Integrated distribution modelling to estimate the national population size of an alpine bird

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Abstract:

1) Estimates of species' population abundances have important ramifications for conservation decision-making. Conservation practice, however, often has to rely on indices of relative abundance rather than absolute estimates. Attempts to estimate large-scale abundance estimates of species are limited by both the availability of data and statistical challenges. New opportunities are, however, emerging as a result of the development of an open data culture.
2) Here we integrate information from two distinct citizen science data sources, opportunistic occurrence data and targeted standardized distance-sampling survey data, to estimate the population size of an alpine bird - the willow ptarmigan, *Lagopus lagopus* - in Norway between 2008 and 2017. Our model combines the strengths of the occurrence data (widespread but coarse) and standardised survey data (spatially restricted but detailed) to estimate ptarmigan population size at both local and national-scales. Using simulations, we also examined the sensitivity of the population size estimates to each data type to guide future data collection.
3) An occupancy-detection model fit to the occurrence data predicted that willow ptarmigan were present in 29% of 5 x 5 grid cells across Norway. Occupancy probability was most strongly affected by habitat covariates. The distance-sampling model predicted that ptarmigan density in the area covered by the line-transect surveys was, on average, 13 individuals per km^2, and most strongly affected by climatic variables. On integration, we predicted a mean annual population size of c. 1.2 million individuals.
4) Most of the uncertainty in the national population size estimate was driven by uncertainty in occupancy in western and central Norway. Hence, data collection

activities might be encouraging in these regions to increase the precision of population size estimate.

5) *Synthesis and applications:* Our study shows the possibilities of new data sources and modelling approaches to provide absolute estimates of species' population sizes, which are often more revealing than relative abundance indices for understanding species' population dynamics and trends. Ecologists can take advantage of the open data revolution, and especially the relative strengths of different available data types, to estimate species' abundance at large spatial scales.

Keywords: citizen science; data integration; integrated distribution models; population abundance; population size; species monitoring; synthesis

Introduction

Species' abundance plays a central role in most ecological and evolutionary processes (Kunin 1998; McGill & Collins 2003). Monitoring programs typically collect abundance data to create indices of the relative abundance of species (Van Strien, Pannekoek & Gibbons 2001; Collen *et al.* 2009), which are sufficient for many questions about trends (Dornelas *et al.* 2019) and drivers of trends (Kolecek *et al.* 2014). However, estimates of species' total or absolute abundances are also important, such as to inform the IUCN red list assessment (IUCN 2012), for reference levels to define conservation targets (Reed *et al.* 2003), or to assign sustainable harvest quotas (Eriksen, Moa & Nilsen 2018). However, few monitoring schemes aim to go beyond abundance indices to estimate the total number of individuals within a population, especially at large spatial scales. With the current reliance on abundance indices, there is a risk that the value of absolute population abundance estimates is overlooked for understanding species' population dynamics and trends.

The main challenge to the quantification of species abundances at large spatial scales is imperfect detection and spatial heterogeneity in abundance (Yoccoz, Nichols & Boulinier 2001; Jones 2011). Imperfect detection arises because some individuals are almost always missed during a survey within a target area (Kéry & Royle 2016). Abundance models that ignore imperfect detection make the simplistic assumption that species' detection probabilities are constant among different places and at different times (i.e. similar fractions of individuals are missed during a survey) (Pollock *et al.* 2002; Johnson 2008). By contrast, models that account for imperfect detection allow for variation in species' detectability and can therefore provide better information on spatial and temporal patterns in species abundance (Pollock *et al.* 2002; Hewson *et al.* 2018). Species' detection probabilities, and in turn total abundance estimates, can be estimated using methods for marked (i.e., tagged) individuals, e.g., mark-recapture (McCrea & Morgan 2014), or for unmarked individuals, such as distance-sampling

77 methods (Buckland *et al.* 2001) or repeat surveys (Botsch, Jenni & Kery 2020). However,
78 these methods are costly in terms of sampling frequency or effort, which means that they tend
79 to be only possible at a small spatial scale for local abundance estimates. Estimating
80 abundance at large spatial scales remains a challenge due to spatial variation in abundance,
81 which means that surveyed areas might be a poor representation of the wider landscape
82 (Buckland & Johnston 2017). This is especially true when the survey was focused on the core
83 habitat of a species.

84 Upscaling of abundance estimates from local-scale abundance data may be possible by
85 combining it with other data types that provide coarser but more widespread information on
86 species' populations (Pagel *et al.* 2014; Isaac *et al.* 2020; Farr *et al.* 2021). Opportunistic
87 occurrence data that have been collected without a common survey protocol, typically from
88 citizen scientists, can potentially provide data over a large spatial scale, including from both
89 core and marginal areas for a species (Kery, Gardner & Monnerat 2010; Soroye, Ahmed &
90 Kerr 2018). In the last decade, hierarchical models have been developed that deal with the
91 inherent biases within such opportunistic citizen science data (van Strien, van Swaay &
92 Termaat 2013; Isaac *et al.* 2014). Moreover, recent studies have also shown how different
93 types of data, including abundance and occurrence, can be combined together to increase the
94 sample size and spatial coverage (Miller *et al.* 2019; Isaac *et al.* 2020).

95 Here, we show how occurrence data and abundance data can be combined by using
96 integrated modelling to estimate total abundance for an iconic alpine species. More precisely,
97 we estimate the national population size of the willow ptarmigan *Lagopus lagopus* in Norway.
98 This species is thought to have already undergone a large decline in the 20th century
99 (Lehikoinen *et al.* 2019). Moreover, as an alpine species, it is especially vulnerable to on-
100 going and future climate change (Bowler *et al.* 2020). We combined information on density,
101 from distance-sampled line-transect surveys that targeted the core alpine habitat of the

ptarmigan, with occurrence data that provided information on the larger distribution of bird species across Norway. Moreover, we examined the uncertainty of the model to identify which geographic regions might be further sampled to improve the national population size estimate.

