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## ARTICLE

# A modeling approach to forecast local demographic trends in metapopulations

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## Abstract

Predicting animal population trajectories into the future has become a central exercise in both applied and fundamental ecology. Because demographic models classically assume population closure, they tend to provide inaccurate predictions when applied locally to interconnected subpopulations that are part of a larger metapopulation. Ideally, one should explicitly model dispersal among subpopulations, but in practice this is prevented by the difficulty of estimating dispersal rates in the wild. To forecast the local demography of connected subpopulations, we developed a new demographic model (hereafter, the two-scale model) that disentangles two processes occurring at different spatial scales. First, at the larger scale, a closed population model describes changes in metapopulation size over time. Second, total metapopulation size is redistributed among subpopulations, using time-varying proportionality parameters. This two-step approach ensures that the long-term growth of every subpopulation is constrained by the overall metapopulation growth rate. It implicitly accounts for the interconnectedness among subpopulations and avoids unrealistic trajectories. Using realistic simulations, we compared the performance of this new model with that of a classical closed population model at predicting subpopulations' trajectories over 30 years. While the classical model predicted future subpopulation sizes with an average bias of 30% and produced predictive errors sometimes >500%, the two-scale model showed very little bias (<3%) and never produced predictive errors >20%. We also applied both models to a real dataset on European shags (*Gulosus aristotelis*) breeding along the Atlantic coast of France. Again, the classical model predicted highly unrealistic growths, as large as a 200-fold increase over 30 years for some subpopulations. The two-scale model predicted very sensible growths, never larger than a threefold increase over the 30-year time horizon, which is more in accordance with this species' life history. This two-scale model provides an effective solution to forecast the local demography of connected subpopulations in the absence of data on dispersal rates. In this

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context, it is a better alternative than closed population models and a more parsimonious option than full-dispersal models. Because the only data required are simple counts, this model could be useful to many large-scale wildlife monitoring programs.

#### KEYWORDS

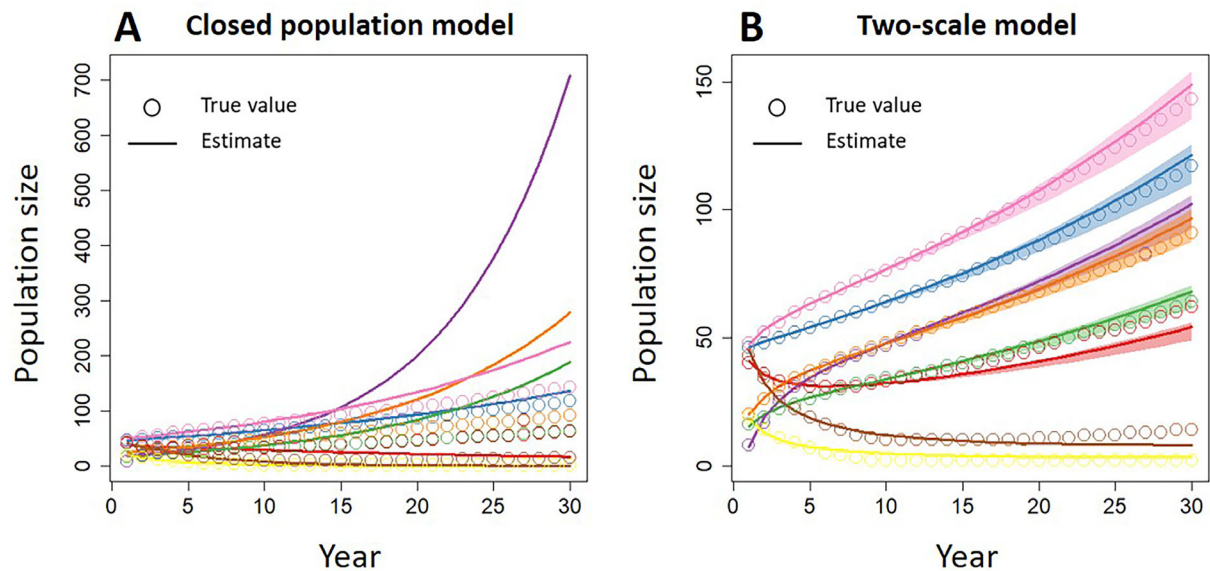
dispersal, open-population models, population viability analysis, predictive modeling, seabird demography, wildlife management

## INTRODUCTION

Forecasting animal population trends into the future has become a central endeavor in both basic ecology and wildlife conservation (Lacy, 2019; Morris & Doak, 2002; Mouquet et al., 2015). This predictive exercise, often referred to as population viability analysis (Beissinger & McCullough, 2002; Boyce, 1992), is indeed a cornerstone of scientific studies that aim at (1) projecting the demographic consequences of some disturbance (e.g., habitat fragmentation) on animal populations (e.g., Morita & Yokota, 2002) or (2) comparing the consequences of alternative management scenarios (e.g., Ferreras et al., 2001). Demographic projections generally rely on models that assume geographic closure (Earl, 2019; Jeglinski et al., 2023), meaning that a population's trajectory is not influenced by dispersal processes but is only driven by births and deaths (Boyce, 1992). The main reason for making this assumption is that immigration and emigration rates are usually very hard and costly to estimate in the wild (Cayuela et al., 2018; Miller et al., 2019). However, the validity of this simplifying assumption, and therefore the reliability of population projections, highly depends on the spatial scale at which the demographic model is applied (Thomas & Kunin, 1999). This issue of spatial scale choice, known as the modifiable area unit problem, is highly prevalent in population modeling (Laymon & Reid, 1986) and more generally in ecology (Jelinski & Wu, 1996). On a relatively large scale, when the analysis encompasses an entire metapopulation (Hanski, 1998, 1999), it is sensible to assume geographic closure. Indeed, a metapopulation as a whole can be considered as a closed system dominated by birth and death processes (Goodwin & Fahrig, 1998; Hanski, 1998). On a smaller spatial scale, however, the influence of dispersal on the local dynamics of (sub)populations becomes more important, and closed population models become ill-adapted (Goodwin & Fahrig, 1998). When dealing with wide-ranging connected populations, there is thus a dilemma between the predictive accuracy and the local utility of the demographic predictions that can be made with a closed population model. Indeed, the accuracy of population

