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RESEARCH ARTICLE

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Extension of Pradel capture-recapture survival-recruitment model accounting for transients

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Abstract

- 1. Population growth is the sum of survival and recruitment, and knowledge of these two vital rates is crucial for understanding population dynamics. Moreover, animal populations often contain varying number of transient (i.e. nonresident) individuals that do not contribute to these rates but may bias their estimates. The widely used Pradel (1996, Biometrics, 52: 703) survival-recruitment model for capture-mark-recapture data is only able to handle resident individuals on a fixed study area across a particular study period. Yet, numerous capture-mark-recapture data sets, from a wide range of taxa, feature transient individuals. The most widespread sources of avian demographic data, based on citizen science projects, feature both transient individuals and changes in the study area over time.
- 2. We present an extension of the Pradel model that accounts for the presence of transient individuals and changes in the study area. In contrast to known extensions of the Cormack-Jolly-Seber models in which transients are modelled as a proportion of newly captured individuals, our novel approach models transient individuals as a proportion of all birds captured. In addition, we present a new simple way to visualize the interlinkage of the vital rates produced by our extended Pradel model.
- 3. We demonstrate utilization of the model using capture-mark-recapture data collected by a constant-effort mist-netting citizen science programme in the Czech Republic, presenting demographic rates of two species with different population dynamics. To demonstrate the newly achieved ability to analyse the phenomenon of transience, we show the differences in transience and its temporal trends between wet and dry habitats.
- 4. Removing the limitations of the Pradel model opens up new potential for much wider range of applications. Furthermore, our novel parametrization of transients as a proportion of all birds captured facilitates biological interpretation of the transience parameter and the study of transience as a biological phenomenon. Calculating all demographic parameters in a single model also opens up a unique possibility to take into account their correlated error distributions in follow-up

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analyses. Our model can be further extended in several ways and can serve as a basic building block in a wide range of demographic analyses.

KEYWORDS

capture-mark-recapture, capture-recapture, population growth, Pradel model, recruitment, survival, transients

1 | INTRODUCTION

Population dynamics is one of the most important and interesting phenomena in ecology and conservation. Decomposition of population growth into demographic parameters (survival, recruitment, fecundity, dispersal) can bring a deeper understanding of the drivers of population dynamics. This can be achieved in several ways. A population can be described using different types of data, such as capture-mark-recapture (CMR) data, nest record data, dead recovery data, or counts of individuals (Sandercock, 2006). Such data sets can be then analysed separately, that is, using separate models for each data set to estimate a given demographic parameter. Alternatively, one may take a step further and combine these different data sets in a single integrated population model (IPM), jointly estimating relevant demographic parameters for every age class and linking them together, typically using a Leslie matrix model (Cave et al., 2010; Weegman et al., 2022). In many cases, though, this might not be possible due to the lack of appropriate data. For example, in many species, relatively low philopatry makes it difficult to estimate juvenile survival, and suitable data (e.g. dead recoveries) are rare and sparse.

On the other hand, there are extensive CMR data that may be useful even if they are not sufficient for the construction of proper IPMs. For example, large-scale citizen science projects aim to collect CMR data for birds, profiting from their popularity (e.g. Albert et al., 2016; Robinson et al., 2009). Thanks to the networks of skilled volunteers, these projects cover whole continents over several decades, providing data for many species and habitats. While these CMR data sets themselves do not allow full Leslie matrix analysis, they allow for a very simple decomposition of population growth into survival and recruitment (recruitment comprises the effects of breeding productivity, juvenile survival and immigration in a single parameter). This simple decomposition is possible using the wellknown Pradel (1996) temporal symmetry model, which can estimate survival, recruitment and population growth. This model has become a 'classic' for demographic studies and has been used on wide range of taxa, including birds (Ancona et al., 2017; Saracco et al., 2008, 2020), rodents (Nichols et al., 2000; Polyakov et al., 2021; Schorr, 2012), bears (Clark et al., 2018; Sawaya et al., 2012), leguans (Rodrigues et al., 2021), turtles (Sasso et al., 2006) and toads (Lambert et al., 2016; Muths et al., 2011). The Jolly-Seber model is also capable of this analysis (Kéry & Schaub, 2012), but the Pradel model is more straightforward, as it circumvents the estimation of absolute population sizes.

Both the Pradel and Jolly-Seber models have two essential limitations, however. First, the study area must remain unchanged over the course of the study (Sandercock, 2006). This is generally not true in abovementioned large-scale citizen science projects, where volunteers can join or leave over the course of the project, which inevitably leads to a turnover of study sites and consequent changes in the study area. A second and even more important limitation of both the Pradel and Jolly-Seber models is that transient individuals are not taken into account. Transients are individuals just passing through, not contributing to the local (resident) population and its demographic rates, and they are thus very unlikely to be recaptured. Therefore, transience lowers the apparent survival of newly captured individuals compared to those already captured before. Ignoring transience in a model thus leads to substantial bias in estimated vital rates. This is not an infrequent problem, since transience is a very common phenomenon in many taxa (Genovart & Pradel, 2019; Oro & Doak, 2020).