Materials and methods

Occurrence data

Occurrence data for Norway were downloaded from GBIF and the Species map service of the Norwegian Biodiversity Information Centre. Data are collected by variable methods and are best regarded as opportunistic i.e., without a consistent sampling protocol. We downloaded two sets of data: (1) occurrence data for willow ptarmigan and (2) occurrence data for all birds (Fig. 1). Data for all bird occurrences were used in the statistical analysis to control for spatial and temporal variation in the sampling effort of ornithologists across Norway. The willow ptarmigan occurrence dataset included some observations from the line-transect surveys; however, we did not discard them from the occurrence data set since they still provided valid occurrence observations. Both sets of data were filtered by removing: duplicate observations (with the same date, species and geographic coordinates); those with coordinate uncertainty greater than 5 km; those with geographic coordinates with less than three decimal places and those outside our temporal scope of 2008-2017. We focused on records during the breeding season between May and September. The occurrence data were mapped to a reference grid comprising 5 x 5 km grid cells that covered the extent of Norway (limited to grids that overlapped at least 50% with mainland Norway). This resolution should account for limited local movement of the ptarmigan within the summer season and aligned with the mean length of the line-transect surveys (see next section).

Line-transect survey data

We used a dataset of line-transect surveys that covered almost the full latitudinal extent of mainland Norway for 2008–2017 (Fig. 1). The surveys come from a structured citizen science program that is coordinated by local and regional initiatives. The program targeted the willow

ptarmigan and focused on its core habitat in alpine areas. Volunteer surveyors follow a common survey procedure using distance-sampling methods, usually in August (Nilsen *et al.* 2020). See Bowler et al. (2020) for more details. We excluded observations made at distances greater than 200 m from the transect line, as well as detections by the surveyor, and not by the trained pointing dogs, at distances > 10 m away from the transect line. We used data from 585 line-transects (mean length of 4.3 km) that were visited in at least 5 years (a median of 10 years) during our study period.

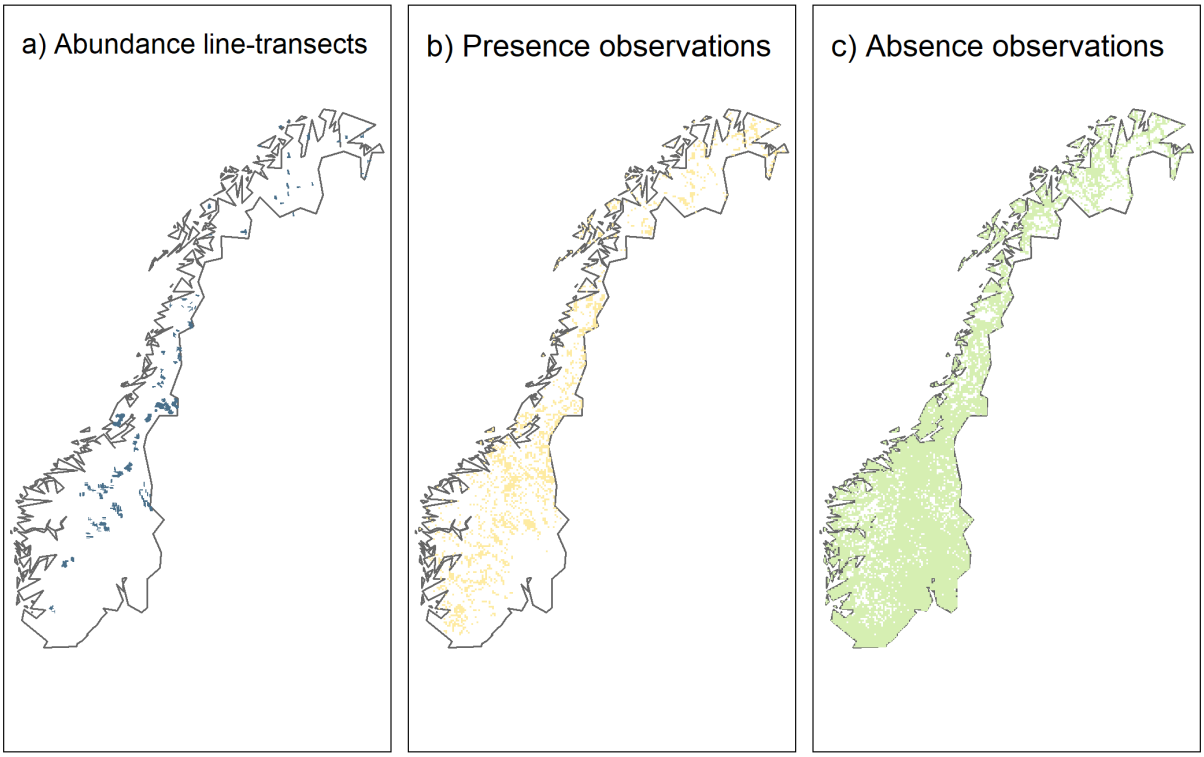

Fig. 1 Maps showing the distributions of each data set: (a) line-transect surveys from structured citizen science that targeted the willow ptarmigan and (b) presence and (c) absence observations for the willow ptarmigan (i.e. bird species were reported on a given date and place but not the willow ptarmigan) from opportunistic citizen science.

144 Environmental covariates

145 *Climate*: We used the EuroLST dataset that provides summary temperature maps derived
146 from reconstructed MODIS LST averaged for 2001–2013 at 250 m resolution (Metz,
147 Rocchini & Neteler 2014). We used data on maximum temperature of the warmest month and
148 minimum temperature of the coldest month.

