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

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# Abstract

Quantifying the temporal and spatial variation in animal demography is a central theme of ecology and important for directing policy. However, field sampling at large spatial extents for long periods of time is cost prohibitive and often politically untenable. Citizen science programs can alleviate these issues by harnessing stakeholders to increase the spatial and temporal resolution of datasets. Yet, many citizen science programs lack data on individual animals making it difficult to model demography. Integrated population models (IPM) offer promise to use multiple streams of data on populations or multiple aspects of a single dataset to estimate key vital rates for populations or communities. We leveraged a large-scale citizen science monitoring program—the “Hønsefuglportalen”— to estimate spatial and temporal variation in demography for willow ptarmigan (*Lagopus lagopus*). The core field sampling approach was line-transect distance sampling with age-specific detections—the latter critical to modelling the population dynamics in the IPM. We explored latitudinal and longitudinal variation in recruitment, survival, and density; patterns of density dependence; and the relationship between recruitment and rodent occupancy using an IPM in a Bayesian framework following open science principles. Overall results were consistent with expectations of ecological theory. Slower life history patterns were observed at higher latitudes and altitudes portending differential effects of climate change on ptarmigan across their range. Observed patterns between rodents and recruitment were consistent with the alternative prey hypothesis (APH); however, spatial variation in the directionality and magnitude of effect were substantial. The robustness of the hierarchical structure of our model was instrumental in elucidating these patterns. Our study highlights the power of citizen science, IPMs, and open science principles to estimate spatial and temporal variation in the demography for a culturally important species.

# Introduction

There is growing demand for biodiversity indicators from international unions, national government, local management bodies, and corporate and industry actors. Such indicators 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 their county- or municipality-level decision making (+ refs?). 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 that 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/>), 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 and requires trained specialists, thus limiting 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 (+ example refs). The exception here are monitoring programmes that succeed in making use of a large number of citizen scientists 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). 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 (+ref to protocol?) and established routines for quality control and annual releases of publicly available data via 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) but large-scale estimation of demographic rates underlying these trends has thus far remained as untapped potential of the dataset. Nilsen and Nater (2023) recently developed a novel integrated distance sampling model (IDSM) which successfully uses the age of idividuals detected along line transects data coupled with radio-telemetry data to estimate not just abundance, but also survival and recruitment across years. In this study, we adapt the model of Nilsen and Nater (2023) 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 abundance across 41 reporting districts and 15 years (2007-2021) for this popular 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). While the main reason for the long-term decline in abundance remain unresolved, willow ptarmigan are considered sentinel species that are sensitive to both climate change and land use changes (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 the gyrfalcon (Franke et al. 2020) . The willow ptarmigan has a relatively fast pace of life (Sandercock, Martin, and Hannon 2005; H. Steen and Erikstad 1996), and can display substantial spatio-temporal variation in demographic rates (**Bowler2020?**). 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; **Bowler2020?**). This tight relationship between the breeding success of ground nesting birds and the rodent cycle is known as the Alternative Prey Hypothesis and has been a central part of Fennoscandian research on grouse population dynamics for many decades (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, they are 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. In addition, as 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 (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 August each year, trained volunteer fieldworkers collect observations of willow ptarmigan and other grouse species (rock ptarmigan *Lagopus muta*, black grouse *Lyrurus tetrix*, capercaillie *Tetrao urogallus*) along predefined line transects. To increase the detection probability, each team of fieldworkers use a pointing dog to locate the birds. Each survey team typically consist of at least two persons (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 noted, 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 made for 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 (refs). The published datasets contain both metadata about the transect surveys (survey date, line transect length and location, study area ID, etc.) as well as 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. In general, the effort is higher in South-Eastern and Central Norway, medium 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 ever observed (i.e. species absence likely due to low habitat suitability) were dropped, resulting in 2077 transects used in the analyses.

### Radio-telemetry study in Lierne

The model of Nilsen and Nater (2023) 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. During the breeding and chick-rearing season (May to July) birds were monitored more often, and during December and January we obtained few 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.

## National-scale integrated model

### Integrated distance sampling model (IDSM) for willow ptarmigan

Nilsen and Nater (2023) 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 deterministic 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 as opposed to just one. For more detailed information on the single-site model, including tests of model performance, see Nilsen and Nater (2023).

### 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](#fig-model)) and enabled sharing of information among areas by explicitly modelling spatial variation alongside shared temporal and residual variation in vital rates and detection parameters.

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

Here, and are the densities of juvenile and adult ptarmigan in survey site (= transect) of area in year , respectively. Both juveniles and adult survive from year to with an area- () and year- () specific survival probability , and survivors produce the next generation of juveniles according to an area- and year-specific recruitment rate ().