For the Cormack-Jolly-Seber (CJS) survival model, the solution to account for transients is already well known (Cave et al., 2010; Johnston et al., 2016; Pradel et al., 1997). Seniority, the probability that a resident animal was already present in the previous year, is equivalent to the survival parameter in the time-reversed capture histories (Nichols, 2016; Sandercock, 2006). It is thus possible to use two independent CJS models (one for the original capture histories, the other for time-reversed ones) to estimate survival and seniority, and then derive population growth and recruitment post hoc (Labonne & Gaudin, 2005), while fully accounting for transience. However, this approach does not allow the calculation of proper confidence intervals for the post hoc derived parameters (Labonne & Gaudin, 2005), since the two separated CJS models do not provide a joint distribution of survival and seniority and their correlated error structure. It would thus be highly preferable to find a solution to account for transients in the Pradel (1996) temporal symmetry model, which estimates both survival and seniority simultaneously.

For the Pradel model, though, a solution accounting for transients was not available, and this has often been mentioned as a limitation of the Pradel model (Ahrestani et al., 2017; Saracco & Rubenstein, 2020). Many studies using the Pradel model have found the presence of transience, but have not been able to address it properly (Giroux et al., 2021; Rodrigues et al., 2021; Tenan et al., 2014). Using the original Pradel model on data with transients leads to a strong bias in the estimates of survival, seniority (and thus also recruitment) and capture probability (Orgeret et al., 2014), which can lead to poor model fit (Sasso et al., 2006). Thus, handling such a prevalent phenomenon in CMR models is a high priority (Sandercock, 2006).

Here, we have developed an extension of the Pradel model that addresses the presence of transient individuals as well as changes in the study area. This extension enables estimation of recruitment, survival and population growth in a single model, and has the potential to boost the use of data from large-scale citizen science programmes.

THEORY 2

The main objective of the model presented in this study is to use CMR data to decompose the realized population growth rate λ_t (the relative population change from occasion t to the next occasion t + 1) of a resident adult population to the sum of survival ϕ_t (the proportion of individuals surviving from occasion t to occasion t +1) and recruitment b_t (the rate of addition of new individuals to the population; see Table 1 for exact parameter definitions):

$$\lambda_t = \phi_t + b_t. \tag{1}$$

Survival also includes potential emigration (thus, it is apparent survival); recruitment, besides the individuals reaching adulthood, also involves the potential immigration of adults. The relative proportion of survival in population growth rate is called seniority, and can be calculated as

$$\gamma_{t+1} = \phi_t \,/\, \lambda_t. \tag{2}$$

The Pradel (1996) model uses CMR data to estimate any of the above four vital rates. Any two of these can be chosen as the primary parameters of the model; the other two vital rates can be calculated from these post hoc. In accord with the original Pradel (1996) study, we chose the time-symmetric parametrization, which uses survival and seniority as the primary demographic parameters.

MODEL ASSUMPTIONS AND 3 NOTATION

The sampling scheme considered is a capture-mark-recapture scheme that consists of k temporal occasions (e.g. years). The sampled area is assumed to have remained unchanged throughout the study period. There are two types of animals: residents, which inhabit the study area (their demography is the focus of interest); and transients, which are just passing through, and therefore their chance of being available for subsequent recapture is assumed to be zero (Cave et al., 2010; Pradel et al., 1997). Upon second capture, the animal is considered a confirmed resident. Other assumptions follow Pradel (1996): animals are captured and individually marked or just noted if already marked, and immediately released; no mark is lost or misread; there is no temporary emigration (except possibly random); and animals have independent fates. On a given occasion, all resident individuals, newly captured or recaptured, have the same probability of being captured. Nothing is assumed about the capture

probability of transients. See Table 1 for the notation of the symbols used in this study.

MODEL DEFINITION 4

In this section, we describe our extension of the Pradel (1996) model to account for transient individuals. First, we will describe the basic version of the model, corresponding to the original Pradel (1996) model. In the next step, we will describe two practical, optional extensions of the basic model, which can come in handy for a wide variety of CMR schemes.

The input data, that is, the capture histories of individual animals, are summarized in two matrices, called m-arrays: F-summarizing the capture histories of residents and transients up to the second capture (including those captured only once); and R-for residents from the second capture onwards (see Figure 1 for illustration; for exact definitions, see Table 1). Similar data structure is present in the familiar 2 age-classes CJS model (see e.g. Kéry & Schaub, 2012, Chapter 7.10.3). The organization of input data into m-arrays speeds up the computation significantly and allows the likelihood to be described more simply.

We describe the model likelihood in three parts (see Figure 1):

- (i) the probability of the first capture, conditional on being captured during the study $-f_{t}^{*}$;
- (ii) the probability of the second capture, conditional on the first capture $-f_{i,t}$ (the animal can be resident or transient);
- (iii) the probability of subsequent recaptures, conditional on the second capture $-r_{i,t}$ (i.e. the animal is a confirmed resident).