149 *Habitat*: We used a vegetation map of Norway, which used satellite data to classify land cover
150 at 30 m resolution into 25 classes (Johansen, Aarrestad et al. 2009). The land classes were
151 aggregated into percentage cover of: mountain birch forest; boreal/lowland forest; bogs with
152 dense field layer; swamps/bogs with sparse field layer; open areas with dense field layer; open
153 areas with sparse field layer and snowbeds, following Kvasnes et al. (2018) (Table S1).

154 *Treeline:* Elevation was extracted from a digital elevation model of Fennoscandia at 10 m
155 resolution (https://kartkatalog.geonorge.no/). Treeline data at 100 m resolution was extracted
156 from Blumenrath & Hanssen (2010). We calculated the deviation of the elevation from the
157 predicted treeline for each grid cell.

158 *Region*: We obtained spatial polygon data on the administrative regions that subdivide
159 Norway (https://gadm.org/, level 2).

160 Covariate data were matched to the occurrence data by averaging values within the 5 x 5 km
161 grid cells and to the abundance data by averaging within circles (with areas of 25 km^2 to
162 match the area of the grid cells) centred on the centroids of each line-transect.

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Statistical analysis

Selection of environmental variables

We included both linear and quadratic effects of all continuous covariates in the models described below. We used variable indicator selection by multiplying the Gaussian prior on each covariate with a Bernoulli indicator variable that modified whether the variable was included in the model or not (Rushing et al. 2019). Alternative approaches were considered but they gave similar results (see SI).

Occurrence data

To estimate the probability of occurrence of willow ptarmigan, we first constructed a detection history for each 5 x 5 km grid cell. The spatial and temporal unit of our analysis was a visit, defined by a list of species observations collected on a given date in a given grid cell. For each visit, we created a binary indicator to reflect whether willow ptarmigan was included among the reported bird species (1=yes, 0=no). Hence, following others (van Strien, van Swaay & Termaat 2013), absence data (non-detections) for ptarmigan were inferred from observations of other bird species on a given visit. We used occupancy-detection models to analyse the detection/non-detection of species on a visit, which have been used in previous studies using similar heterogeneous data (Kery, Gardner & Monnerat 2010; Outhwaite *et al.* 2020) and tested in simulation studies (Isaac *et al.* 2014). In occupancy-detections models, the detection probability of a species is estimated by the number of times a species was/was not reported during repeat visits to the same grid. We assumed closure (i.e. period of no change in occupancy during repeat visits) between April and October of each year.

Letting $z_{i,t}$ refer to the true occupancy status for a species in grid *i* in year *t*, we modelled occupancy probability (ψ) as a function of fixed effects of the environmental covariates and a series of random effects to account for clustering of the data in space and time (spatial: administrative region and grid cell; temporal: year).

Hence, our occupancy model was:

$$z_{i,t} \sim Bernoulli(\psi_{i,t})$$

$$logit(\psi_{i,t}) = \beta_0 + \beta_e\, EnvironVars_i + Grid_i + Region_i + Year_t$$

Detection probability (p) was modelled for each visit *j* to a given grid in a given year, and allowed to vary with variables expected to be most associated with species visibility and abundance (open habitat cover, temperature and tree line). Following Outhwaite (2020), survey effort was modelled as a function of list length, i.e., number of species reported on a visit (a categorical variable – a single species, a short list (2-4 species), or a longer list – set as the reference level). Random effects for year and region were also included.

$$logit(p_{i,t,j}) = \beta_0 + \beta_{det}\, EnvironVars_i + \beta_{si}\, single\_list_j + \beta_{sh}\, short\_list_j + Year_t + Region_i$$

The observed detection data for the willow ptarmigan, *y* (0 for non-detection or 1 for detection) on each visit are then assumed to be drawn from a Bernoulli distribution conditional on the presence of the species in that grid cell and year:

$$y_{i,t,j} | \, z_{i,t} \sim Bernoulli(z_{i,t} \,.\, p_{i,t,j})$$

The models were run in JAGS with 20,000 iterations and 10,000 burnin, with vague priors. The Rhat statistics and traceplots were used to check for convergence.

Line-transect survey data

We fitted a distance-sampling detection model to estimate the effective strip width of each transect (Buckland *et al.* 2001). We modelled the perpendicular distances of ptarmigan observations from the transect line as a half-normal distribution, following an earlier study (Bowler *et al.* 2020). On the transect line, we assumed perfect detection – a common assumption in distance-sampling (Buckland *et al.* 2001). We modelled sigma - the parameter of the half-normal distribution that reflects the rate of distance-decay of detections - to be dependent on group size (i.e. the number of birds in each observation). To account for any spatial autocorrelation in sigma, we also included a random effect for region.

$$log(sigma_{i,t}) = \beta_0 + \beta_{GS} GroupSize_{i,t} + Region_i$$

The effective strip width of each transect (*i*) in each year (*t*) was calculated from sigma by (Buckland *et al.* 2001):

$$ESW_{i,t} = \sqrt{\frac{(\pi * sigma_{i,t}{}^2)}{2}}$$

We then used the estimated effective strip width (ESW) and transect length (TL) to relate the total number of individuals observed along each transect, N, to the latent variable, ptarmigan density, D, (abundance per km^2) for each transect i in year t :

$$Ptarmigan\_Obs_{i,t} \sim Negative\ Binomial(N_{i,t}, r)$$

$$N_{i,t} = D_{i,t} \times TL_{i,t} \times ESW_{i,t} \times 2$$

We assumed that the number of individuals, $N_{i,t}$ followed a negative binomial distribution with constant dispersion parameter *r*. Like for occupancy, density was modelled as a function

of fixed effects of the environmental covariates and random effects to account for clustering of the data in space and time (spatial: administrative region and grid cell; temporal: year).

$$ln\, D_{i,t} = \beta_0 + \beta_e\, EnvironVars_i + Grid_i + Region_i + Year_t$$

To spatially align the line-transect density predictions with the grid-level occupancy predictions, each line-transect was associated with the 5 x 5 km grid cell that overlapped with the line-transect centroid coordinates. The density per km estimated for each line-transect was then scaled to the associated 5 x 5 km grid by multiplying by 25, on the assumption that the line-transect was a representative sample of the grid. The models were run in JAGS with 50,000 iterations and 25,000 burnin, with vague priors. The Rhat statistics and traceplots were used to check for convergence.

