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## Assessing the effect of density on population growth when modeling individual encounter data

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**Abstract.** The relative role of density-dependent and density-independent variation in vital rates and population size remains largely unsolved. Despite its importance to the theory and application of population ecology, and to conservation biology, quantifying the role and strength of density dependence is particularly challenging. We present a hierarchical formulation of the temporal symmetry approach, also known as the Pradel model, that permits estimation of the strength of density dependence from capture–mark–reencounter data. A measure of relative population size is built in the model and serves to detect density dependence directly on population growth rate. The model is also extended to account for temporal random variability in demographic rates, allowing estimation of the temporal variance of population growth rate unexplained by density dependence. We thus present a model-based approach that enable to test and quantify the effect of density-dependent and density-independent factors affecting population fluctuations in a single modeling framework. More generally, we use this modeling framework along with simulated and empirical data to show the value of including density dependence when modeling individual encounter data without the need for auxiliary data.

**Key words:** *Audouin's Gull; capture-recapture; Gibbs variable selection; open population estimation; population dynamics; Pradel model; rate of population change; temporal symmetry model.*

### INTRODUCTION

Because a population cannot grow indefinitely, it is expected that density will eventually check population growth (Malthus 1798). At the opposite, low levels of density have also been found to sometimes limit population growth (Allee et al. 1949). The first phenomenon (negative density dependence) will result in population fluctuations around the carrying capacity (Sibly and Hone 2002) while the second (positive density dependence) will precipitate population decline. It follows that the way density regulates population dynamics influences persistence time of threatened populations as well as the sustainable harvest rate of exploited populations (Lande et al. 2003). The study of the strength and form

of density dependence is thus fundamental to the understanding of processes that regulate temporal and spatial variation in population size (Lack 1954, Ricker 1954, Andrewartha and Birch 1986).

It has always been challenging to demonstrate density dependence in real populations. There are practical, theoretical, and technical difficulties in tackling the problem (Lebreton 2009). First, population size and hence density is notoriously difficult to measure accurately; second, density is only a proxy for interactions among individuals and is thus a noisy measure of what actually occurs; but probably the main obstacle is statistical: successive densities and changes in density are obviously strongly related, a fact that must be acknowledged in any model. Early attempts focused on fitting the theoretical logistic growth model (Verhulst 1838, Pearl and Reed 1920) but were inconclusive (Slobodkin 2001). Among the extant approaches, retrospective studies analyze variation of population growth rate over time by

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focusing on the realized population growth rate between two successive time steps as  $\rho_i = N_{i+1}/N_i$ , where  $N_i$  is population size at time  $i$ . However, abundance estimation in open populations can be biased when the error in the counts around the true population size (observation error) is not accounted for, leading to spurious detection of density dependence (Dennis et al. 2006, Freckleton et al. 2006, Lebreton 2009). State-space models is another approach that can reduce bias in parameter estimates when population counts are the only data available (Clark and Bjørnstad 2004), however separating observation variance from process variance is only possible when the observation error is relatively small (Knappe 2008). In addition, negative autocorrelation between successive estimators may lead to an overestimation of temporal variance of population growth rate (an overestimation of  $N_i$  biases  $\rho_i$  low but biases  $\rho_{i-1}$  high).

Some methods, based on individual encounter histories, are currently available to assess the impact of density on demographic rates while accounting for imperfect detection. Schofield and Barker (2008) and Schofield et al. (2009) propose to study the effect of density on recruitment and survival. However, density dependence may be effected differently in different years. For instance, for a given density, it may entail a reduced survival in years of high fecundity whereas survival will remain high in years of low fecundity. Methods that allow to study the effect of density directly on population growth rate are thus needed. The approach proposed by Schofield et al. (2009) can be reparameterized so that recruitment rate is defined as the difference between population growth rate and survival (Nichols 2016) thus allowing modeling in terms of population growth rate.