projections tends to increase with the spatial scale of the predictive scope (e.g., focusing solely on the whole metapopulation size), because one is less likely to violate the closure assumption at larger scales (Beissinger & McCullough, 2002; Earl, 2019). However, broadscale predictions are usually less useful than site-specific ones, especially in the context of wildlife conservation (Clapham et al., 2008). Unfortunately, population units that are of primary interest to inform wildlife conservation decisions are often much smaller than what could sensibly be considered as a *geographically closed* population (Moritz, 1994).

The main risk when forecasting local demographic trajectories of interconnected subpopulations using a closed population model is to overestimate the trend of subpopulations that have recently experienced a positive balance of immigrants (see Figure 1A for an illustration of this effect). Consider the case of an initially small subpopulation that consistently receives a large number of immigrants each year. For several years, this subpopulation will experience a realized growth rate that largely exceeds the overall metapopulation's growth rate. However, such a large growth rate cannot be sustained for very long. Over time, as the size of this subpopulation increases, the relative contribution of immigration to its growth will necessarily decrease because, *proportionally speaking*, the production of new dispersers by other subpopulations cannot keep up the pace. Immigrants must indeed come from somewhere, and the rate of production of new dispersers is necessarily constrained by the metapopulation's growth rate. Ultimately, the growth rate of that immigration-subsidized subpopulation is not independent of the dynamics happening in the rest of the metapopulation. In such a situation, a closed population model will necessarily overpredict the growth of this subpopulation because it assumes that demographic trends are independent among subpopulations. This bias is due to the fact that the strong but transitory growth rate, experienced by this immigration-subsidized subpopulation, is being blindly projected forward over a long period. Because population growth is an exponential process, this bias can quickly become extremely severe



**FIGURE 1** Example of demographic predictions, from a single simulated dataset, provided by (A) the classical closed population model, assuming independent growth among subpopulations; and (B) the two-scale model. The classical model largely overestimates the growth of some subpopulations, while the two-scale model provides accurate predictions.

(see Figure 1A), especially when density dependence is not included in the model (see *Discussion*).

This risk of overprediction is very likely for species with a metapopulation structure, such as colonial seabirds (Jeglinski et al., 2023; Schippers et al., 2009), gregarious bats (Moussy et al., 2013; Reis et al., 2012), small mammals (Olivier et al., 2009; Ozgul et al., 2009), or pond breeding amphibians (Alex Smith & Green, 2005; Semlitsch, 2008). A closed population model will necessarily produce unrealistic projections for any subpopulation (e.g., breeding colony) that has been experiencing a strong initial phase of immigration during the phase of data collection. To avoid this problem, the linkage between local growth and the production of new individuals at the metapopulation's scale must be explicitly stated in the model.

Open population models that incorporate immigration and emigration processes exist (Hanski, 1998; Pulliam, 1988). Their use remains however very limited in the context of most empirical analyses, because estimating dispersal rates in the wild is usually far too difficult and costly (Cayuela et al., 2018; Miller et al., 2019). Even in cases where it might be possible to estimate the rates of local immigrants and local emigrants for a single subpopulation, this will not be sufficient to solve the problem. Indeed, if a high rate of immigrants is estimated locally over a transitory period and then it is projected forward over many years, the positive bias described above will still occur. This is because one still implicitly assumes that the stock of immigrants is unlimited. To avoid this bias, immigration fluxes need to be

constrained in a realistic way, for example, through an explicit linkage between the local demography of subpopulations and the number of migrants they are sending away. In a fully explicit metapopulation model, this requires estimating not only the local dynamics of every subpopulations within a metapopulation, but also the rates of exchange between all possible pairs of subpopulations, which is usually prohibitive (Jeglinski et al., 2023).

To work around this issue, we built an innovative demographic model in which the change of any subpopulation's size is conditional on the overall metapopulation growth. Changes in metapopulation size are modeled first, using a classical "closed population" demographic process. Then, in a second step, total metapopulation size is distributed among all local subpopulations. This two-step process ensures that the growth of any subpopulation remains constrained by the number of individuals actually present in the metapopulation. This new modeling approach, named "two-scale model," was initially developed for the needs of a large-scale research project that aims at quantifying the cumulative impact of offshore wind energy development on the population dynamics of seabirds breeding along the French Atlantic coast. To assess the performance of this two-scale model, we first ran a simulation study. Next, we applied the model to a real dataset on European shags (*Gulosus aristotelis*). In both cases, the predictive performance of the two-scale model was compared with that of a classical closed population model assuming independent demographic trajectories among subpopulations.

## MODELING APPROACH

### Two-scale model description

Hereafter, we use the term *subpopulation* to refer to a local population connected to other local populations inside a larger metapopulation (Hanski, 1998, 1999). Consider the case of  $I$  subpopulations connected by dispersal. The only data collected from each subpopulation are annual count censuses, without any form of individual identification, such that no information is available to estimate immigration and emigration rates. These types of “simple count” data are extremely frequent in wildlife monitoring. Formally, we describe the census data  $C_{i,t}$  as the number of animals (e.g., number of breeding pairs) counted in each subpopulation  $i = \{1, \dots, I\}$  each year  $t = \{1, \dots, T\}$ .