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| 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 year t. Ad[x,t] = adults in year t. R[x,t] = recruitment rate in year t. S[x,t] = survival probability from year t to t+1. Note that the additional site (=transect) dimension, “j”, is omitted for the sake of illustration. |

The initial densities, and are modelled for each site (= transect) as random realizations of log normal distributions with area-specific log means () and log standard deviations (). Survival () and recruitment (), on the other hand, are assumed to be the same for all sites within a given area and were modelled as:

The global means ,, and the normally distributed spatial random effects, , 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 () of local yearly rodent occupancy () 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 () and otherwise unaccounted for variation through year- and area-specific residual random effects (). 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 (bar the effect of rodent occupancy, [Figure 1](#fig-model)). 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 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 and including 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 (), 2) temporal variation (), 3) residual variation (), and 4) variation in rodent occupancy (). To obtain the proportion variance explained by each of the component, we divided it by the sum of all other components (). The spatial, temporal, and residual variance components were defined as the square of the estimated corresponding random effects standard deviation from the model while was calculated as the variance of all area- and year-specific products.

## 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 abundance, whether to run MCMC chains sequentially or in parallel, etc. A visual representation of the pipeline is also displayed in [Figure 2](#fig-workflow) and for more details on pipeline implementation and options, we refer the reader to the GitHub repository: <https://github.com/ErlendNilsen/OpenPop_Integrated_DistSamp>.

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| 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 (SF) are provided as .pdf files with captions in “SuppFigures\_Captions.txt”.

## 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/km2 in the area “Statskog og Klinga utm.” close to the coast in central Norway to 55.85 [51.699, 60.003] birds/km2 in “Ålen og Haltdalen Fjellstyre” further south near the Swedish border. In general, population density appeared to be lowest in the Northern parts of Norway and highest in the eastern part of central Norway ([Figure 3 (a)](#fig-densA)). Uncertainty in density estimates was relatively consistent, with a few areas (inlcuding the one with the lowest estimated density, “Statskog og Klinga utm.”) sticking out by having substantially less precise estimates ([Figure 3 (b)](#fig-densB)). 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 large number of areas.

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| |  |  |  | | --- | --- | --- | | |  | | --- | | (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](#fig-lam)). 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”).

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| |  |  |  | | --- | --- | --- | | |  | | --- | | (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 population growth rates were estimated for areas with relatively low population densities across latitudes but we did not find evidence for a strong association between population growth rates and population densities overall ([Figure 5](#fig-paramCorrs) A).

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| Figure 5: Posterior summaries (points = posterior medians, lines = 95% credible intervals) of area-specific population growth rate vs. population density (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)](#fig-pVRA)). The global average survival probability across all areas and years () 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)](#fig-pVRB); [Figure 5](#fig-paramCorrs) 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]).

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| |  |  |  | | --- | --- | --- | | |  | | --- | | (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 (intercepts) 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 many areas, the years 2011, 2014, and 2018 not only sported 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](#fig-paramCorrs) 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](#fig-paramCorrs) 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 (truncation distance = 200 m) from 0.435 [0.383, 0.497] to 0.784 [0.688, 0.892], respectively. 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](#fig-varDecomp)). 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.

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| 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 (2023), 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 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/km2 to 55 birds/km2, 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)](#fig-densA). These areas are characterized by more extreme climatic conditions, boasting cold temperatures and – in the North – a short growing season. Resulting reduced primary production limits food availability and as ptarmigan are income breeders using 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 [Figure 4 (a)](#fig-lamA). Nonetheless, recent population declines were also evident in some areas, and particularly in the mountains in central Norway [Figure 4 (a)](#fig-lamA).

Density dependence is an important process to understand in ecology but more so 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 numerous 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)). While we found the highest population growth rates in areas with relatively low density, and relatively low growth rates in high-density areas [Figure 5](#fig-paramCorrs), our analysis did not provide evidence for a strong relationship between density and growth rates across space. However, this is unsurprising as we did find substantial spatial differences in demography, which suggests that carrying capacity too varies over space. Also, support for density dependence in willow ptarmigan has been mixed. Myrberget (1988) observed no change in productivity despite a 50% decrease in abundance. Conversely, Pedersen et al. (2004) found strong overwinter negative density dependence and they posited that immigration was the vital rate that responded to changes in density. Low survival rates appeared to have a one-year lag following abundance peaks. This pattern could be a result of negative density dependence that went undetected when looking at the ensemble of samples across the 41 areas. Negative density dependence has been shown in willow ptarmigan populations which may explain explain reduced survival following years with elevated densities (Pedersen et al. 2004).Future work should explore different time-lags for density and population growth and the possibility for non-linear effects.

Overall, annual recruitment rates showed a spatial pattern that was inversely related to that of annual survival, with lower recruitment rates co-occurring with higher survival rates (and lower densities) and vice-versa [Figure 5](#fig-paramCorrs), as we would expect based on life history theory (Stearns 1992). Furthermore, the areas with relatively lower recruitment and higher survival were primarily found in the northern parts of Norway and in the mountainous region in the central part of the country, which aligns with previous studies finding 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).