Data integration

We followed the principle of a zero-inflated model to predict species abundance per 5 x 5 km grid cell over the whole extent of mainland Norway. A zero-inflated model assumes that species abundance is generated by two processes: one governing whether a grid is suitable for occupation and a second process governing the abundance of the species at suitable grids. We used the aforementioned occupancy-detection model for the first process and the distance-sampling model for the second process. Previous attempts to data integration have often used a joint-likelihood approach, which means that the ecological models were assumed as the same in each dataset (Miller et al. 2019). However, there is debate about whether occurrence and abundance are really outcomes of the same point processes governing the distribution of individuals (Kéry & Royle 2016). In our case, we felt justified in modelling each dataset separately based on the large differences in spatial extent between the two datasets and geographic space – the line-transects specifically targeting the alpine habitat of the ptarmigan.

Moreover, our datasets were not entirely independent (some of the presence observations came from the line-transect surveys) and a joint-likelihood approach could have over-estimated the precision in the estimated abundance.

We integrated the information in each dataset via multiplication of samples from the posterior distribution of grid-level predictions from the occupancy model and the distance-sampling model for each year. These models were used to make predictions of realized abundance to all grids across Norway, as follows:

$$Realized\ abundance_{i,t} = PredictedAbund_{i,t} \times Pr(Occupancy)_{i,t}$$

To estimate the national population size, we summed the predictions across all grid cells. For comparison, we used a simpler approach, similar to the approach used by BirdLife International, which estimates total population abundance by multiplication of the estimated area of occupancy with estimated mean density. In our case, area of occupancy was based on the number of occupied grid cells predicted by the occupancy model (i.e. sum of the z across all grid cells) while mean density was the mean density predicted across all line-transects.

Model validation and predictive performance

Within-sample: We carried our posterior predictive checks by calculating a Bayesian p-value. Bayesian p-values close to 0 or 1 would indicate poor model fit (Kéry & Royle 2016). For the line-transect model, this was based on a Pearson chi-square statistics for the observed number of birds and for simulated values from the fitted model in comparison with the expectation of the linear predictor of the model. The p-value is then how often the discrepancy for the observed data is larger (or smaller) than the discrepancy for the simulated data. For the occupancy model, the Pearson chi-square statistic was calculated for the total number of birds

detected each year and for the simulated values from the fitted model, in comparison with the expected number from the fitted values (Tobler *et al.* 2015; Broms, Hooten & Fitzpatrick 2016). We also used area under the curve (AUC) to quantify the discrimination of the occupancy model (Zipkin, Grant & Fagan 2012) and mean absolute deviation (MAD, average deviation between observation and predictions) for the line-transect model.

Out-of-sample: The latitudinal range of the data was split into 25 blocks that were systematically assigned to one of five folds (Fig. S1). We repeated the models described above five times - training using four of the folds (e.g., folds 1-4) and using the remaining fold (e.g., fold 5) for testing. For each fold we calculated the AUC to quantify the discrimination of the occupancy model (Zipkin, Grant & Fagan 2012), and MAD for the line-transect model. These statistics were calculated for the middle year of the time-series. Random site and region effects were not included in the models for cross-validation since the levels within the training dataset were not always within the test dataset.

Uncertainty analysis

We used Monte Carlo simulation to examine how uncertainty in the grid-level predictions of occupancy and abundance led to uncertainty in the national population size estimates. We compared the effects of uncertainty of predictions for each grid and each data type by propagating uncertainty through for each grid and data type while holding constant the values for the remaining grids and data type. Specifically, uncertainty was examined by taking all grid values (except for one focal grid) for occupancy probability and abundance to be the mean of the posterior from the fitted model (i.e., the best estimate) but randomly sampling occupancy or abundance values from their posterior distributions for the remaining focal grid. For each random sample, a new total population size was arrived at calculating the realised

abundance (occupancy x abundance) of each grid and then summing the values across all grids. Random sampling was repeated 1000 times and the standard deviation of the total population sizes was calculated across the replicates.