First, we model metapopulation growth using a classical closed population approach:

$$N_{t+1} = \lambda \times N_t,$$

where  $N_t$  is the metapopulation size (i.e., the sum of the sizes of all subpopulations;  $N_t = \sum_{i=1}^I n_{i,t}$ ) in year  $t$ , and  $\lambda$  represents the interannual growth rate at the metapopulation scale. At this scale, because it is assumed that  $\lambda$  results only from birth and death processes, it corresponds to the true overall demographic trend and it is necessarily constrained by the species' life history strategy.

Second, we model the size ( $n_{i,t}$ ) of each subpopulation  $i$  in year  $t$  by redistributing the metapopulation size ( $N_t$ ) among the  $I$  subpopulations:

$$n_{i,t} = \gamma_{i,t} \times N_t,$$

where  $\gamma_{i,t}$ , which we call the *redistribution* parameter, is the proportion of  $N_t$  allocated to subpopulation  $i$ . Parameter  $\gamma_{i,t}$  does not model an explicit demographic mechanism. It is only a convenient way of capturing the trajectory of a given subpopulation, conditionally on the overall metapopulation size, with a single parameter. It is therefore important to understand that this parameter does not explicitly represent a local immigration/emigration rate. Rather, parameter  $\gamma_{i,t}$  is a latent (unknown) combination of local survival, reproduction, immigration, and emigration rate. This proportion  $\gamma_{i,t}$  varies among subpopulations, allowing each of them to receive its own specific fraction of the total metapopulation size  $N_t$ . In addition,  $\gamma_{i,t}$  must vary across years to ensure that each subpopulation has its own

demographic trajectory. Without year variation on  $\gamma_i$ , every subpopulation would be forced to reach the same local demographic trend (i.e., the trend of the whole metapopulation). Across-year variation on  $\gamma_i$  is modeled using a simple linear temporal effect, which provides enough flexibility for our purpose while avoiding overparameterization (a single degree of freedom is added). Because of the constraints  $\gamma_{i,t} \in [0; 1]$  and  $\sum_{i=1}^I \gamma_{i,t} = 1$ , this trend is modeled using an intermediary parameter ( $w_{i,t} \in \{-\infty; +\infty\}$ ), which is an unscaled equivalent of  $\gamma_{i,t}$ . The linear temporal trend is written as follows:

$$w_{i,t} = \beta_{0,i} + \beta_{1,i} \times (t - 1),$$

where  $\beta_{0,i}$  represents the intercept for subpopulation  $i$ , that is, the unscaled fraction of  $N_t$  received by subpopulation  $i$  in year 1; and  $\beta_{1,i}$  represents the slope of the linear temporal trend for subpopulation  $i$ . The year- and subpopulation-specific values of  $\gamma_{i,t}$  are then obtained by scaling values of  $w_{i,t}$  on the  $[0; 1]$  interval, as follows:

$$\gamma_{i,t} = \frac{w_{i,t}}{\sum_{i=1}^I w_{i,t}}.$$

This last step ensures that the constraint  $\sum_{i=1}^I \gamma_{i,t} = 1$  is satisfied.

Finally, we model the observation process giving rise to local count data  $C_{i,t}$ , using a normal distribution:

$$C_{i,t} \sim \text{Normal}(n_{i,t}, \sigma^2),$$

where  $n_{i,t}$  is the true mean subpopulation size in year  $t$  and  $\sigma^2$  is the variance due to the imperfect observation process. It is common practice to use a normal distribution to allow for overcounts (false positives) and undercounts (false negatives), both of which can occur during seabird colony counts, but alternatively a lognormal or a Poisson process might be used (Schaub & Kéry, 2021). Without intra-annual replicated counts, note that stochastic process variance and observation error variance are actually confounded. If replicated counts were available, we could choose to model the observation process differently, including, for instance, a detection probability parameter (Royle, 2004; Williams et al., 2002).

In this model formulation, the parameters to be estimated are: (1)  $\lambda$ , the metapopulation growth rate; (2)  $\beta_{0,i}$  and  $\beta_{1,i}$ , the intercept and slope, respectively, of the linear temporal trend which determine the value of the

redistribution parameter  $\gamma_{i,t}$ ; and (3)  $\sigma^2$ , the variance of the observation process. All other parameters (e.g.,  $\gamma_{i,t}$ ) are latent variables in the model, which are derived from these basic parameters. Census data  $C_{i,t}$  are sufficient to estimate all model parameters, such that none of these parameter values need to be arbitrarily fixed by the user.

## Closed population model description

In the closed population model, the demographic growth of each subpopulation  $i$  is simply modeled as follows:

$$n_{i,t+1} = \lambda_i \times n_{i,t},$$

where individual growth rates  $\lambda_i$  are independent and follow a lognormal distribution:

$$\lambda_i \sim \text{LogNormal}(\lambda_0, \sigma_\lambda^2),$$

with  $\lambda_0$  being the mean growth rate and  $\sigma_\lambda^2$  its variance across subpopulations. The observation process is modeled exactly as in the two-scale model (see above).

In this model formulation, the parameters to be estimated are (1)  $\lambda_0$  and  $\sigma_\lambda^2$ , which are hyperparameters governing the probabilistic distribution of subpopulation growth rates  $\lambda_i$ ; and (2)  $\sigma^2$ , the variance of the observation process. Census data  $C_{i,t}$  are sufficient to estimate all model parameters, such that none of these parameter values need to be arbitrarily fixed.

