An integrated open population distance sampling approach for modelling age-structured populations

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Abstract

Estimation of abundance and demographic rates for populations of wild species is a challenging but fundamental issue for both management and research into ecology and evolution. One set of approaches that has been used extensively to estimate abundance of wildlife populations is Distance Sampling (DS) methods for line or point transect survey data. Historically, DS models were only available as closed population models, and did not allow for the estimation of changes in abundance through time. The advent of open population formulations based on the DS framework greatly extended the scope of the models, but much untapped potential remains in models that estimate temporal dynamics not only in abundance but also in the underlying demographic rates. Here, we present an integrated distance sampling approach that utilize age-structured survey data and auxiliary data from marked individuals to jointly estimate population density and the demographic rates (recruitment rate and survival probability) that drive temporal changes density. The core of the resulting model is, in essence, equivalent to both an integrated population model and a matrix population model with two age classes: juveniles and adults. The integrated framework allows making full use of the available data by effectively combining line transect and telemetry data, and can easily be adapted to include additional and/or different data types. Moreover, as demographic rates often respond to environmental variation, our approach also supports direct estimation of the effects of such environmental covariates on demographic rates. Through a comprehensive simulation study we show that the model is able to adequately recover true population and vital rate dynamics. Subsequent application to data from a study of willow ptarmigan (Lagopus lagopus) in Norway showcases the frameworks ability to recover both fluctuations and trends in population dynamics and highlights its potential applicability to a wide range of species surveyed using distance sampling approaches.

1. Introduction

Estimating abundance and demographic rates for wildlife populations is an integral part of basic and applied ecology (Skalski, Ryding, and Millspaugh 2005; Williams, Nichols, and Conroy 2002). Over the last few decades, tremendous progress has been made towards this end. This progress is partly driven the development and application of new field data collection methods and approaches, such as citizen science data (Danielsen et al. 2022), camera trap data (Hamel et al. 2013) and the collection of environmental DNA data (Beng and Corlett 2022). In addition, developments of novel statistical methods alongside decreases in computational costs now allow researchers to estimate abundance and demographic rates in situations where it was not feasible before (Zipkin et al. 2021). Combined, these advances put us in a much better position for estimating quantities needed for population management (Williams, Nichols, and Conroy 2002) and indices relevant for large scale policy applications, e.g. Essential Biodiversity Variables (Kissling et al. 2018).

Until recently, joint estimation of population dynamics and demography has relied mostly on data from marked individuals and associated open-population capture-mark-recapture models (Schaub and Kery 2021). While such methods can provide valuable information for both ecological research and management, collecting the necessary data is typically costly and logistically challenging to implement over large areas. Monitoring programmes focusing on abundance trends over larger areas, on the other hand, are typically based on data from unmarked animals. One often used approach for such surveys is to structure data collection around the distance sampling (DS) method. DS has been used for estimating animal abundance in a wide range of contexts and for a variety of taxa (Buckland et al. 2015). One reason for the method's popularity is that it does not require repeated visits to the same sites for estimating detection probability. This makes DS particularly useful for implementation in participatory monitoring programs, allowing stakeholders to take part in the data collection process.

The most common implementations of DS models have long used closed-population formulations, and thus do not allow formulating a process model that projects abundance across years based on estimates of population growth rate (λ) or underlying demographic rates Buckland et al. (2015). In recent years, DS approaches have been extended in many ways, including applications that estimate changes in abundance over time in open populations via a hidden state model representing population dynamics (Moore and Barlow 2011; Sollmann et al. 2015; Schaub and Kery 2021). This has greatly extended the potential of DS approaches for studying ecological dynamics across time and space. However, while these latter frameworks may allow to accurately quantify population changes, they typically provide little information on the drivers of these changes, i.e. the underlying vital rates. In fact, if the data does not contain information about the age (and/or sex-) structure of the surveyed population, there is no straightforward way to estimate demographic rates from such data. On the contrary, if age (and sex) of detected individuals can be determined, this information can be used to provide information on recruitment rates and survival probabilities. Nilsen and Strand (2018), for example, used a model based on harvest statistics and observations of population age structure to estimate population abundance and demographic rates without the need for any additional data from marked individuals.

Concurrent with the development of more sophisticated DS models, another group of models has emerged and rapidly gained popularity, not least for their ability to disentangle demographic processes underlying population dynamic: integrated population models (IPMs, Schaub and Kery 2021). Through joint analysis of multiple datasets, IPMs allow simultaneous estimation of population size and composition, as well as all vital rates that form part of an underlying age- or stage-structured population model. Since both DS models and IPMs estimate population size/density, a combination of the two frameworks has the potential to provide good estimates of both population- and demographic parameters by maximizing knowledge gained from transect surveys by augmenting them with other available data (e.g. Schmidt and Robison 2020).

In this study, we present a new IPM (IDSM, integrated distance sampling model) which integrates data from line transect distance sampling survey data and survival data from marked birds. The model's core is a stage-structured matrix population model that projects population size from one time step to the next based on underlying survival and recruitment rates. Below, we first present the model and assess its robustness and performance through application to simulated data. We then apply the model to real data collected from a willow ptarmigan (*Lagopus lagopus*) study in Central Norway. Because demographic rates are often affected by environmental covariates (e.g. rodent abundance in the case of willow ptarmigans), we also illustrate how such covariates can be included in the modelling framework.