Integrated population models (IPMs; Besbeas et al. 2002) allow estimation of the strength of density dependence not only on demographic rates but also on the derived population growth rate (Abadi et al. 2012). However, IPMs rely on the combination of different sources of information, which may not always be simultaneously available, and testing for density dependence directly on population growth rate is possible only using a two-step approach where growth rate estimates are regressed on population size. To our knowledge, there are no model-based approaches currently available that enable to formally test and quantify the strength of density dependence directly on population growth rate from capture-mark-reencounter (CMR) data in a single modeling framework.

Unlike any other approach that exists to estimate and model population growth and associated vital rates using CMR data from open populations, the temporal symmetry approach, also known as the Pradel model (Pradel 1996), combines the standard-time and the reverse-time approaches in a unique likelihood, allowing inference on population growth rate. Like other approaches (Schwarz 2001, Pledger et al. 2003, 2010, Link and Barker 2005), the Pradel model simultaneously incorporates the survival and recruitment processes,

where the latter includes both local recruitment and immigration, and estimated mortality includes permanent emigration. However, the Pradel model likelihood can be parameterized with population growth rate  $\rho$  as a structural parameter, thus allowing to test biological hypotheses directly on  $\rho$ . In addition, a Bayesian formulation of the Pradel model permits the hierarchical modelling of the biological and sampling processes and allows the extension of the original fixed time effects structure to random time effects (Tenan et al. 2014b).

At this point, density can be integrated in the model, only as an external covariate. This is not very satisfactory as the changes in density and population growth are obviously related and considering an external measure of density and the population growth rate parameters of the model as independent is obviously wrong. In this paper we derive a measure of relative population size directly from the CMR data, and use it to detect density dependence within the same model. In this way, we circumvent the statistical difficulty inherent in density-dependent models of having the same quantity, namely density, at the same time estimated and the driver of its own changes.

Here we propose a new Bayesian hierarchical formulation of the temporal symmetry approach that allows quantification of the effect of population size on population growth rate and, more generally, the study of density-dependent and density-independent (i.e., environmental) factors that affect temporal variation of population growth rate. Such decomposition into deterministic and stochastic components is important to the assessment of the effects of environmental change on population dynamics.

We illustrate the modeling approach with simulated data, to investigate the effectiveness of detecting density-dependent effects on population growth rate, and we apply the approach to encounter histories of a long-lived seabird. More generally, we use the modeling framework along with simulated and empirical data to explore the value of including density dependence when modeling individual encounter data.

## METHODS

### *The temporal symmetry model*

Consider a homogeneous population of individuals sampled using a CMR protocol at a single study site during  $s$  successive occasions. We follow the notation of the original paper of Pradel (1996) and assume that neither removals nor introductions derive from the capture-recapture procedure. In the full likelihood developed for the temporal symmetry model, information of individual capture histories is summarized, for each occasion  $i = 1, \dots, s$ , as the number of (1) total animals observed ( $n_i$ ), (2) observed for the first time ( $u_i$ ), and (3) observed for the last time ( $v_i$ ). The parameters of the full likelihood in Pradel (1996) are  $\phi_i$ , the survival

probability from  $i$  to  $i + 1$ ;  $p_i$ , the probability of being captured/encountered at time  $i$ ;  $\gamma_i$ , the seniority probability, i.e., the probability that an animal present at  $i$  was already present at  $i - 1$ ;  $\xi_i$ , the probability of not being seen before  $i$  when present at  $i$ ;  $\chi_i$ , the probability of not being seen after time  $i$  when present at  $i$ . Parameters  $\gamma_i$  and  $\xi_i$  are the reverse-time analogues of  $\phi_i$  and  $\chi_i$  used in the Cormack-Jolly-Seber (CJS) model.

We can express the expected number of animals alive at both occasions  $i$  and  $i + 1$  in forward- and reverse-time order respectively and equate them:  $N_i \phi_i = N_{i+1} \gamma_{i+1}$ , where  $N_i$  denotes abundances at sampling occasion  $i$  (Fig. 1a). Population growth rate can thus be derived as a function of survival and seniority probability with the following approximate equality:  $\rho_i = N_{i+1}/N_i \approx \phi_i/\gamma_{i+1}$ .