## Model implementation

In the applications described below, we implemented both closed population and two-scale models in a Bayesian framework that relied on Markov chain Monte Carlo (MCMC) posterior sampling. The MCMC approach allows combining the retrospective and prospective components of the analysis very easily, as follows. In addition to fitting the model to the  $T$ -year count data (i.e., retrospective analysis), we simply added 30 years of NAs to the dataframe to obtain predictions of future subpopulation sizes across a 30-year time horizon.

In all cases, we used uninformative priors. For parameters  $\beta_{0,i}$  and  $\beta_{1,i}$  of the two-scale model, which are components of a proportionality parameter ( $\gamma_{i,t}$ ) and thus only take strictly positive values, we used a uniform distribution on (0, 100). For parameter  $\lambda$  of the two-scale model and parameter  $\lambda_0$  of the closed population model, we used a uniform distribution on (0, 10). We note that a value of  $\lambda > 1.5$  is virtually impossible for a long-lived

species, such as the European shag studied in this paper, so setting the upper boundary to 10 is largely uninformative. For parameter  $\sigma_\lambda^2$  of the closed population model, we used a uniform distribution on (0, 20).

For all the analysis presented below, we ran three parallel chains of 55,000 MCMC samples each, with a burn-in period of 5000 samples. Adequate convergence of MCMC chains was checked through a visual assessment of sample path plots and using the R-hat diagnostic of Brooks–Gelman–Rubin (Brooks & Gelman, 1998). We decided that chain convergence was reached if R-hat  $< 1.01$ .

## APPLICATIONS

### Simulations

Annual abundances at eight connected subpopulations were simulated for 40 years. The initial metapopulation size was always set to  $N_0 = 240$ . For subpopulations, new values of initial size  $n_{i,0}$  were randomly drawn at each simulation from a multinomial distribution, with individual probability parameters  $p_i$  themselves drawn from a uniform (0,1) distribution to ensure enough variability in  $n_{i,0}$  among subpopulations and across simulations. Starting from  $n_{i,0}$ , local abundances were simulated forward in time as the result of two successive and demographically explicit processes. First, the interannual dynamics of local births and deaths were modeled using constant *intrinsic* growth rates  $\lambda_i$  that were specific to each subpopulation  $i$ . Note that we use the term *intrinsic* to refer to the contribution of births and deaths only to a population's growth rate. Second, interannual dispersal events between subpopulations were simulated using a  $I \times I$  matrix of dispersal rates in which each subpopulation  $i$  had its own level of attractiveness based on two parameters: (1) *site fidelity* “*sf*” determined the probability that any individual would remain inside its current subpopulation (i.e., not emigrating); (2) *heterogeneity in attractiveness* “*ha*,” which can take values between 0 (no heterogeneity) and 1 (maximum heterogeneity), controlled the amount of heterogeneity in attractiveness among subpopulations. With  $ha = 0$ , an individual leaving its subpopulation would have the same probability of dispersing to any other subpopulation. With  $ha > 0$ , some subpopulations would be more attractive than others, and a dispersing individual would have a higher probability of ending up in one of them. This simulation model is, mechanistically speaking, more realistic than the two-scale statistical model described above. Our goal was indeed to simulate data as realistically as possible to make a stringent test of the robustness of the statistical model.

We simulated datasets for the following values of parameters  $sf$  and  $ha$ — $sf = \{0.3, 0.5, 0.7, 0.9\}$  and  $ha = \{0.50, 0.75, 1.00\}$ —to represent a wide range of parameters. We did not include scenarios with very low heterogeneity in attractiveness (e.g.,  $ha = 0$ ) because such scenarios did not seem realistic. This led to a total of 12 simulation scenarios, which were run both in the context of a growing (set 1) and declining (set 2) metapopulation. For the first simulation set, the average metapopulation growth rate was set to  $\lambda = 1.03$ , and we parameterized the *intrinsic* growth rates of the eight subpopulations as follows: 0.96, 0.98, 1.01, 1.03, 1.04, 1.06, 1.07, and 1.10. For the second simulation set, the average metapopulation growth rate was set to  $\lambda = 0.98$ , with the eight subpopulation intrinsic growth rates taking the following values: 0.91, 0.93, 0.96, 0.98, 0.99, 1.01, 1.02, and 1.05. We also ran an additional simulation set (Appendix S1: Table S3) for a stable metapopulation ( $\lambda = 1.00$ ).