2. Methods

2.1 An integrated distance sampling model

Our open population integrated distance sampling model (IDSM) consists of two major components: a latent structured population model and a set of likelihoods for data originating from distance sampling surveys and auxiliary survival monitoring. In the example case, these auxiliary data come from a radio-telemetry study, but in principle other types of capture-recapture data can also be used.

2.1.1 Age-structured population model

The population model follows a post-breeding census and includes two age classes: juveniles (young of the year) and adults (> 1 year of age, Figure 1). This structure is inspired by earlier models for our focal species, the willow ptarmigan (+ref), and is commonly used for populations of passerine and game birds (Williams, Nichols, and Conroy 2002; Schaub and Kery 2021). In the context of our willow ptarmigan case study (see below), the census falls into late summer and coincides with the annual distance-sampling survey in August.

Both juveniles and adults survive from year t census to year $t + 1$ census with survival probability S_t. As ptarmigan can reproduce already as 1-year old, all survivors then produce offspring in late June which recruit into the population as juveniles just prior to the census in year $t + 1$ according to a recruitment rate R_{t+1}. The changes in densities (numbers) of juveniles and adults in the population, D_{juv} and D_{ad}, can thus be expressed as

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

or, alternatively, in matrix notation as

$$\begin{bmatrix} D_{juv,t+1} \\ D_{ad,t+1} \end{bmatrix} = \begin{bmatrix} S_t * R_{t+1} & S_t * R_{t+1} \\ S_t & S_t \end{bmatrix} \begin{bmatrix} D_{juv,t} \\ D_{ad,t} \end{bmatrix}$$

Note that recruitment rate R is defined as juveniles/adult (not juveniles/female). We also make the simplifying assumption that there is no age- or sex-dependence of vital rates, but this assumption could be relaxed by including additional auxiliary data (Israelsen et al. 2020; Sandercock et al. 2011).

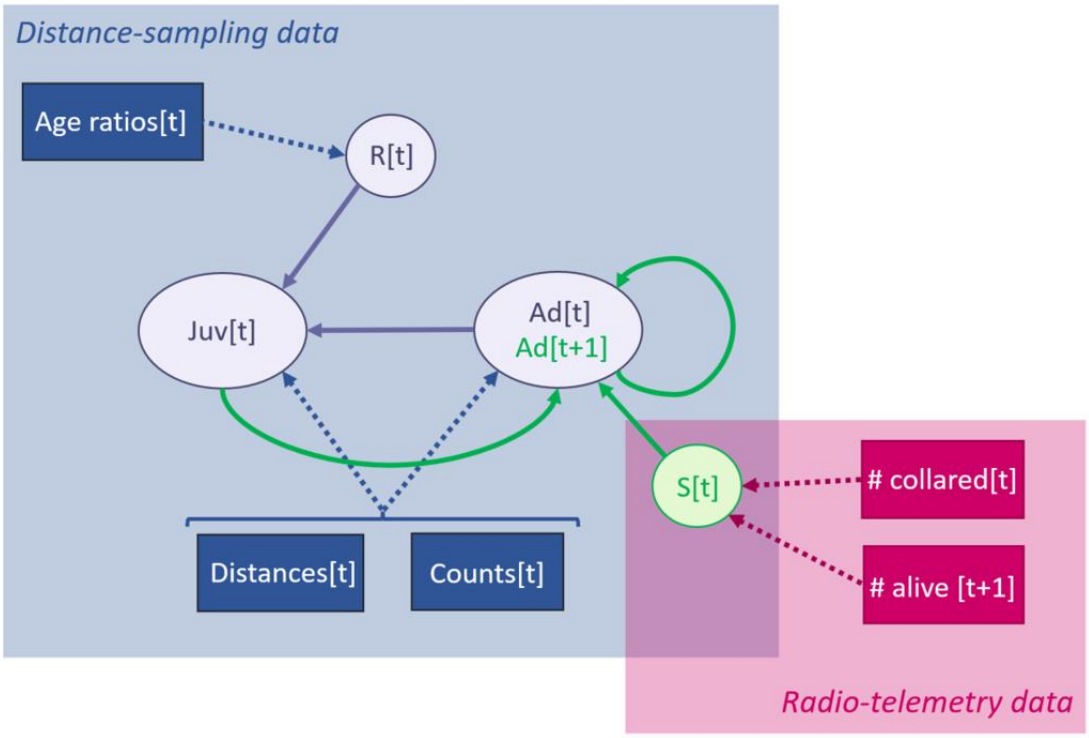

Figure 1: Simplified graphical representation of the ptarmigan life cycle with two age classes and the data sources included in the integrated distance sampling model. Juv[t] = juveniles in year t. Ad[t] = adults in year t. R[t] = recruitment rate in year t. S[t] = survival probability from year t to t+1.