We focus on the likelihood parameterization that incorporates population growth rate  $\rho$  as a structural parameter, in addition to survival  $\phi$  and detection probability  $p$ . We refer to Appendix S1 for further details on model formulation.

#### Modeling density dependence

In order to extend the temporal symmetry model to account for density dependence on population growth rate, we note that population size ( $N_{i+1}$ ) at time step

$i + 1$  is composed of survivors from time  $i$ , i.e., individuals that were already present in the population at time  $i$  ( $A_{i \rightarrow i+1}$ ) and recruits ( $B_{i+1}$ ), where  $B_{i+1}$  includes both local recruits and immigrants (Fig. 1b). We can describe the relationship between the number of individuals in common at the two successive time steps ( $A_{i \rightarrow i+1}$ ) and population size  $N_i$  by using a binomial distribution with probability parameter the survival probability  $\phi_i$ :

$$A_{i \rightarrow i+1} \sim \text{Bin}(N_i, \phi_i). \quad (1)$$

We can also describe the relationship between  $A_{i \rightarrow i+1}$  and  $N_{i+1}$  using a negative binomial distribution involving the seniority probability, that is the probability that an animal present at  $i + 1$  was already present at time  $i$ :

$$B_{i+1} \sim \text{Neg-Bin}(A_{i \rightarrow i+1}, \gamma_{i+1}). \quad (2)$$

In other words,  $N_{i+1}$  is the number of independent Bernoulli trials that must be performed with probability of success  $\gamma_{i+1}$  until the  $A_{i \rightarrow i+1}$  survivors are obtained.  $B_{i+1}$  is thus the number of failures in this hypothetical experiment.

The estimate of population size,  $N_i$ , obtained in this way can be used for the assessment of density dependence, circumventing the statistical difficulties identified with external estimates (Lebreton 2009). There are yet two specific difficulties with this estimate: it is well known that, in the fully time-dependent Jolly-Seber model, initial population size is not estimable; a second difficulty is that population size estimation is very sensitive to capture heterogeneity (Link 2003). The first difficulty can be circumvented by imposing some constraint that renders initial population size estimable, but, unless there is a good reason for imposing such a constraint, a safer approach consists in assessing density dependence only at the occasions where population size is estimable. The second difficulty will be nullified if density dependence is examined on relative population sizes. Indeed, unlike population size, change in population size, i.e., population growth rate, is extremely robust to capture heterogeneity (Marescot et al. 2011). Using a linear relationship for the way population size affects population growth rate achieves this aim as the scale factor relating any measure of relative population size and absolute population size is then confounded with the slope of the effect. For the sake of robustness, we thus suggest privileging a log linear relationship of the form

$$\log(\rho_i) = \alpha + \beta N_i + \epsilon_i \quad (3)$$

with  $\epsilon_i \sim \text{Norm}(0, \sigma^2)$ , or alternatively

$$\log(\rho_i) = \alpha + \beta \log(N_i) + \epsilon_i \quad (4)$$

in which case the log scale factor will be confounded with the intercept. Other forms of the relationship in Eq. 4 could also be explored.