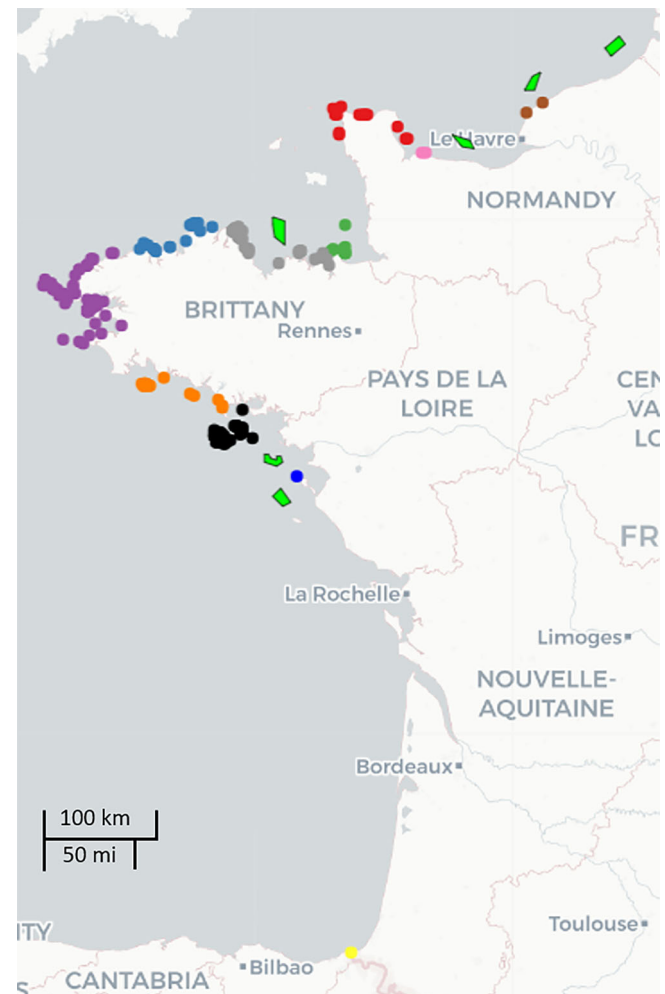
A total of 200 datasets were simulated for each scenario within each simulation set. Each dataset simulated was analyzed with both the two-scale model and the classical closed population model, using an MCMC posterior sampling procedure performed with package NIMBLE (de Valpine et al., 2017) in program R version 4.1.0 (R Core Team, 2020). From the 40 years of local abundances simulated in each dataset, only the first 10 years were used as empirical count data to estimate parameters, while the next 30 years were set as NAs to let the model predict the “future” trajectory of each subpopulation. For the sake of simplicity and clarity, we assumed counts without error, which means that the number of animals in the count data is equal to the true number of animals present in a given subpopulation. The observation variance was thus set to  $\sigma^2 = 0$  in both models. Nonetheless, additional simulations were performed to assess the robustness of the results in the presence of varying levels of observation errors (Appendix S2).

Predictive model performance was assessed using only model predictions for the 30-year forecasting period. To compare the performance of the two models, we used measures of (1) relative bias, that is, bias scaled by the parameter value, and (2) root mean squared error (RMSE), a measure that combines both bias and imprecision. We remind that predictive accuracy is high when the RMSE is close to 0.

## Real data

Both closed population and two-scale models were applied to annual count data collected during the breeding season at European shag colonies distributed along

the French Atlantic coast. These data were collected from multiple sources (local NGOs) and used for the need of a study aiming at quantifying the impact of collisions with offshore wind turbines on shag populations. The European shag is a partially migratory species (Grist et al., 2014) distributed all across the Eastern part of the North Atlantic, from Morocco to Norway, and across the Mediterranean basin. In France, most breeding colonies are located in the northern part of the Atlantic coast and along the Channel Sea (Figure 2), where shags are present all year round. Like many colonial seabirds, European shags are highly philopatric (Aebischer, 1995; Barlow et al., 2013). However, they still display some level of dispersal, and we know that their dispersal rate quickly decreases with distance from their colony of birth (Barlow et al., 2013). With the rapid development of



**FIGURE 2** Map of the 234 European shag colonies (dots) on the French Atlantic and Channel Sea coast. Each color corresponds to a subpopulation, which consists of one or several colonies. The delimitation of these subpopulations was based on the proximity of colonies to seven French offshore windfarms (green polygons) that have been authorized in the area (see Appendix S1).

offshore wind energy along the French Atlantic coast, there is growing concern about the potential impact of wind turbine collisions on European shag demography, which is already sensitive to oceanographic changes (Fortin et al., 2013). Given the spatial distribution of shag colonies in relation to the windfarms' planned locations (Figure 2), we expect some colonies to be more exposed to collisions than others. It was thus necessary to project the European shag demography at a scale finer than the whole Atlantic coast. Annual count data on European shag colonies were collected between 2006 and 2016. Each year, as part of routine seabird surveys, the number of "Apparently Occupied Sites" (AOS) at a given colony was counted by field observers. An AOS is defined as one or two shags present at a nesting site, with or without the presence of nesting material (Monnat & Cadiou, 2004). Counts in AOS are typically used as a proxy of the number of breeding pairs or reproductive females in seabird survey programs (e.g., Deakin et al., 2022; Newson et al., 2008). In the text below, we refer to it as the "number of breeding pairs."

In total, 234 colonies were monitored during this 11-year period, but not every colony was surveyed every year. The number of colonies surveyed each year varied between 50 and 140, with an average of 90 (SD = 30.6). Only 27 colonies were present and surveyed every single year between 2006 and 2016, while 109 colonies were present or have been surveyed only once during this period. On average, a colony was surveyed 4.2 years (SD = 3.7). Shag pair abundance was also very heterogeneous across colonies (mean = 38.3, SD = 81.2), spanning from a single pair being present some years on the smallest colonies, up to 1004 pairs for the largest one. For this analysis, the 234 colonies were aggregated in 11 subpopulations, based on their proximity to planned offshore windfarms, using the grouping procedure defined in Appendix S3. To build subpopulation-scale abundance data, we simply summed the count data across all the colonies included in a given subpopulation. Because the proportion of colonies surveyed within a given subpopulation varied across years, we had to include a proportionality correction parameter in the observation process model (Appendix S4). We note that in this analysis, unlike in the simulation study, we did not assume perfect detection and therefore did not set the observation variance  $\sigma^2$  to 0. In both models, this parameter  $\sigma^2$  was fully estimated from data through the Bayesian MCMC procedure. However, because our count data lack intra-annual replication, interannual process variance and observation variance are both confounded in  $\sigma^2$ .

For this analysis, the MCMC procedure was performed in JAGS (Plummer, 2003), using the jagsUI (Kellner, 2024) package in program R version 4.1.0

(R Core Team, 2020). We added 30 years of NAs to the 11-year count data to obtain subpopulation projections from both fitted models.