2.1.2 Likelihoods for distance sampling data

The implementation of the modelling framework we present makes three assumptions about the distance sampling survey: 1) the survey consists of line transects, 2) animals may be detected alone or in groups, and 3) juveniles and adults can be distinguished during surveys. These assumptions are inspired by our willow ptarmigan case study (details below). Our model includes three likelihoods for different components of the age-structured distance sampling data. First is the likelihood for the perpendicular detection distances from line transect, y, which are linked to distance-dependent detection probability p through a half-normal detection function:

$$p = exp\left(-\frac{y^2}{2\sigma^2}\right)$$

where σ is the half-normal detection parameter. We assumed σ to vary among years (index t) but not between transect lines or animal group size. Following Moore and Barlow (2011), the resulting σ_t can be used to calculate effective strip width (esw_t) and, consequently, average detection probability per line transect with a truncation distance W according to:

$$esw_t = \sqrt{\frac{\pi * \sigma_t^2}{2}}$$
$$\widehat{p_t} = esw_t / W$$

The average detection probability $\widehat{p_t}$ is an integral part of the second data likelihood which relates the observed number of animals in each age class a, $obsN_{a,j,t}$ (j = transect) to the corresponding true number per transect, $N_{a,j,t}$:

$$obsN_{a,j,t} \sim Poisson\left(\widehat{p_t} * N_{a,j,t}\right)$$

$N_{juv,j,t}$ and $N_{ad,j,t}$ are then linked back to the population model by converting them to densities through multiplication with $2L_{j,t}W$ (where $L_{j,t}$ is length of transect j in year t, and W is the truncation distance).

The third data likelihood focuses on the counts of adults ($obsAd_{j,t}$) and juveniles ($obsJuv_{j,t}$) observed during the distance sampling surveys and links them to year-specific recruitment rate:

$$obsJuv_{j,t} \sim Poisson\left(R_t * obsAd_{j,t}\right)$$

2.1.3 Likelihood for radio-telemetry data

The final likelihood is for the auxiliary telemetry data. It is set up under the assumption of perfect detection, and hence known fates, of animals bearing transmitters and links the numbers of animals released at the start of season k of year t to the number of survivors at the end of the same season:

$$survivors_{k,t} \sim Binomial\left(released_{k,t}, Sk_t\right)$$

Here, Sk_t is the seasonal survival probability, and annual survival probability, S_t is calculated as $S1_t * S2_t$.

2.1.3 Hierarchical models with time-variation in parameters

Vital rates (survival probabilities S, recruitment rates R) and detection parameters (half-normal detection parameters σ) can all be modelled as time-dependent in our framework. For both the tests with simulated data and the case study described below, we implemented log-normally distributed random year effects on all parameters except survival, which was set to be constant. In the case study, we additionally included an effect of rodent occupancy (see details below) on log recruitment rates, resulting in the following model:

$$log(R_t) = log(\mu_R) + \beta * RodentOcc_t + \epsilon_t$$

where μ_R is the baseline recruitment rate, β the slope of the effect of rodent occupancy, and ϵ_t the normally distributed random effects.

2.2 Model testing with simulated data

We assessed the model's overall performance and ability to estimate abundance, demographic rates, and detection parameters without bias by testing it on simulated data. We generated a total of 10 simulated datasets in five steps. First, we simulated 15-year time-series of survival and recruitment rates from biologically plausible values for averages and – in the case of recruitment – among-year variation in demographic rates (survival was held constant across years). Second, we used the yearly demographic rate and realistic initial population densities to simulate stochastic population dynamics in 50 distinct sites. Third, we simulated the grouping of individuals in each site by first determining the expected number of groups in a site (based on the average group size of 5.6 from our ptarmigan data) and then distributing individuals among groups via multinomial trials. Fourth, we assigned a distance from transect line to each group and simulated the line transect survey in all 50 sites across 15 years. Finally, we simulated 5-year time-series of radio-telemetry data (= survival from one year to the next) for a subset of individuals (30 per year on average) using the simulated survival probabilities for each relevant year. We then fit the IDSM to each of the 10 simulated datasets three times, using distinct seeds for both simulating initial values and initiating and running the MCMC. Model implementation for simulated data tests was largely identical to that for real data and is described in detail below.

2.3 Case study

The willow ptarmigan has a circumpolar distribution (Fuglei et al., 2020), and lives year-round in heterogeneous alpine and artic ecosystems. In Norway, there has been a long-term decline in the willow ptarmigan abundance across more than a century (Hjeljord and Loe 2022), but in the last few decades abundance trends has fluctuated both in time and space. In Scandinavia, willow ptarmigan is a valued game species (see e.g. Andersen et al. (2014)), and there have been several long-term research projects devoted to understanding how they respond to environmental variation and harvest management (Israelsen et al. 2020; Sandercock et al. 2011). A key insight from across several study areas is the the annual recruitment rate (i.e. R_t in our model, as outlined above) is highly variable, and is affected both by spring conditions (Eriksen et al. 2023) and the abundance of small rodents, which constitute alternative prey for common predators (i.e. the Alternative Prey Hypothesis; see Hagen (1952); Kausrud et al. (2008); Bowler et al. (2020)). Adult survival show less inter-annual fluctuations (Israelsen et al. 2020), although spatial (and potentially temporal) variation due to e.g. harvest management is evident when comparing across studies (Israelsen et al. 2020).

Our case study was based on an ongoing long-term research project on willow ptarmigan in Lierne municipality in Central Norway (approximately 62.4 degrees north and 13.2 degrees east). The study area is located in a sub-alpine ecosystem, and the landscape is a mosaic of open heath and shrub vegetation (dominated by Ericacea, willow shrub *Salix spp*., and dwarf birch *Betula nana*), interspersed with bogs and forest patches (mainly birch *Betula spp*.). The climate is strongly seasonal, with snow typically covering the ground from October/November through April/May.