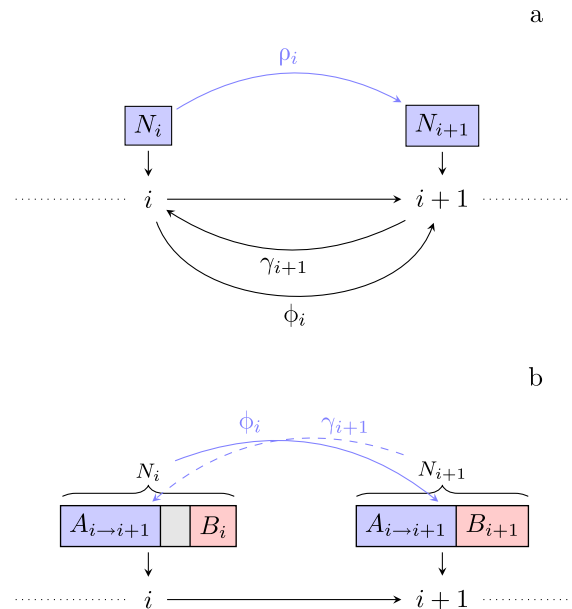


FIG. 1. (a) Graphical representation of the relationship between population size at time  $i$  ( $N_i$ ), population growth rate ( $\rho$ ), seniority ( $\gamma$ ), and survival ( $\phi$ ) probabilities in the temporal symmetry model. (b) Relationship among the parameters of the density-dependent temporal symmetry model. Number of survivors and recruits are denoted by  $A$  and  $B$ , respectively. The empty gray cell represents the portion of individuals that, along with some individuals among the recruits at  $i$ , will exit the population between  $i$  and  $i + 1$ .

In this way, we can examine whether higher or lower population sizes affect population growth rate differently (i.e., whether there is some form of density dependence) in a fairly robust way. The random term here ( $\epsilon_i$ ) accounts for temporal variance of population growth rate unexplained by density dependence, as well as for the fact that population size is but a proxy for the interactions among the individuals in the population (Lebreton 2009). Environmental covariates that may move the level at which density dependence operates may also be introduced in the relationship. In this paper, we intend to examine the performance of the core part of the model using simulations. We take year 2 as a reference year, use the cumulative growth rate since this year as a (relative) index of population size,  $P_i = N_i/N_2$ , and relate  $P_i$  to population growth rate  $\rho_i$  as follows:

$$\log(\rho_i) = \alpha_p + \beta_p \log(P_i) + \epsilon_{p,i} \quad (5)$$

with  $\epsilon_{p,i} \sim \text{Norm}(0, \sigma_p^2)$ . A Poisson prior distribution is used for  $N_1$ . Note that  $N_2$  is the first estimable population size and, for that reason, it represents a logical benchmark for accumulating population growth. However, years other than the second one can be chosen as a reference for the index of population size. Finally, note that  $\rho_i$  must be larger than  $\phi_i$  to ensure the seniority parameter to lie between 0 and 1. This additional constraint thus applies to the random variables  $\epsilon_{p,i}$ .

#### Simulation study

We used simulated data to assess the performance of the estimators in detecting density dependence. We also examined the frequency of estimated spurious density-dependent effects in the simulation replicates. For each scenario, we generated 100 data sets of individual capture histories from an initial population size  $N_1 = 200$ , for  $s = \{5, 10, 15\}$  sampling occasions, different degrees of density dependence ( $\beta_p = \{0.0, -0.2, -0.4, -0.8\}$ ) and of population growth rate intercept ( $\rho_0 = \exp(\alpha_p) = \{0.98, 1.00, 1.40\}$ ). We considered a total of 36 scenarios deriving from all possible combinations of  $s$ ,  $\beta_p$ , and  $\rho_0$ , following the model in Eq. 5 and with unexplained temporal random variation  $\sigma_p = 0.1$ . The model in Eq. 5 was also used to fit the simulated data. Survival and detection probability were simulated and modeled with random time variation, i.e.,  $\text{logit}(\phi_i) = \alpha_\phi + \epsilon_{\phi,i}$  and  $\text{logit}(p_i) = \alpha_p + \epsilon_{p,i}$ , with  $\epsilon_{\phi,i} \sim \text{Norm}(0, \sigma_\phi^2)$  and  $\epsilon_{p,i} \sim \text{Norm}(0, \sigma_p^2)$ . The following parameter values were used for data simulation:  $\phi_0 = \text{expit}(\alpha_\phi) = 0.5$  and  $p_0 = \text{expit}(\alpha_p) = 0.8$ , where  $\text{expit}$  is the inverse-logit function,  $\sigma_\phi = 0.1$ , and  $\sigma_p = 0.4$ .