## RESULTS

### Simulations

Our simulation study reveals that the two-scale model provides much more accurate predictions than a classical closed subpopulation model assuming independent demographic trajectories among subpopulations (Figure 1, Tables 1 and 2). This result holds whether the metapopulation is growing, declining, or stable (see Appendix S1 for detailed results of each scenario). This result also remains valid in the presence of observation error (Appendix S2).

The difference in performance between both models is particularly striking for the prediction of future subpopulation sizes. Across years and space, the classical model tended to overpredict future subpopulation sizes. Across all the scenarios assessed, the averaged bias was 26.5%, with a minimum bias of 9.7% and a maximum bias of 47.6% (Tables 1 and 2). Our new two-scale model, on the other hand, showed very little bias, with a tendency toward a slight underestimation of future subpopulation sizes. The averaged bias was  $-3.6\%$ , with all biases falling inside the  $-6.7\%$  to  $0.3\%$  range (Tables 1 and 2). The difference in terms of RMSE on that parameter is even more marked. The classical model has an averaged relative RMSE of 110% versus only 10% for the two-scale model.

When focusing on the subpopulation with the largest rate of growth, the difference in performance between the two models is even more salient. The classical model predicted that subpopulation's size at the 30-year time horizon with an error of 415% on average, which means a fivefold overestimation. Across the scenario assessed, this error varied between 175% and 734%, highlighting that the classical model was never able to provide an accurate prediction of the future size of the fastest growing subpopulation. In contrast, the two-scale model displayed an average predictive error of  $-4.4\%$ , with an error range between  $-16.8\%$  and  $9.5\%$ . Here also, the tendency was a slight underestimation, but this was not a systematic pattern observed for every scenario (Appendix S1).

As far as predicting growth rates, our new model also performed systematically better than the classical model, but the differences were less noticeable (Tables 1 and 2). In terms of subpopulation-specific growth rates, the classical model had a  $-2\%$  bias and a 5% RMSE, while our



**TABLE 1** Summary results of the first simulation set for a growing metapopulation ( $\lambda = 1.03$ ).

Performance metric	Demographic parameter	Closed population model		Two-scale model	
		Average	Min–max range	Average	Min–max range
RMSE	$n_{i,t}$	124.7%	65.4% to 196.7%	9.7%	4.8% to 18.2%
RMSE	$\lambda_i$	4.5%	2.6% to 10.6%	1.4%	0.4% to 2.8%
RMSE	$\lambda_0$	1.9%	0.9% to 2.8%	0.3%	0.2% to 0.6%
Bias	$n_{i,t}$	29.7%	11.2% to 47.6%	−2.6%	−6.7% to 0.3%
Bias	$\lambda_i$	−1.7%	−5.1% to 0.0%	0.0%	−0.2% to 0.6%
Bias	$\lambda_0$	1.9%	0.9% to 2.8%	−0.2%	−0.6% to 0.0%
Error	$n_{\max,T}$	364.5%	174.6% to 558.9%	−0.6%	−16.8% to 9.5%

Abbreviation: RMSE, root mean squared error.

**TABLE 2** Summary results of the second simulation set for a declining metapopulation ( $\lambda = 0.98$ ).

Performance metric	Demographic parameter	Closed population model		Two-scale model	
		Average	Min–max range	Average	Min–max range
RMSE	$n_{i,t}$	95.5%	54.3% to 139.1%	10.2%	6.6% to 14.1%
RMSE	$\lambda_i$	5.5%	3.2% to 12.5%	1.6%	0.6% to 2.6%
RMSE	$\lambda_0$	2.1%	1.1% to 3.0%	0.6%	0.4% to 0.8%
Bias	$n_{i,t}$	23.2%	9.7% to 39.1%	−4.6%	−6.6% to −2.5%
Bias	$\lambda_i$	−2.2%	−6.1% to −0.1%	−0.5%	−0.7% to 0.0%
Bias	$\lambda_0$	2.1%	1.1% to 3.0%	−0.6%	−0.8% to −0.3%
Error	$n_{\max,T}$	466.0%	236.2% to 734.2%	−8.2%	−16.1% to −3.9%

Abbreviation: RMSE, root mean squared error.

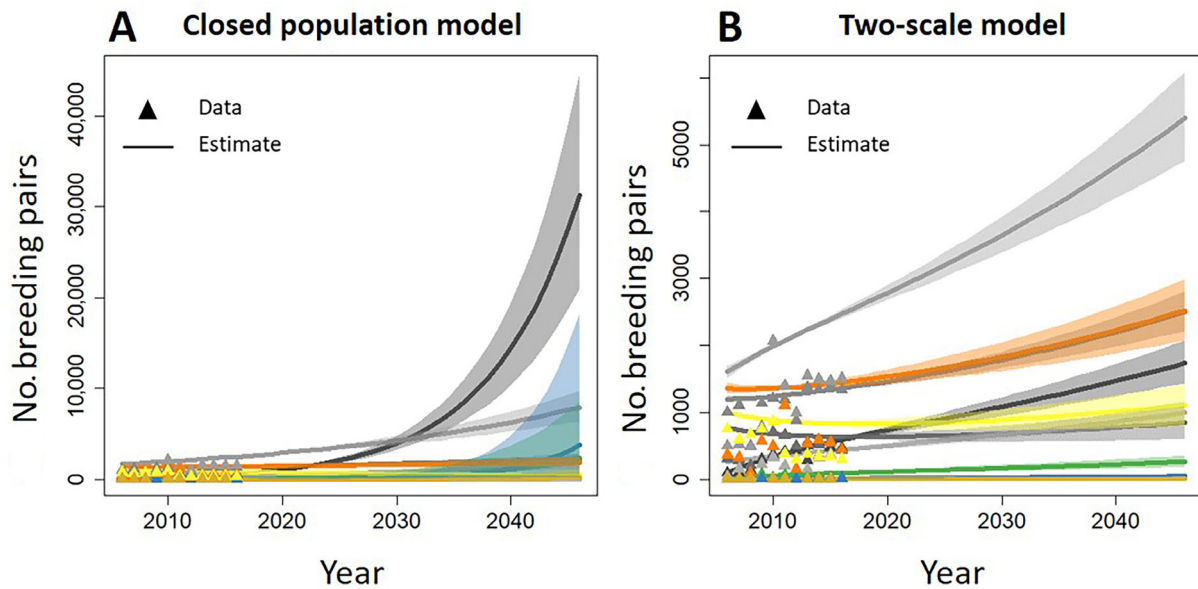
new model showed a −0.2% and 1.5% RMSE. Regarding the overall metapopulation growth rates, the biases were of 2% and −0.4% for the classical model and our new model, respectively.