From this study system, two datasets were used for the case study:

1. Data from a line transect survey program targeting willow ptarmigan operated under the natural resources management authorities (2007-2021, ongoing)

2. Data from an individual-based monitoring programme based on radio collared willow ptarmigan (2015-2021, ongoing)

Line transect survey data were collected in August each year, prior to the annual autumn harvest season, as part of the program "Hønsefuglportalen". Hønsefuglportalen is a national program for line transect surveys of tetraonid birds, and the effort is directed mainly towards willow ptarmigan habitats. In our case study, we used data from the western part of Lierne municipality. Line transects are surveyed by trained volunteers that use pointing dogs to locate the birds. When located, the geographical coordinate, perpendicular distance from the sampling line, the number of birds in the group, as well as the age (juvenile or adult) and sex of the birds are recorded. As the surveys are conducted in early August, juveniles can be distinguished from adults by their smaller body size. Males and females are manly distinguished by the sound (males often make a characteristic sound when being flushed. Nevertheless, mis-identification can occur, and in addition a proportion of the birds are registered as "unknown" age and/or sex. Since 2019, data has been collected through a mobile app tailormade for this project, which is available trhough App Store (for ios phones) and Google Play (for Android phones). Before 2019, field workers reported their data through a dedicated web portal. After data are collected and reported, they undergo several steps of quality control: first by local contacts and subsequently by personnel at the Norwegian Institute for Nature Research (NINA). The data are then standardized based on the Darwin-Core standard (Wieczorek 2012), and made publicly available as a sampling-event data set published through GBIF (Nilsen et al. 2023). For additional description of the data collection procedures, see (Bowler et al. 2020; Kvasnes, Pedersen, and Nilsen 2018; Nilsen et al. 2023).

The individual longitudinal study based on radio collared willow ptarmigan was conducted in 2015-2021. Each winter (in February-March), willow ptarmigan were located at night using snowmobiles and large hand nets with prolonged handles, as described in (Israelsen et al. 2020). To prevent birds from flying off before the field personnel were close enough to capture them, a high-powered head lamp was used to dazzle the birds. After capture, birds were placed in an opaque bag to reduce stress. They were then fitted with a uniquely numbered leg ring (~ 2.4g) and a Holohil RI-2BM or Holohil RI-2DM radio transmitter (~ 14.1g) and subsequently released. The radio transmitters had an expected battery lifetime of 24 months (RI-2BM) or 30 months (RI-2DM), and included a mortality circuit that was activated if a bird had been immobile for 12 hours. We monitored the birds throughout most of the year by triangulation from the ground at least once a month for 10 months of the year (February – November) by qualified field personnel. If a mortality signal was emitted from a transmitter, we attempted to recover it as soon as possible to determine cause of death. A number of birds dispersed out of the main study areas and was thus out of signal range for field personnel on the ground. To avoid loss of data, we conducted aerial triangulation using a helicopter or airplane three times a year (May, September and November) in the years 2016-2020.

2.4 Bayesian model implementation

We implemented the model in a Bayesian framework using NIMBLE version 1.0.1 (Valpine et al. 2017) in R version 4.3.1 (R Core Team 2023). The likelihood for line transect observation distances was set up using a custom half-normal distribution developed by Michael Scroggie as part of the "nimbleDistance" package (https://github.com/scrogster/nimbleDistance). We used non-informative uniform priors (with biologically reasonable boundaries where possible) for all parameters. We assumed constant survival and time-varying recruitment rate in models fit to both simulated and real data.

For the model fits to simulated and real data we ran 3 and 4 MCMC chains with NIMBLE's standard samples for 500k and 100k iterations, respectively. 300k and 40k and thereof were discarded as burn-in prior to thinning with factors 5 and 20 , leaving us with 40k and 3k posterior samples per chain (total of 120k and 12k samples per run), respectively. Posterior samples from the model fitted to real data are available at Nilsen and Nater (2024) (in folder PosteriorSamples_LierneCaseStudy).

3. Results

3.1 Model performance on simulated datasets

Posterior distributions for parameters estimated in three model fits to each of 10 simulated data sets are shown in Figure 2 and Figure 3. Overall, the IDSM was able to correctly estimate both detection parameters and demographic rate parameters from all 10 simulated datasets without any systematic bias. The replicate runs for each dataset resulted in very similar posterior distributions, demonstrating that the models converged towards the same posterior distributions irrespective of starting values. Estimates of population sizes / densities were also adequate, and are presented in the supplementary materials (available at Nilsen and Nater (2024) in folder SimCheck_byDataSet).