The mean across the 100 replicates of the Bayesian point estimate of the posterior mean for each parameter was calculated, along with the root mean squared error and the proportion of times the 95% Bayesian credible interval (BCI) for the estimate encompassed the real value (coverage). We used coverage to evaluate the ability of the model to accurately estimate the parameters.

Normal prior distributions with mean zero and variance 10 were used for the intercept of population growth rate ( $\alpha_p$ ) and the parameter for intensity of density dependence on growth rate ( $\beta_p$ ). A Uniform(0,1) distribution was used for the intercept of survival ( $\phi_0$ ) and encounter probability ( $p_0$ ). A Uniform(0,2) distribution was used for the temporal random standard deviation of population growth rate ( $\sigma_p$ ) and survival ( $\sigma_\phi$ ), and a Uniform(0,4) distribution was used for the temporal random standard deviation of encounter probability ( $\sigma_p$ ).

#### Application to bird data

We illustrate our approach by assessing the strength of density dependence on the growth rate and survival of a population of a long-lived seabird, the Audouin's Gull (*Ichthyophaga audouinii*). To this end, we analyzed mark-resight data of sexually mature gulls ( $\geq 3$  yr old, 4,286 individuals) that were individually marked only at fledging using a plastic ring with a unique alphanumeric code and resighted at the Ebro delta colony (Spain) during the breeding season (April–July) in the period 1992–2003. The same data were analyzed by Tavecchia et al. (2007), who bring evidence for negative density dependence on survival and, in a separate analysis, on population growth rate using counts on the whole local breeding population for the period 1981–2003.

We applied the same model described above and used to fit the simulated data. In addition, we used the Gibbs variable selection approach (O'Hara and Sillanpää 2009, Tenan et al. 2014a) to estimate the degree of support for the inclusion of density dependence on the survival and population growth rate linear predictor. To do so, the parameter for the intensity of density dependence ( $\beta$ ) was multiplied by an “inclusion parameter”  $\omega$ , a latent binary variable with a Bernoulli prior distribution with parameter 0.5:

$$\log(\phi_i) = \alpha_\phi + \omega_\phi \beta_\phi \log(P_i) + \epsilon_{\phi,i} \quad (6)$$

$$\log(\rho_i) = \alpha_p + \omega_p \beta_p \log(P_i) + \epsilon_{p,i} \quad (7)$$

Detectability was modeled as random time varying. Model-averaged parameter estimates were derived. Priors were the same as those used in the model fitted to the simulated data, except for  $\sigma_\phi$  and  $\sigma_p$  that were drawn from a Uniform(0,5) distribution. See Appendix S1 and Data S1 for details on the Bayesian variable selection.

#### Model implementation

The density-dependent Pradel model was fitted using the Markov chain Monte Carlo (MCMC) framework. Summaries of the posterior distribution were generated from three Markov chains initialized with random starting values, run for 3,000,000 iterations after a 100,000 burn-in, and thinned every 300 draws to reduce data storage.



The Bayesian implementation of the temporal symmetry model is done by using the so-called “zeros trick” (Spiegelhalter et al. 2007) that allows the specification of an arbitrary likelihood in the BUGS language; for further details see Appendix S1 in Tenan et al. (2014b). Models were implemented in program JAGS (Plummer 2003), called from R (R Core Team 2012) using the jagsUI R package (Kellner 2016). For details about the code for data simulation and modeling see Data S1.