## Real data

As expected, the classical demographic model assuming population closure at the local scale forecasted much larger growths for some subpopulations than our two-scale model (Figure 3, Table 3). For instance, the classical model predicts that subpopulation no. 1 will grow from ca. 600 breeding pairs in 2016 to ca. 31,600 pairs by 2046 (Table 3), which represents a 51-fold increase in 30 years. This is a very unlikely scenario that would require a consistent growth of 14% each year. Our model, on the other hand, predicts a much more credible subpopulation size of ca. 1700 pairs in 2046. This represents a threefold increase in 30 years and would require an average annual growth rate of 7%. A similar pattern is observed for subpopulation

no. 8 (Table 3), which was holding only 17 breeding pairs in 2016. The classical model predicts a 213-fold increase of this subpopulation, which is expected to reach ca. 3600 pairs by 2046. On the other hand, our model only predicts a threefold increase with a final subpopulation size of ca. 48 breeding pairs. Overall, average predictions of subpopulation sizes by 2046 range between 27 and 31,600 pairs for the classical model, versus a range comprised between 10 and 5400 pairs for the new model.

At the metapopulation scale, despite the fact that the overall growth rate seems fairly similar between the two models ( $\lambda = 1.05$  for the classic model vs.  $\lambda = 1.02$  for the new model), the metapopulation size after 30 years predicted by the classical model ( $N_{TH} = 52,253$ ) is 3.4 times larger than that predicted by the two-scale model ( $N_{TH} = 15,433$ ). The metapopulation growth prediction from the classical model represents a 6.6-fold increase over 30 years, which does not seem realistic for such a long-lived species. From the two-scale model, the prediction is only a 1.9-fold increase, a result that appears much more sensible.



**FIGURE 3** Projections of European shag populations' trajectories from each model. Note the difference in scale of the y-axis between the two graphs.

**TABLE 3** Summary results from the European shag data analysis.

Subpopulation	Initial <sup>a</sup> population size	Predicted population size (after 30 years)		Annual growth rate	
		Closed population model	Two-scale model	Closed population model	Two-scale model
1	626	31,617	1734	1.14	1.07
2	627	345	850	0.98	1.00
3	1368	2300	2498	1.02	1.02
4	2480	7927	5391	1.04	1.03
5	445	1792	996	1.05	1.03
6	5	27	10	1.05	1.03
7	95	2082	264	1.10	1.06
8	17	3655	48	1.19	1.09
9	1442	1845	2521	1.01	1.02
10	817	458	1109	0.98	1.00
11	5	204	13	1.12	1.05
Metapopulation	7925	52,253	15,433	1.05	1.02

<sup>a</sup>Population size in 2016 ( $t = 11$ ), that is, at the end of the data period.

## DISCUSSION

The two-scale demographic model presented in this study provides an efficient approach to forecast the local growth of multiple subpopulations interconnected by dispersal. Because the only data required to implement this model are annual subpopulation counts, it should prove useful in many situations. Indeed, most wildlife monitoring programs that are routinely conducted around the

world, notably in the context of omnibus surveillance monitoring (Nichols & Williams, 2006), consist of simple head counts without any form of individual identification or any other means of estimating dispersal rates (Pollock et al., 2002; Yoccoz et al., 2001).

As shown by the results from our simulations and real data analyses, this model is a better alternative than closed population models, which inappropriately assume independent subpopulation trajectories and, as a

consequence, systematically overpredict the growth of some subpopulations or even that of the metapopulation as a whole. Moreover, in the absence of ancillary information on dispersal rates, the two-scale model provides a more parsimonious and thus more relevant alternative than full-dispersal models, which consider bidirectional exchanges between every possible pairs of subpopulations. For  $m$  subpopulations, a full-dispersal model would require estimating  $m^2$  dispersal rates (i.e.,  $m \times m$  dispersal matrix), while the two-scale model only requires estimating 2- $m$  redistribution parameters ( $m$  intercepts [i.e.,  $\beta_{0,i}$ ] and  $m$  temporal slopes [i.e.,  $\beta_{1,i}$ ]). This gain in number of parameters is achieved because the redistribution of individuals across space is modeled in a centralized top-down fashion (i.e., unidirectional vertical transfer), instead of considering full bidirectional horizontal transfers. Although our approach consists of a phenomenological model that does not seek to accurately reflect how dispersal mechanisms really occur in the wild, it provides a convenient and fully identifiable model that allows estimating and forecasting local subpopulation trajectories with good accuracy, in the absence of dispersal data.