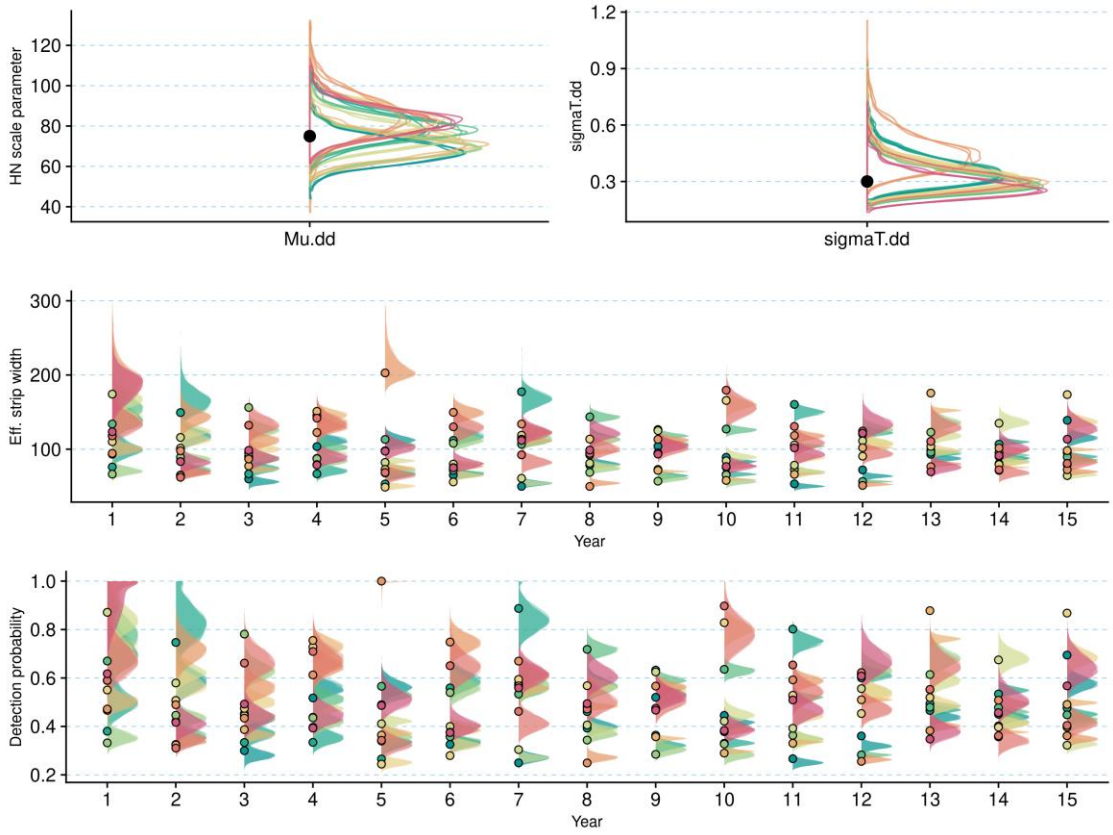

Figure 2: Detection parameters estimated from 10 distinct sets of simulated data (= colors). Upper panel depicts model parameters, and lower panels show derived estimated of effective strip width and mean detection probability. Dots represents true values (black for global values, colored for dataset-specific values), and density plot represent the posterior distributions for each model run.

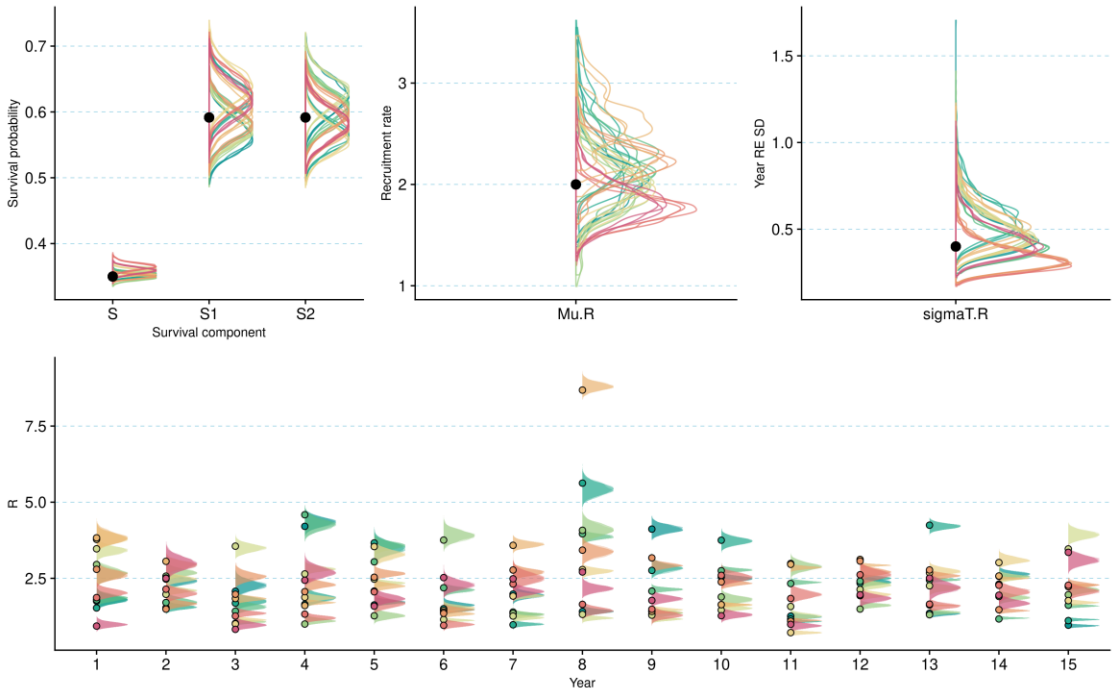

Figure 3: Demographic rate parameters estimated from 10 distinct sets of simulated data (= colors). Upper panel show annual and seasonal survival probabilities, hyperparameters for the random effects model for recruitment (mean and sd), and lower panel show annual estimates of the recruitment rate. Dots represent true values (black for global values, colored for dataset-specific values), and density curves represent the posterior distributions from each model run.

3.2 Case study on willow ptarmigans in Central Norway

Having evaluated the overall performance of our model on simulated data, we used data from our case study in Lierne as a case study to estimate abundance, vital rates and detection probabilities from a real-world data set. Ptarmigan population density increased markedly across the study period, from < 10 ptarmigan / km^2 in 2007 to > 35 ptarmigan / km^2 in in 2021 (Figure 4). The increase was most distinct from 2016 and onward.