## RESULTS

### *Simulation study*

The temporal symmetry model achieved the nominal 95% coverage for all the survival and encounter probability parameters in almost all the 36 scenarios (Appendix S1: Table S1–S3). The lowest coverage for population growth rate parameters was achieved in the absence of density dependence in the simulated data ( $\beta_p = 0$ ) where coverage was between 0.87 and 0.94 for the intercept  $\rho_0$ , and in the range 0.45–0.94 for the intensity parameter  $\beta_p$ . In other words, in the absence of density dependence in the simulated data, the model detected spurious density dependence in <9% of the simulation replicates (the complementary of coverage for  $\beta_p$ ) except for the case with  $s = 15$  sampling occasions,  $\rho_0 = 0.98$  (28% of spurious results) and  $\rho_0 = 1.00$  (55% of spurious results; Fig. 2; Appendix S1: Table S1–S3). Coverage for the temporal random standard deviation of population growth rate ( $\sigma_p$ ) was always close to or higher than the nominal 95% value (Appendix S1: Table S1–S3).

### *Application to bird data*

The posterior probability for the inclusion of the density-dependent effect on survival and population growth rate was  $\Pr(\omega_\phi = 1) = 0.62$  and  $\Pr(\omega_p = 1) = 0.45$ , respectively. Model-averaged posterior estimates for the parameter expressing magnitude and direction of density dependence indicate a negative relationship between population size and both survival and growth rate, despite credible intervals encompass zero ( $\beta_\phi = -0.634$ ,  $-1.457$ – $0.114$ , and  $\beta_p = -0.320$ ,  $-0.779$ – $0.131$ ; mean, 95% BCI; Appendix S1: Table S3). Density dependence explained 40% and 35% of temporal variation in survival and PGR, respectively. An empirical comparison of the observed population growth rate, derived from counts of breeding pairs, and the rate of growth estimated using the density-dependent temporal symmetry approach suggests a substantial agreement between the two quantities (Appendix S1: Fig. S1).

## DISCUSSION

We provide a hierarchical formulation of the Pradel model that explicitly incorporates an internal estimate of

relative population size, which can be used in a model-based approach to formally test and quantify the strength of density dependence directly on population growth rate from capture–mark–reencounter (CMR) data on open populations. In addition, the framework allows the estimation of temporal variance unexplained by density dependence, and can thus be used to quantify the relative contribution of intrinsic factors (i.e., density dependence) and stochastic (density-independent) events affecting population fluctuations. In our application on a long-lived seabird, we showed how a Bayesian variable selection procedure can be used to assess the degree of support for density dependence simultaneously on population growth rate and survival probability in a GLM approach. In addition, we could go beyond the qualitative assessment of the relationship between population size and growth rate in the Audouin’s gull provided by Tavecchia et al. (2007) and estimate the temporal random variance unexplained by density dependence. We believe that explicit estimation of the latter quantity is relevant to the understanding of population dynamics, because the fluctuation of bird populations is often largely affected by stochastic components (Sæther and Engen 2002). Moreover, temporal variance of population growth rate, estimated using a random effect approach, is very relevant to extinction probability (Nichols and Hines 2002) and evolutionary demography (Rees and Ellner 2009).

Density dependence in population growth rate is important for studying population fluctuations in the long term (Knape 2008). Capture–mark–reencounter data have been mainly used to estimate density dependence in life history traits, which in turn influences density dependence in population growth rate (Both et al. 1999, Lande et al. 2002, Tavecchia et al. 2007, Reed and Slade 2008, Fay et al. 2015). However, the connection between vital rates and population dynamics is usually not well defined, making estimation of density dependence on population growth difficult even in the case where life history data are available and density dependence on vital rates is well estimated (Knape 2008). In this context, the density-dependent temporal symmetry framework represents a model-based approach to quantify the strength of feedback of population size on population growth rate and to test for the significance of the effect. In addition, although CMR data are usually more demanding compared to counts, we emphasize that, contrary to population size estimators, population growth rate estimators of CMR models, such as in the Pradel model, are robust to capture heterogeneity among individuals (Hines and Nichols 2002, Pradel et al. 2010). This can be particularly useful when species cannot be easily counted in nature (e.g., many burrowing nesting seabirds, reptiles, and amphibians).