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”) and low subsequent survival (SF “TimeSeries\_pSurv.pdf”), which 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 provides evidence for the Alternative Prey Hypothesis (APH; (Israelsen et al. 2020)). The AHP 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). Conversely, Nyström et al. (2006) suggested that gyrfalcons (a specialized ptarmigan predator) did not respond to rodent populations and did not switch to alternative prey when ptarmigan populations are low. Nonetheless, other predators such as fox could prey switch in response to changing availability of rodents and ptarmigan as shown by Breisjøberget, Odden, Wegge, et al. (2018) and Bowler et al. (2020). However, statistical associations in our study and others is not causal and alternative explanations for this pattern are plausible. The positive association between rodents and ptarmigan could be caused by bottom-up processes such as food availability unrelated to predation. Future work should develop causal models and manipulative experiments to establish causal relationships among top-down and bottom-up processes.

Taken together, this alludes to the large role small rodents play in shaping ptarmigan demography and population dynamics and is further supported by the largely positive effects of rodent abundance on recruitment estimated by our model ([Figure 5](#fig-paramCorrs) C). Once more, the highest latitude and highest altitude areas stood out, sporting the strongest rodent effects (SF “betaR\_Map.pdf”). This may be linked to the overall low ptarmigan densities in these areas, as e.g. Nielsen (1999) found evidence that gyrfalcon predation on ptarmigan was most impactful when ptarmigan densities were low. Notably, the conclusive estimation of overall positive effects of rodent abundance on recruitment in our model was only possible thanks to the integration and sharing of data across multiple areas. When Nilsen and Nater (2023) 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. For example, the cover of ericaceous shrubs as a proxy for food availability or spatially-explicit spring green up dates both measured using remote sensing are ecologicaly plausible and feasibly acquired factors.

Extending the present analysis by including additional covariates 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](#fig-varDecomp) but also relevant for constant spatial and shared temporal variation. Interestingly, we found that a larger portion of variation in recruitment was allocated to spatial than to temporal factors, while the opposite was the case for survival. Contrastingly, ptarmigan nest failure is almost entirely caused by predation which has been shown to vary greatly across years and less across space (Munkebye et al. 2003; Kvasnes et al. 2015, 2014) whereas adult survival has been shown to not very greatly across years (Israelsen et al. 2020). Also, immigration, included in our recruitment term , has been hypothesized to be a spatial process (Kvasnes et al. 2015). This conundrum could be a result of the limited spatial replication of many previous studies that we were able to address with our approach. Future research could help rectify these discrepancies by including more mechanistic relationships between environmental factors and vital rates.

## Implications for management

Management decisions made at the resolution of large geo-political 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 […] The results from our study suggests that management decisions should be spatially refined and ideally informed by knowledge about the “local” population processes. […]

Besides pointers on how to adjust management of ptarmigan and their habitat, 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 using a common protocol and training programme, as well as data processing pipeline. 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 spatio-temporal variation in demography and population dynamics at a large scale but also with good spatial resolution. 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. […]

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), for example, 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 accounted for by adding an additional layer of hierarchy to observation process (see e.g. REF), which could further be used to also account for error in judging the observation distance (e.g. **marques2004?**). Another potential source of bias in our IDSM is related to failure to correctly assign the age class of observed birds. Nilsen and Nater (2023) 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 (+ref). In our case, however, juveniles are likely more prone to misclassification due to […] . 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. for 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](#fig-pVR), 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). 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 (**lawson2020?**). 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](#fig-dens)). 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. […] 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 […] The most relevant source of data to be included into the IDSM framework in the near future, however, is harvest data. 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; **nater2021?**). Harvest effects on willow ptarmigan have been studied previously yet uncertainties persist (Sandercock et al. 2011; Aanes et al. 2002; Pedersen et al. 2004; Willebrand and Hörnell 2001). For example, the strength and shape of density dependence and how harvest may induce population sinks because of Allee effects (Kvasnes et al. 2015)). Modelling allee effects, or better yet predicting where they are likely to occur if over-harvest occurs, requires a spatially-explicit understanding of harvest and its impact on local populations. Because harvest effort, thus rates, can vary dramatically over time and space (Breisjøberget, Odden, Storaas, et al. 2018) easily repeatable analyses that can be done continually would prevent prolonged over-exploitation. Harvest effects may interact with other (emergent) factors such as climate change and habitat degradation making the need to be identify triggers for policy changes paramount (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](#fig-workflow). Modern applied ecology needs research to be published not just as manuscripts, 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. 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.

# Acknowledgements

TBA … We are grateful to the participants in the “Hønsefuglportalen” and their dog helpers that collected ptarmigan observations. Additionally, we would like to thank Bernardo Brandão Niebuhr dos Santos for his help with spatial data visualization. J. A. Martin was supported by a Fulbright Fellowship and the Norwegian Institute for Nature Research that facilitated this collaboration.

# 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 (key b49a2978-0e30-4748-a99f-9301d17ae119), Statskog (key 6a948a1c-7e23-4d99-b1c1-ec578d0d3159), and FeFo (key c47f13c1-7427-45a0-9f12-237aad351040), respectively.

The auxiliary radio-telemetry data, rodent occupancy data, and 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 (Zenodo citation TBA).

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