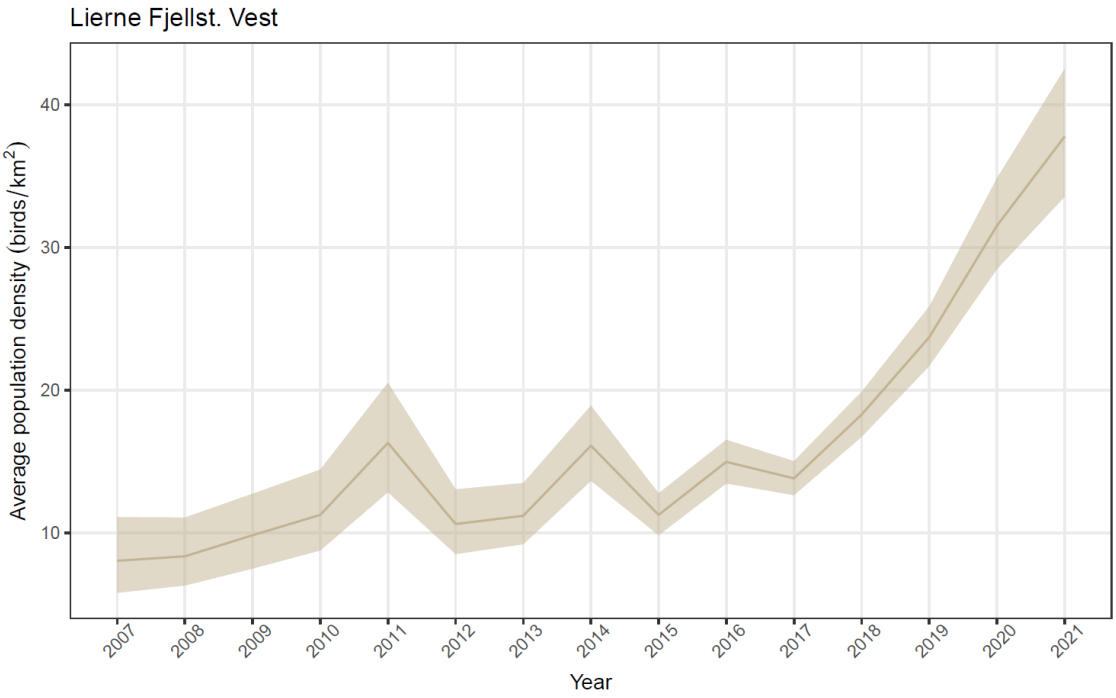

Figure 4: Estimated density of willow ptarmigans in Lierne from 2007 to 2021. Solid line represents the posterior median, ribbon marks 95% credible interval.

Average survival probability for August - January (S_1) was estimated at 0.46 (95% C.I = 0.42 - 0.51) while average survival probability for February - July (S_2) was estimated as 0.64 (95% C.I = 0.59 - 0.7) (Figure 5 A). Annual survival probability S, given by the product of S_1 and S_2, was estimated at 0.3 (95% C.I = 0.29 - 0.31), Figure 5 A).

Recruitment (R_t) was allowed to vary across years (see model specification), and estimates displayed large inter-annual variability (Figure 5 C, Figure S1). While the mean (baseline) recruitment μ_R was estimated as 2.9 (95% C.I = 2.5 - 3.4) the yearly recruitment rates ranged from 1.2 in year 2012 to 4.9 in year 2007.

Given the available data, the IDSM was not able to estimate a clear effect of small rodent abundance on ptarmigan recruitment (slope-paramater for the z-standardized rodent occurrence data = 0.037 ; 95% C.I. = -0.216 - 0.248, see supplementary figure "Rep_betaR.R.png" in Nilsen and Nater (2024)).