We also note that the realized population growth rate ( $\rho$ ) estimated by the Pradel model, contrary to the projected population growth rate ( $\lambda$ ) commonly derived from a projection matrix model, accounts for the

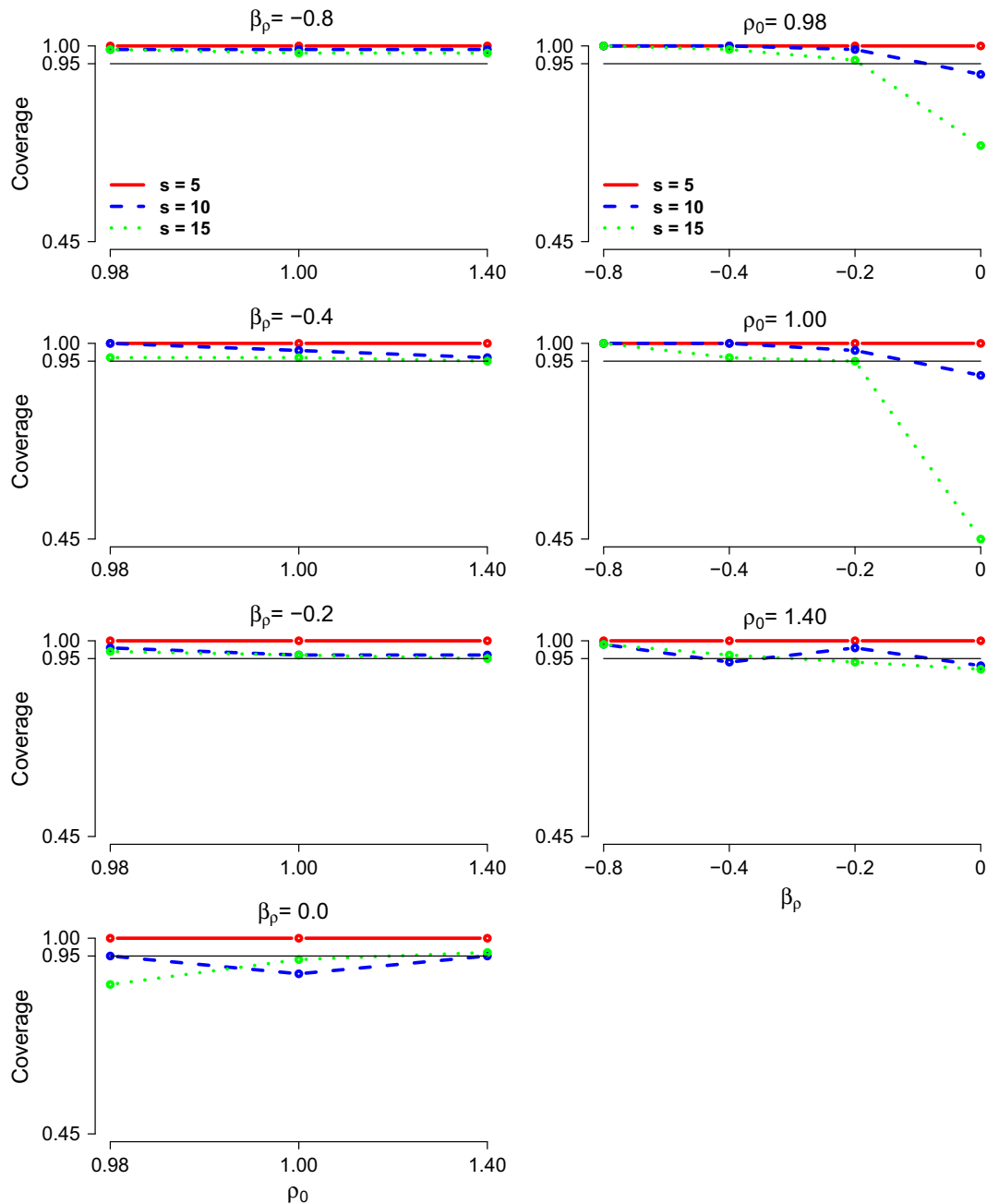


FIG. 2. Performance of the parameter coverage across the 100 simulation replicates, for different values of the population growth rate intercept on real scale  $\rho_0 = \{0.98, 1.00, 1.40\}$ , the parameter for intensity of density dependence on log scale  $\beta_p = \{0.0, -0.2, -0.4, -0.8\}$ , and the number of sampling occasions  $s = \{5, 10, 15\}$ . The horizontal solid line indicates the nominal 95% coverage.