Traditionally, demographic forecasting has been based on closed population models and therefore primarily carried on single and isolated (sub)populations (Lacy, 2019). A specific method, called multiple-population viability analyses (Wenger et al., 2017), allows predicting demographic trajectories for several (sub)populations but only if they are fully isolated from each other (Legault, 2005; Neville et al., 2020). In both cases, because the focal entities defined as “populations” are isolated fragment of a species’ distribution range (e.g., Lunney et al., 2007), the assumption of geographic closure can genuinely be made. However, when viability analyses are performed at spatial scales that encompass several connected subpopulations, only two methods have been available so far. First, a site occupancy approach can be used (MacKenzie et al., 2006; Sjögren-Gulve & Hanski, 2000). Such metapopulation viability analyses are able to predict probabilities of colonization and extinction for each subpopulation (e.g., Howell et al., 2020; Schtickzelle & Baguette, 2004), but they do not provide any insight on local demography (Sjögren-Gulve & Hanski, 2000). Second, we can treat the whole metapopulation as a unique focal “population” and use a classical closed population model (e.g., Frick et al., 2017). This approach is valid because the closure assumption is met at the metapopulation scale (Goodwin & Fahrig, 1998), but it cannot produce the local predictions that are usually wanted (Clapham et al., 2008).

Our main motivation for developing the two-scale model was to solve the issue of unrealistic demographic booms in subpopulation predictions. An alternative to

avoid this issue would be to include density dependence in every local subpopulation. This would actually provide a more mechanistic and realistic solution, but we found two important issues with that approach. First, although density dependence has been reported in many instances (Bonenfant et al., 2009; Brook & Bradshaw, 2006; Sánchez-Lizaso et al., 2000), there is usually no guarantee that a given subpopulation actually experiences density dependent regulation of its growth (Horswill et al., 2017; Sánchez-Lizaso et al., 2000). Second, the strength and shape of density dependence are very hard to estimate from a simple time series of population counts, especially when observation uncertainty cannot be properly accounted for (Knappe & de Valpine, 2012; Lebreton & Gimenez, 2013). Our two-scale model was specifically developed to deal with limited data, and in such a situation, it would seem impossible to estimate density dependence parameters for multiple subpopulations with a decent level of accuracy.

Like in any forecasting exercise that aims at making anticipatory predictions (Maris et al., 2018), the projections produced by the two-scale model rely on the assumption that recent historical conditions, which were driving subpopulation trends, will persist in the future (Mouquet et al., 2015). More specifically, this model first assumes that the future metapopulation growth will remain consistent with its trend over the recent past, an assumption that is very common in most PVA analyses (Boyce, 1992; Lacy, 2019). Second, the two-scale model assumes that dispersal rates among subpopulations, captured through redistribution parameters  $\gamma_{i,t}$ , follow a constant linear trend over time, which might not totally reflect the true changes of dispersal dynamics in the metapopulation. As mentioned above, these assumptions of constancy are a common issue in every anticipatory prediction endeavor, independently from the type of modeling approach being used (Maris et al., 2018; Mouquet et al., 2015).

Currently, the model is formulated to analyze single count data (i.e., only one count per colony per year), because these are often the only data available, as is the case for the present European shag case study that motivated the development of this approach. With this formulation, imperfect detection cannot explicitly be accounted for and observation variance cannot be disentangled from true interannual process variance. Additional simulations (see Appendix S2) showed that the model’s performance was barely affected by moderate levels of observation errors (CV between 10% and 50%). Nonetheless, we know that intra-annual repeated counts are a much more reliable source of information to account for observation errors (Williams et al., 2002), especially when one seeks to disentangle interannual process variance from

observation variance (Ahrestani et al., 2013; Nichols et al., 2009). Repeated count data could easily be incorporated in this model, simply by adding one level of indexing (i.e., repetitions  $k$ ) to the count data ( $C_{i,t,k}$ ) in the observation process. In addition, one could easily consider alternative ways of modeling the observation process, including, for example, a parameter for individual detection probability, as is done in N-mixture models (Royle, 2004).

Forecasting future population trends at both large and local scales is an exercise of growing interest to research ecologists, wildlife managers, and decision makers (Houlahan et al., 2017; Mouquet et al., 2015; Sutherland & Freckleton, 2012). However, making reliable predictions often requires large amounts of data that can be difficult or costly to obtain (Yoccoz et al., 2001). This issue is further complicated by the fact that the monitoring of animal populations that span across large areas is rarely done in the context of a single, well-planned wildlife program (Pollock et al., 2002). Often, like in our European shag example, surveys at different locations are performed independently by different entities (e.g., local NGOs) that each have their own monitoring schedule. As a consequence, not every subpopulation is surveyed every year, which results in a fair number of missing surveys in the dataset. For instance, in our shag example, the global dataset contained 63% of missing counts (i.e., colony  $\times$  year surveys). Despite this, the two-scale model was able to estimate and forecast subpopulation trajectories with decently narrow CIs (see Figure 3B), which suggests a good robustness to missing data. Nonetheless, there surely is a limit to the amount of missing data that can be tolerated by the model before its predictions become unreliable, an important question that should be investigated in the near future.

## AUTHOR CONTRIBUTIONS

Thierry Chambert and Aurélien Besnard designed the model. Thierry Chambert built the model and ran simulations. Antoine Chabrolle and Nicolas Sadoul gathered and assembled the data. Thierry Chambert analyzed the data. Thierry Chambert wrote the first draft of the manuscript, and all authors contributed significantly to its content.

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## CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Chambert, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.13901493>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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