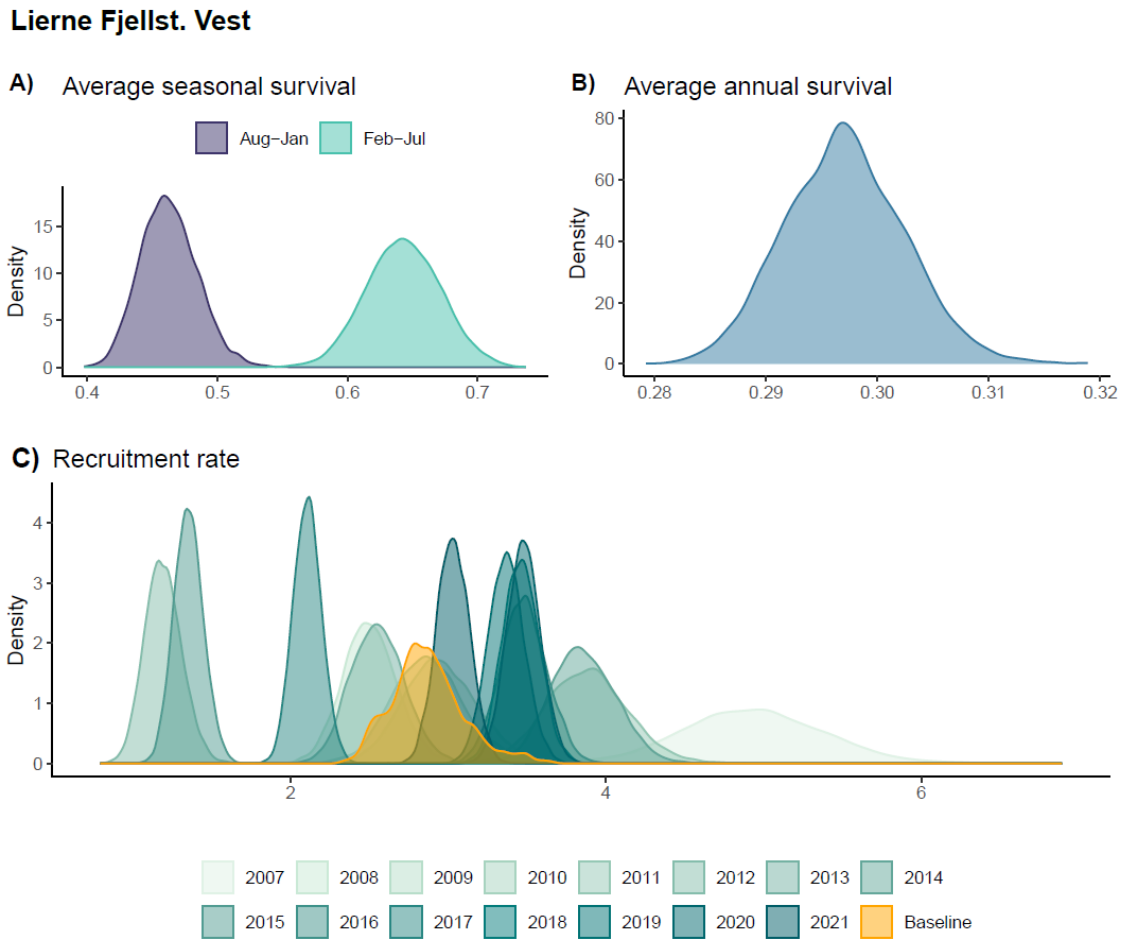

Figure 5: Posterior densities of A) seasonal survival, B) average annual survival, and C) recruitment rate. For the latter, the yellow distribution is for the intercept, representing a baseline recruitment rate when rodent occupancy is low. The turquoise distributions are for year-specific estimates or recruitment rate, with darker colors indicating later years.

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Discussion

We developed an integrated populaiton model that jointly analyses line transect distance sampling survey data and data from marked individuals to estimate population abundance, survival probabilities, and recruitment rates over time. We first used simulated data to examine the model's ability to recover the underlying parameters when they were known. We then fitted the model to data from an ongoing field study on willow ptarmigan in Norway to showcase its applicability to real wildlife monitoring data.

Open population formulations of the distance sampling model have previously been presented (Sollmann et al. 2015; Bowler et al. 2020; Moore and Barlow 2011), and in these studies also applied to various ecological systems. The model presented here extends those previous applications by formulating the underlying population process model as a stage-structured matrix model (Caswell 2000) in which the matrix elements are represented by annual survival probabilities and recruitment rates. While this has been the common approach for a range of other statistical modelling frameworks, including the growing suite of models falling into the category of integrated population models (Schaub and Kery 2021), the integration of mechanistic population models into distance sampling frameworks is rather new. The resulting modelling framework allow us to make maximum use of distance sampling data in combination with auxiliary information both from the distance sampling survey itself (i.e. information on age, sex, etc. of observed animals) and from other types of monitoring, and enables estimation not only of changes in population density but also of underlying vital rates over time.

In general, the model did a very good job at recreating the underlying parameters when fitted to simulated data where the true values are known. The simulated data sets were based on relatively wide ranges of parameter values, yet we did not find the model to have any particular problems or biases recovering the original parameters used in simulations. When the input data are unbiased (with respect to the underlying model formulation) we therefore consider the model to be able to extract unbiased and meaningful demographic parameters from age-structured distance sampling data.

Real data, however, are likely to be subject to certain biases, and such biases might result in biased parameter estimates unless accounted for. One type of bias that is likely to be common for age-structured distance sampling data arises from failure to (correctly) classify the age class of observed individuals. In our case study on willow ptarmigan in Norway, such misclassification is likely to happen at an unknown rate, even if the size difference between adult and juvenile birds are quite substantial during the survey. Moreover, The probability for misclassificiation might be related to both the timing of the survey (e.g. mid August rather than early August), it might vary between observers, and even by survey conditions. Observations with incorrectly classified age have the potential to introduce bias in the IDSMs relative estimates of survival and recruitment. This is due to the way it useses the distance sampling data to estimate survival and recruitment rates. In our process model, the population growth rate (λ) is determined by the survival and recruitment rate in the following way: $\lambda = S + (S * R)$, and this creates a dependence between the demographic parameters. If the age ratio in the data are biased or contain frequent misclassifications, this is likely to affect the relative contribution of survival and

recruitment to the growth rate. To get an idea of the potential effect of this on parameter estimation, we checked the sensitivity of the output of the model fit to real data with regard to the treatment of birds classified as "unknown sex and age" by the field personnel (see Methods). In the model version presented in the results section, we made the assumption that these birds were in fact juveniles. Comparing estimates to an alternative scenario in which we discarded all birds classified as "unknown sex and age" (see supplementary figures in Nilsen and Nater (2024)) we found that – as expected – estimated population density was virtually unaffected by the treatment of "unknown sex and age" observations, while the annual demographic parameters shifted proportional to the amount of "unknown sex and age" observations in the given year (towards higher recruitment and lower survival). Thus, biases in the reported age ratios may affect estimated of demographic rates, but not so much population density. Since the proportion of "unknown sex and age" observations in our ptarmigan case study was rather low, potential biases in estimates resulting from age misclassification are expected to be small. Nonetheless, future developments of the IDSM modelling framework should focus on ways of accounting explicitly for misclassification of age class in the field.