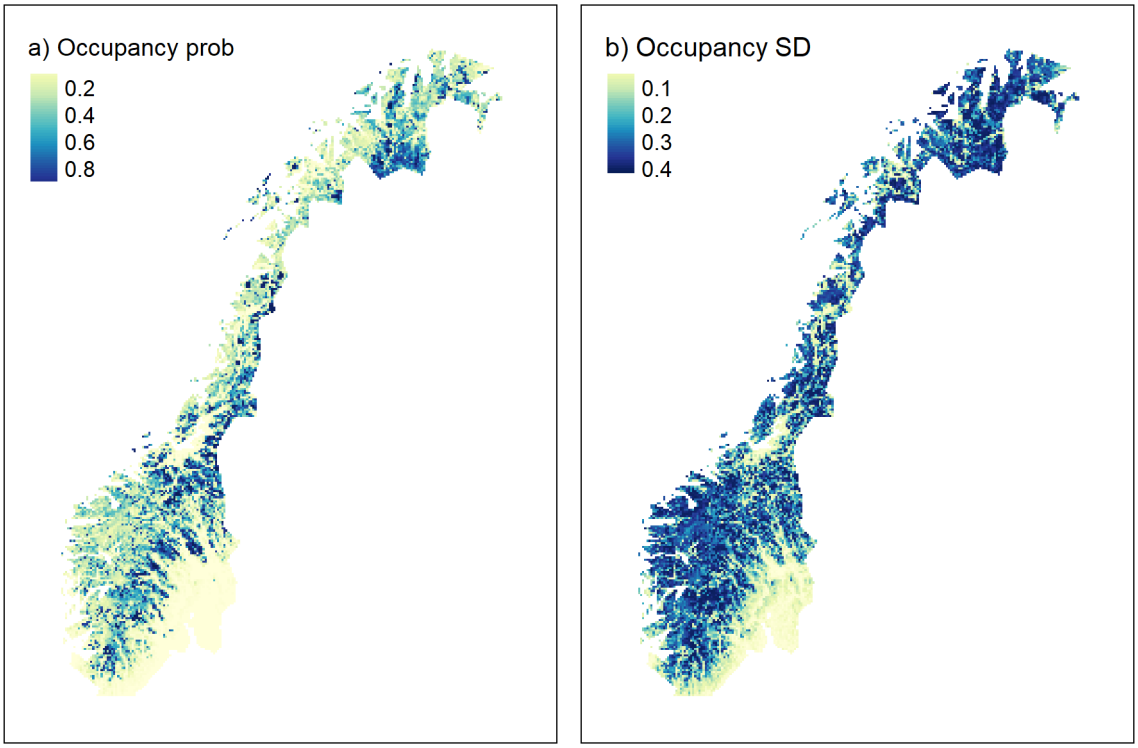
All analyses were performed in R 4.1.0.

Results

Occupancy

Observations of at least one bird species were reported in 75.7% (n = 8927) of the 5 x 5 km grids that covered mainland Norway. In the study period, willow ptarmigan were reported at least once in 21.3 % (n=1898) of the sampled grids. Mean detection probability (i.e. probability to detect a ptarmigan if it is present within a grid) was 0.16 (95% CI = 0.14, 0.18). Detection probability was lower on visits reporting single (95% CI = -0.64, -0.49) or short species lists (95% CI = -1.08, -0.91), and greater in areas with more open habitat (95% CI = 0.47, 0.57), colder temperatures (95% CI = 0.29, 0.45) and higher tree lines (95% CI = 1.20, 1.73).

Mean occupancy probability across all grid cells was 0.29, but there was substantial spatial variation (Fig. 2). Occupancy probability was most positively affected by tree line (quadratic effect, with lower density at the highest tree lines), open dense vegetation, bog cover, mountain birch forest and temperature (Fig. S2). The Bayesian p-value was 0.47, suggesting no fit issues. AUCs were high (occupancy model median AUC = 0.97; detection model median AUC = 0.96). Cross validation showed that the detection model was weaker than the occupancy model, but AUCs on the test dataset were still reasonably good (Table S2).



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334 Fig. 2 Occupancy probability estimates of willow ptarmigan across Norway (a) and standard
335 deviation of the estimate (b) from the occupancy-detection model. Each pixel is a 5 x 5 km
336 grid.

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338 Density

339 The 585 line-transects were placed within 302 (2.6 %) of the 5 x 5 km grids. Along each
340 transect, a median of six ptarmigan (interquartile range = 3–11) were observed each year. The
341 average effective strip width of the line-transects was 100 m (interquartile range = 90–110 m)
342 and was positively affected by ptarmigan group size (95% CI of coefficient on sigma = 0.37,
343 0.40), i.e., larger groups had higher detection probability at greater distances. Mean density of
344 willow ptarmigan per km^2 was estimated as 13 (interquartile range = 9–16) across all line-
345 transects (Fig. 3). Variable indicator selection supported the importance of variables related to
346 temperature (maximum and minimum temperature) and tree line (Fig. S3). For fit measures,

the model predictions were strongly correlated with the observed data (r = 0.93; Fig S4); the mean absolute deviation was 2.39 (for the line-transect mean count) or 4.9 (for year-specific transect predicted count), and the Bayesian p-value was 0.58, suggesting no fit problems. Also, cross-validation suggested no great loss of fit between the test versus training datasets (Table S2).

