Kate Watermeyer, Giovanni Caggiano, Elizabeth A Fulton, Simon Ferrier, and Emily Nicholson. 2021. "Matching Biodiversity Indicators to Policy Needs." *Conservation Biology* 35 (2): 522–32.

Storch, Ilse. 2007. "Conservation Status of Grouse Worldwide: An Update." Journal Article. *Wildlife Biology* 13 (sp1): 5–12. https://doi.org/10.2981/0909-6396(2007)13[5:csogwa]2.0.co;2.

Valpine, Perry de, Daniel Turek, Christopher J Paciorek, Clifford Anderson-Bergman, Duncan Temple Lang, and Rastislav Bodik. 2017. "Programming with Models: Writing Statistical Algorithms for General Model Structures with NIMBLE." *Journal of Computational and Graphical Statistics* 26 (2): 403–13.

Ver Hoef, Jay M, Erin E Peterson, Mevin B Hooten, Ephraim M Hanks, and Marie-Josèe Fortin. 2018. "Spatial Autoregressive Models for Statistical Inference from Ecological Data." *Ecological Monographs* 88 (1): 36–59.

Waldock, Conor, Rick D Stuart-Smith, Camille Albouy, William WL Cheung, Graham J Edgar, David Mouillot, Jerry Tjiputra, and Loïc Pellissier. 2022. "A Quantitative Review of Abundance-Based Species Distribution Models." *Ecography* 2022 (1).

Willebrand, Tomas, and Maria Hörnell. 2001. “Understanding the Effects of Harvesting Willow Ptarmigan Lagopus Lagopus in Sweden.” *Wildlife Biology* 7 (3): 205–12. https://doi.org/10.2981/wlb.2001.025.

Williams, Byron K, James D Nichols, and Michael J Conroy. 2002. *Analysis and Management of Animal Populations*. Academic Press.

Wilson, Scott, and Kathy Martin. 2011. “Life-History and Demographic Variation in an Alpine Specialist at the Latitudinal Extremes of the Range.” *Population Ecology* 53 (3): 459–71. https://doi.org/10.1007/s10144-011-0261-x.

Zimmerman, G. S., W. A. Link, M. J. Conroy, J. R. Sauer, K. D. Richkus, and G. Scott Boomer. 2010. “Estimating Migratory Game-Bird Productivity by Integrating Age Ratio and Banding Data.” *Wildlife Research* 37 (7): 612–22. https://doi.org/10.1071/WR10062.