contribution of both local recruits and immigrants. The possibility of considering immigration for inference on population growth rate can be particularly important in open populations of highly mobile species, where inter-population dispersal can release population trajectories from the effect of environmental stochasticity even when the latter affects local vital rates (Tavecchia et al. 2016).

In our example, however, recruitment includes only local recruits and no immigrants, since data are based only on individuals marked in the same colony as fledglings. In addition, we note that the recruitment rate of marked individuals to the adult population ( $\geq 3$  yr old gulls) is influenced by variability in the proportion of fledglings that are ringed each year. For example, if there is a 20%

increase in the number of fledglings in a given year but, due to logistics, there is only capture effort capacity for a 5% increase in the number of fledglings ringed, the recruitment process to the adult stage after a lag of three years would be underestimated. In our case, we adjusted the number of individuals marked to the observed total number of fledglings each season.

Sæther and Bakke (2000) highlighted that the estimation of temporal variance of demographic traits is crucial when predicting population trends in prospective analysis. An increase of temporal variance in demographic rates with high sensitivity, produced by environmental changes, will reduce mean population growth rates and threaten population viability. The density-dependent Pradel model can be used to test density dependence not only on population growth but also, and simultaneously, on the associated vital rates, while quantifying the temporal variance unexplained by population size and identified extrinsic factors. We note that modeling density dependence on population growth rate can also be possible by expressing the Schofield et al. (2009) approach in terms of population growth rate and survival probability. However, beyond the model used to fit the CMR data, we believe our results support the value of including density dependence when modeling CMR data, with no need for auxiliary information.

The simulation study showed that the risk of estimating spurious density dependence can be high under specific conditions (2 out of 36 scenarios; Appendix S1: Table S3). In this case model performance may be affected by prior specification. Furthermore, the present simulation study does not explore model performance in testing density dependence simultaneously on both structural parameters, i.e., population growth rate and survival/seniority probability. However, in our application we tested for intraspecific density dependence on both population growth rate and survival. Possible interspecific density-dependent effects could also be tested on both structural parameters, where a proxy of interspecific density dependence can be the size of the population of the sympatric and competing Yellow-legged Gull (*Larus michaellis*) (Tavecchia et al. 2007). The possibility to test hypotheses on the hyperparameter ( $\sigma$ ) regulating the temporal variation in population growth rate (and associated vital rates) unexplained by density dependence, is also at hand. In addition, treating positive density dependence (Allee effect) is possible, and potential extensions of the linear predictor for the structural parameters to a change point model formulation (Lunn et al. 2012) may account for both positive and negative density dependence.

Population growth rate estimate obtained from the temporal symmetry model may be biased in the presence of non-random temporary emigration. Although, temporary emigration can be handled by embedding the time-symmetric approach in a robust design sampling protocol, we acknowledge the need for further

investigation on the potential effect of the relationship between population density and temporary emigration to estimation. In addition, we highlight that the realized population growth rate used in the temporal symmetry approach is a measure of the rate of change of the age class (presumably adults) to which the encounter histories belong, which is not necessarily equivalent to the growth rate of the whole population.

Finally, we note that density dependence may also be tested on recruitment and population growth rate using the model parameterization that includes seniority probability and population growth rate as structural parameters. More investigation is however needed to explore potential biases in the estimation of model parameters and related effects.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2595/supinfo>

## DATA AVAILABILITY

Code for data simulation and modeling is available on Figshare: <https://doi.org/10.6084/m9.figshare.7415264>.