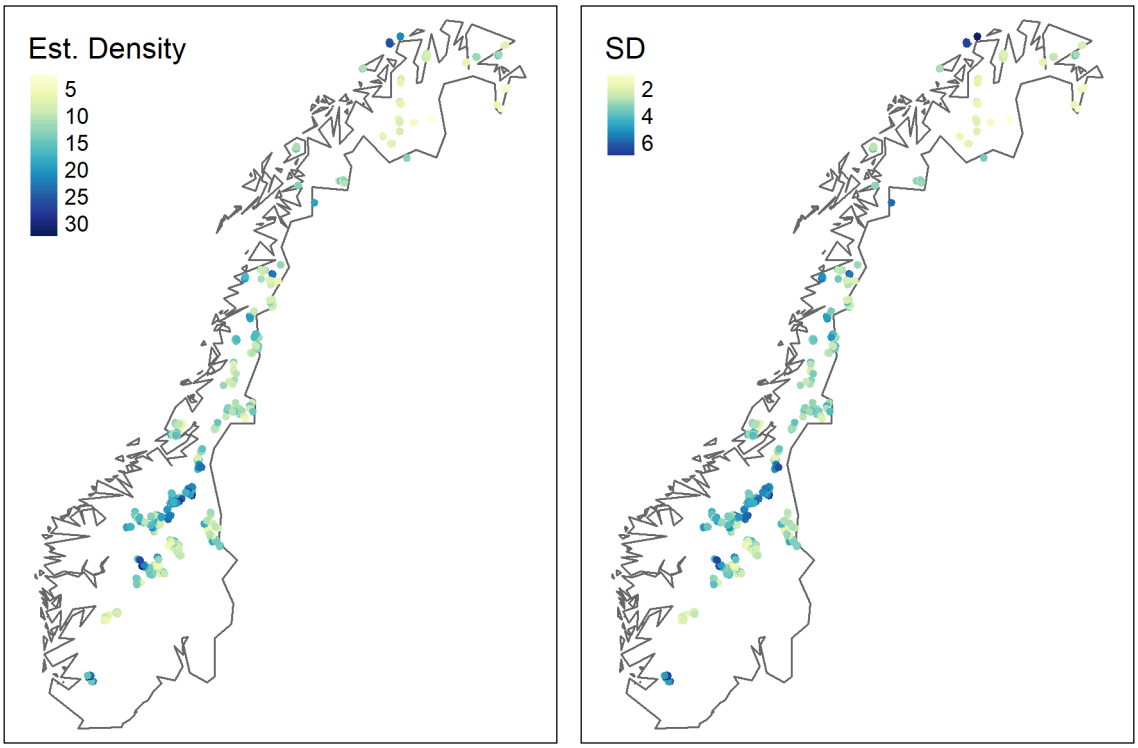


Fig. 3 Ptarmigan density estimates (abundance per km^2) (left) and standard deviation of the estimate (right) from the distance-sample model of the line-transect survey data. Each dot reflects the location of a line-transect.

Data integration and total population size

Abundance was highest in central Norway and lowest in the southeast and north (Fig. 4). Summed across all grids, total abundance, on average across years, was 1,164,379 (95% CI = 1,053,149 to 1,307,195) (Fig. 5a). This estimate was generally similar for all three approaches taken to select the environmental variables for the most parsimonious model (Fig. S5). Year-

specific predictions varied between 778,310 and 1,703,192 individuals, on average (Fig. 5b; see Bowler et al. 2020 for discussion on the drivers of cyclic dynamics). The simpler model to estimate total abundance (i.e., predicted number of occupied grids x mean density) led to a similar prediction of the total population size: 1,207,997.

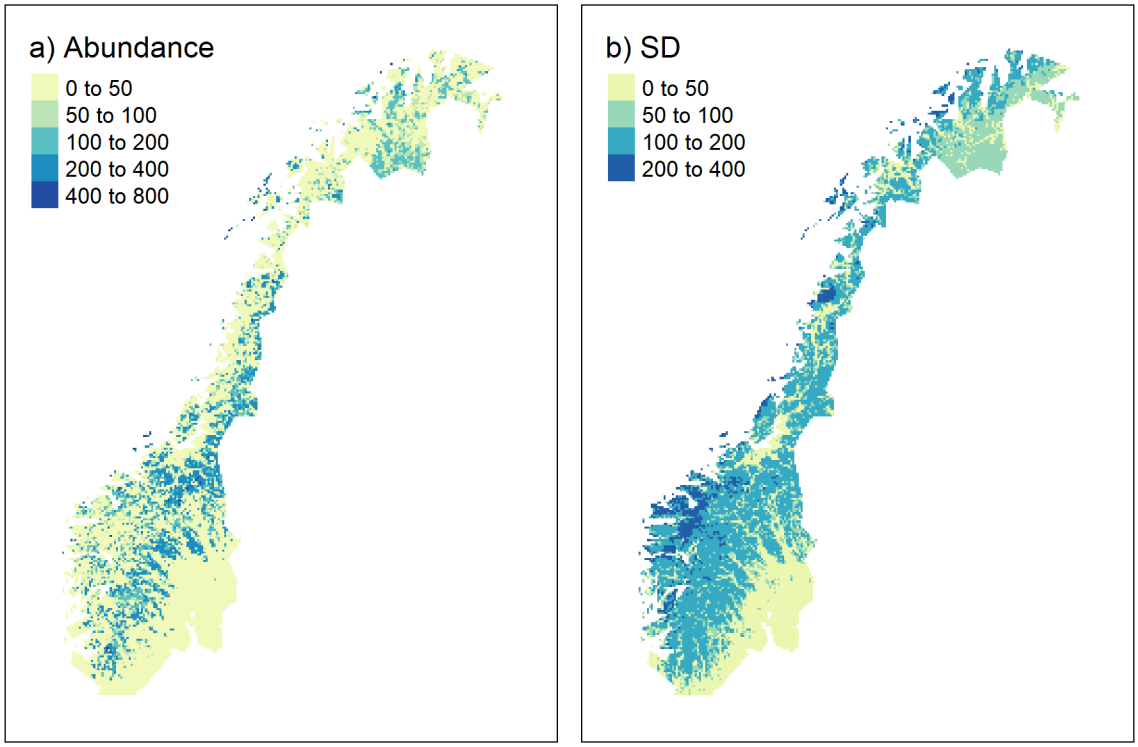
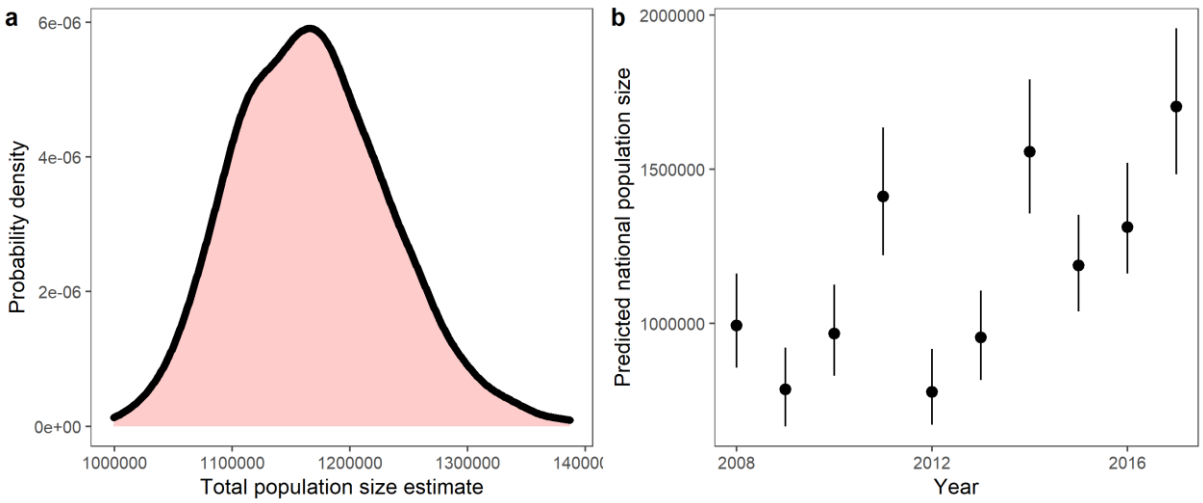


Fig. 4 Integrated model predictions of abundance within each 5 x 5 km grid (left) and its standard deviation (right). The predictions combine information from both the line-transect surveys and the occurrence observations.