The density estimates that we derived from the case study on Willow ptarmigan in Norway is comparable to previous estimates from across Norway (see e.g. Sandercock et al. (2011); Kvasnes, Pedersen, Solvang, et al. (2014)). Throughout the study period from 2007 - 2021, the density increased markedly, but the reason for this increase is not known. Compared to previous studies on ptarmigan (see e.g. (Israelsen et al. 2020; Sandercock et al. 2011)), we could have expected somewhat higher estimates of survival probability. One potential reason for the overall lower estimates obtained here is that our IDSM analysis assumed constant survival over the period 2007-2021 while survival, in reality, may have changed over time. If survival in more recent years, when telemetry data was collected (and the study of e.g. Israelsen et al. (2020) was carried out) was higher than in earlier years – something that seems likely given population increase over recent years – an average over the entire time period is expected to be lower. On a different note, we can also not exclude the possibility of a small degree of bias in survival estimates due to misclassification of age in the data (see above), especially seeing as the IDSM's recruitment rate estimates also appear somewhat high compared to other studies on willow ptarmigan (Eriksen et al. 2023; Kvasnes, Pedersen, Storaas, et al. 2014; Steen et al. 1988). Note however that the last period of the study period in Lierne, there was substantial increase in the density (ref Figure 2), which might indicate that the recruitment and/or survival rates were high in this period.

In addition to estimating demographic rates from line transect data, the IDSM also allows including relevant environmental effects on the demographic rates themselves, and not just on population growth rate as a whole (λ). In the ptarmigan case study we thus attempted to investigate the effect of small rodent abundance (approximated as the proportion of transect lines on which rodents were reported each year) on recruitment rate. Unfortunately, we were not able to detect a clear effect of rodent abundance due to large uncertainty associated with the estimate (see supplementary figures in Nilsen and Nater (2024)). This may seem somewhat surprising given that such a pattern has been reported repeatedly in the literature (see e.g. Bowler et al. (2020)). We speculate that there are at least three potential (non-mutual) explanations to this result. The first is that our covariate

data may not have been well suited for estimating effects on recruitment. The data on rodent abundance was heavily zero-inflated, and the annual variation in the index was rather small otherwise, making for a covariate with relatively little information content. While this may be partially a consequence of how these data are collected, it is also well known that the amplitude and regularity of the rodent cycles has been fading in recent decades (Kausrud et al. 2008; Cornulier et al. 2013), and our study area might be no exception. Lack of peak rodent years in the time series to which we fitted the model may thus also have contributed to making effect estimation challenging. Second, it is possible that rodent effects were obscured by other, potentially stronger, covariate effects. Previous research has shown that ptarmigan recruitment is also sensitive to the weather in the late winter and spring (before and during the breeding season); as we did not fit any weather covariates to the model so there is a possibility that strong unaccounted for effects of spring conditions in certain years may have masked any remaining effects of small rodent abundance. Finally, the data set used in this analysis is relatively short (15 years), leaving us with somewhat limited statistical power to detect effects of temporal covariates . Taken together we therefore do not consider this study as a particularly strong test of the underlying effect of small rodent fluctuations on ptarmigan recruitment rates. It is worth noting that future applications could increase statistical power by including either more years of data or capitalizing on space-for-time substitution as the Norwegian ptarmigan monitoring programme spans many more locations beyond Lierne. Bowler et al. (2020), for example, used data from the same sampling program but from more areas using a simpler open population DS model, and detected a very clear signal from small rodent abundance on ptarmigan population growth rate. An extension of our IDSM to include data from multiple areas therefore constitutes a promising approach for investigating to which extent similar results emerge by linking environmental covariates to the actual demographic rates and not only just to the resulting population growth rates.

The new IDSM framework presented here is relevant for many wildlife populations that are surveyed using line transect sampling that includes additional information on age, sex, and/or life stages of the observed individuals. Following the integrated modelling philosophy, the IDSM also allows for the integration of auxiliary data. In our application here, we integrated data from radio-telemetry of marked birds, which explicitly supported the estimation of survival probabilities. The IDSM framework is very flexible, however, and open to the inclusion of additional/other auxiliary data that contains information on demographic rates or population size/density. Moreover, hierarchical nature of the model makes is straight forward to adapt to different species and to include different suites of environmental covariates on the demographic rates. Finally, it constitutes a modelling framework that is well suited for extension to multiple areas and thus able to capitalize on space-for-time substitution to produce large-scale and spatially explicit estimates of population density, demographic rates, and environmental effects from large-scale (participatory) monitoring.

Author contributions

EBN Lead - Drafted the model code; Lead - Wrote first version of ms; Lead - Data collection; Contributed - Modelling and analyses

CRN Lead - Updated, further developed, and finalized model code; Lead - Modelling and analyses; Contributed - Wrote first version of ms

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Conflict of interest disclosure

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

Data and code availability

The raw data from the line transect surveys is deposited on GBIF and can be accessed freely via the Living Norway Data Portal (https://data.livingnorway.no). The work here is based on version 1.7 of the dataset "Tetraonid line transect surveys from Norway: Data from Fjellstyrene" (Nilsen et al. 2023).

The auxiliary radio-telemetry data and rodent occupancy data, and all code used for wrangling, analysing, and visualizing data and results 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 1.3 of the code (ChloeRNater et al. 2024).

Supplementary figures and posterior samples from the model run on the real data are available as a time-stamped open archived on Open Science Framework (Nilsen and Nater 2024).

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