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373 Fig. 5 (a) Posterior distribution of the estimated national population size of willow ptarmigan.
374 (b) Annual predictions of the population size; points are lines show means and 95% credible
375 intervals (see Bowler et al. 2020 for analysis of the cyclic dynamics).

376

377 Uncertainty analysis

378 Uncertainty in the grid-level occupancy estimates had larger effects on the uncertainty of the
379 national abundance estimate than uncertainty in the grid-level abundance estimates (median
380 SD caused by each: 32 vs 81) (Fig. 6). Uncertainty in the grid-level occupancy estimates was
381 most influential along the western coast of central and southern Norway (Fig. 6). Uncertainty
382 in the abundance estimates had the greatest effect within the core alpine areas where the
383 density of ptarmigan is the highest. The lowest uncertainty for both data types was in the
384 forested areas of southeast Norway, explained by the expected low abundance and occupancy.
385 Grids with high uncertainty in both occupancy and abundance were found in central Norway.

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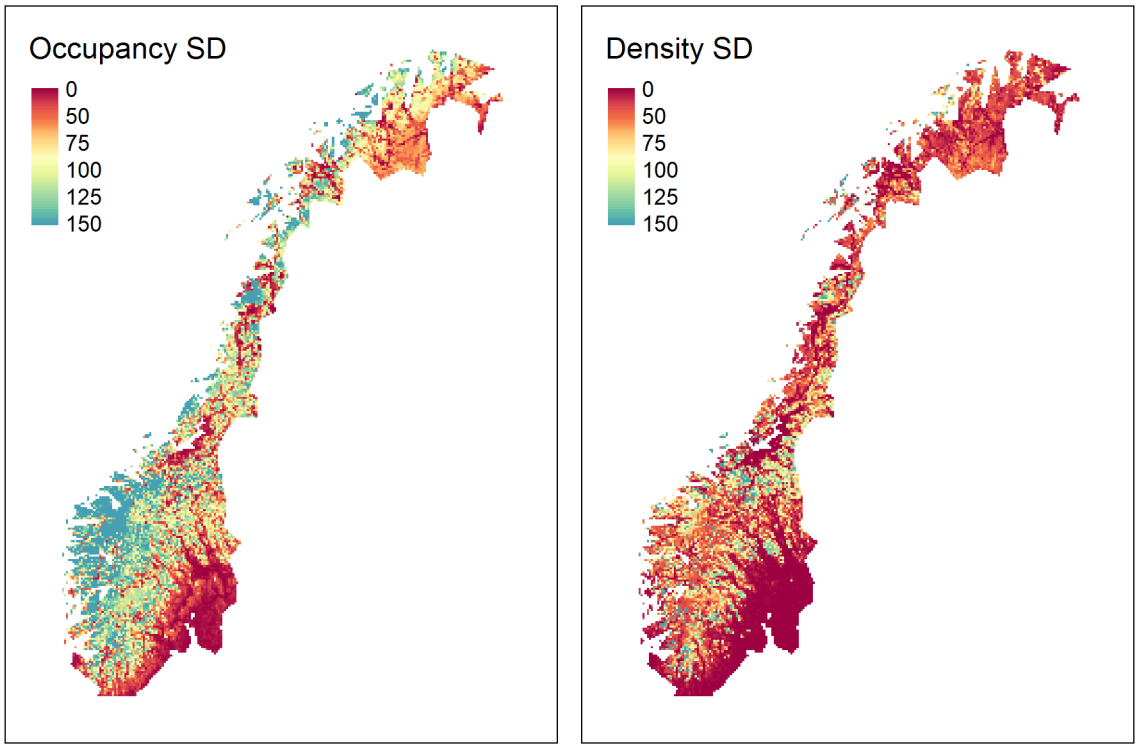

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389 Fig. 6 The impact of grid-level uncertainty in the predictions of occupancy and abundance on
390 the uncertainty (standard deviation of estimate) of the national population size. To facilitate
391 comparison, the same colour scale is used for each map.

Discussion

The cultural shift towards open data has created new opportunities for ecologists to model species' populations, but at the same time, new challenges to develop ways to combine the different data types that are available. We show how abundance data and occurrence data can be combined to produce predictions of total population abundance for a species over a nationwide extent. Our approach takes advantage of the contrast between types of data and citizen science: coarse but spatially extensive occurrence data from opportunistic citizen science and detailed but spatially restricted abundance data from structured citizen science. We used the model to produce the first estimate of the national population size of our study species – an average of c. 1.2 million individuals of willow ptarmigan in Norway in the study period 2008-2017 – and to identify geographic regions where more data are needed to improve the national estimate.

Our approach combines elements of past approaches for estimating avian population sizes but in a spatially-explicit hierarchical model. Previous approaches have typically extrapolated available density estimates over the known range of a species (Thogmartin *et al.* 2006; Musgrove *et al.* 2013; Stanton *et al.* 2019). Callaghan et al. (2021) recently produced global population size estimates for bird species based on relationships between regional abundance estimates and the number of eBird observations. Birdlife International produces global population size estimates by combining average density information with estimates of area of occupancy (http://datazone.birdlife.org/species/spcpop). However, these models are typically not spatially-explicit and/or do not propagate all the uncertainty in the density and occupancy estimates.

Recently, new approaches for data integration have been developed, combining different types of monitoring data, including presence-only, presence-absence and abundance (Miller *et al.* 2019). In so-called integrated distribution models, multiple data streams are

417 combined in the same hierarchical model that explicitly separates the observation/sampling
418 process affecting the observed data from the true state or ecological process affecting the
419 species (Isaac *et al.* 2020). Use of a Bayesian framework also simplifies the process of
420 retaining all the underlying uncertainty in the different components of the model during
421 integration. Several alternative approaches have been proposed for data integration (Pacifici *et*
422 *al.* 2017; Miller *et al.* 2019; Simmonds *et al.* 2020), but the most commonly used method so
423 far is based on a joint-likelihood approach, which uses different data streams to jointly infer
424 the ecological processes, such as land-use and climate effects. The joint-likelihood approach
425 has been most often applied to combine presence-only and presence-absence data (Simmonds
426 *et al.* 2020), but there are also applications for combining abundance and occurrence data
427 (Bowler *et al.* 2019; Farr *et al.* 2021). Simulation studies show that data integration in this
428 way can increase the precision of parameter estimates, including covariate effects (Farr *et al.*
429 2021) and temporal trends (Hertzog *et al.* 2021), by increasing the sample size of data
430 informing the model. However, the joint-likelihood approach requires making the strong
431 assumption about identical ecological processes generating each data type, and it remains
432 unclear when joint-likelihood is robust to deviations from this assumption (Simmonds *et al.*
433 2020; Suhaimi, Blair & Jarvis 2021).

434 While it has been argued on theoretical grounds that abundance and occurrence are
435 outcomes of the same processes affecting the distribution of individuals (Kéry & Royle
436 2016), empirical data analyses support different species dynamics for occupancy and
437 abundance (Dennis *et al.* 2019). In our case, we allowed the models for occurrence and
438 abundance to be independent and not to share information, justified by the large differences in
439 spatial scale and habitats sampled by each dataset. The distance-sampling abundance survey
440 was dedicated to the willow ptarmigan and targeted its core alpine habitats; by contrast, the
441 occurrence datasets came from observers reporting any bird species across the range of

habitats available across Norway. Hence, we rather assumed that each dataset provided different information on the process affecting the species' abundance and distribution, which was supported by the estimated covariate effects – land cover variables explained variation in occupancy while climatic variables mostly explained variation in abundance at occupied sites. Further simulation studies could explore how the optimal integration approach varies with the spatial scale and coverage of each data stream.

Regardless of the data integration approach, population size estimates will always contain some uncertainty, which might limit the application for conservation and management. Recent studies have begun to consider how citizen scientists might be nudged to collect data in specific geographic regions to make the data more informative (Callaghan *et al.* 2019). Often these regions include those with the least amount of data and hence proportionally under-sampled compared to other regions. However, the value of further data collection in a geographic region can be more complex and depend on factors such as the habitat preference and habitat breadth of the species. For the willow ptarmigan, regions with dense forest cover have low occupancy uncertainty, regardless of data availability, because it is not found in these habitats, and this can be easily modelled with the right covariates. Our analysis suggested that uncertainty in occupancy was especially high in western central and southern Norway, where habitat might be suitable but there are less data. Hence, targeted data collection in these areas may be most beneficial. However, as a caveat, this analysis did not consider other causes of uncertainty, including model structure, which also might be further investigated, but we used a typical range of habitat and climate covariates.

We applied our method to the willow ptarmigan in Norway, which currently has the IUCN status of "least concern", but like similar montane species, has been declining across Fennoscandia (Lehikoinen *et al.* 2019), although this was not evident during the recent time-frame of our study. Hence, knowledge of its population size could be important for future red

list decisions. As this species interacts with a range of other species in alpine regions - as both a herbivore and as prey, its absolute abundance also has implications for other species in the food web (Bowler *et al.* 2020). Moreover, the ptarmigan is a game species and information on population size is one of the factors determining harvesting quotas (Eriksen, Moa & Nilsen 2018).

Methods for data integration arrive at a time when ecologists have increasing access to diverse open datasets on species' occurrences and abundances. Since different datasets come with different strengths and weaknesses, stronger inferences can often be made by combining multiple sources rather than focusing on a single data source. Because of the rarity of large-scale abundance data, the value of absolute population size estimates is increasingly overlooked in ecological research. Hence, data integration is particular exciting for studies of the abundance dynamics of species. Currently data integration is rather used retrospectively, for analysis of available data, but as the tools become commonplace, data integration might be planned already in the design stages of monitoring schemes to maximize the complementarity of different datasets and expected benefits of integration.

Author contributions

DB led the project, in discussion with EN. DB performed the analysis and wrote the first draft. EN revised and edited the paper.

Acknowledgements

The authors declare no conflicts of interest. The study was supported by the Research Council of Norway (grant no. 251112) and by base funding from the Norwegian Institute for Nature Research, and from the Environment Agency of Norway supporting the line-transect survey. DB also appreciates the support of the German Research Foundation (DFG) for funding the sMon working group (Trend analysis of biodiversity data in Germany) through the iDiv (DFG FZT 118, 202548816).

Data availability

All data (species and environmental) used in the analysis will be archived in the Dryad database. Updated data for the line-transect survey are also available via GBIF (Nilsen E B, Vang R & E 2021; Nilsen E B *et al.* 2021; Nilsen E.B., Vang R. & J.I. 2021). Code for the analysis are available at: https://github.com/bowlerbear/ptarmiganUpscaling and will be archived at Zenodo on acceptance.

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