Each part is conditioned on the previous one; part (i) is conditional on being captured during the course of the whole study. Part (iii) corresponds to a regular CJS model; parts (ii) and (iii) together correspond to a CJS model with transient individuals (Cave et al., 2010; Pradel et al., 1997).

First, we need a few auxiliary definitions. As in Pradel (1996), we define the probability of a first capture, i.e. the probability that a resident individual captured on occasion t was not captured before:

$$\xi_t = (1 - \gamma_t) + \gamma_t (1 - p_{t-1}) \xi_{t-1}$$

$$\xi_1 = 1.$$
(3)

To account for the presence of transient individuals, our extension of the Pradel model introduces a novel parametrization of residency probability (r_{\star}^{c}) , relative to the number of all individuals captured in year t. This is a principal change compared to the well-established extensions for transient individuals in survival CJS models (Cave et al., 2010; Johnston et al., 2016; Pradel et al., 1997). In the CJS models, the residency/transiency probability is parametrized as a proportion of individuals captured for the first time (as in our r_{t}^{F} parameter), an approximation that is necessary and acceptable in the context of CJS models but not biologically meaningful. This can be seen from a simple case where the numbers of residents and transients remain constant, and the number of newly recruited individuals also does

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TABLE 1 Notation of the symbols used in this study, for the basic model and its two optional extensions (see 'Model extension 1' and 'Model extension 2').

Input data	
k	Number of temporal occasions
F _{i,t}	Number of animals captured for the first time at occasion <i>i</i> and first recaptured at occasion <i>t</i> (<i>i</i> , $t = 1k$; $t \ge i$)
<i>F</i> _{<i>i</i>,<i>k</i>+1}	Number of animals captured for the first time at occasion <i>i</i> and never recaptured again
F _{i,*}	Number of animals captured for the first time at occasion <i>i</i> (<i>i</i> -th row sum of matrix F ; $F_{i,*} = \sum_{t=1}^{k+1} F_{i,t}$)
F *	Vector of row sums of matrix $F; F^* = (F_{1,*}, F_{2,*}, \dots, F_{k,*})$
R _{i,t}	Number of animals recaptured at occasion <i>i</i> (i.e. confirmed residents) and next recaptured at occasion <i>t</i> (<i>i</i> =1 <i>k</i> -1; <i>t</i> =2 <i>k</i> ; <i>t</i> > <i>i</i>)
$R_{i,k+1}$	Number of animals recaptured at occasion <i>i</i> (i.e. confirmed residents) and never recaptured again

Primary model parameters

ϕ_t		Survival probability: the probability that a resident animal present on occasion t will be present on occasion $t+1$ (apparent survival); $t=1 \dots k-1$
γ_t		Seniority probability: the probability that a resident animal present on occasion t was already present on occasion $t-1$
p _t	p(c r) ^b	Capture probability: the probability that a resident ^a animal present on occasion t is captured on occasion t
rt ^C	p(r c) ^b	Residency probability (within all captured individuals ^a); the probability that an animal captured on occasion <i>t</i> is a resident
ω		Probability of the confirmation of residency status for the newly captured resident (e.g. by a recapture within the occasion of the first capture or by direct cues confirming residency); in the CMR schemes where this is irrelevant, it will be naturally estimated as zero

Derived parameters and other symbols								
N _t		Resident population size on occasion t (latent and not estimated by the model)						
I _t		Index of population size on occasion $t\left(I_t = \frac{N_t}{N_1}\right)$						
λ_t		Realized population growth rate of residents between year t and t+1; $\lambda_t = N_{t+1} / N_t = \phi_t / \gamma_{t+1} = \phi_t + b_t$						
b _t		Recruitment rate: the number of animals entering the resident population on occasion <i>t</i> + 1 divided by the number of animals already present in the resident population on occasion <i>t</i> (this parameter is often denoted by letter <i>f</i>)						
r _t ^F	p(r f & c) ^b	Residency probability (within newly captured individuals): the probability that an animal captured for the first time on occasion t is a resident						
ξ _t	p(f r) ^b p(f r & c) ^b	Probability that a resident animal present on occasion <i>t</i> was never captured on previous occasions; or, equivalently, the probability that resident animal captured on occasion <i>t</i> was captured for the first time						
f_t^*		Probability that an animal captured during the study is captured for the first time at occasion t						
f _{i,t}		Probability that an animal captured for the first time at occasion <i>i</i> is first recaptured at occasion <i>t</i>						
$f_{i,k+1}$		Probability that an animal captured for the first time at occasion <i>i</i> is never recaptured again						
r _{i,t}		Probability that an animal recaptured at occasion <i>i</i> (i.e. confirmed resident) is next recaptured at occasion <i>t</i>						
<i>r</i> _{<i>i</i>,<i>k</i>+1}		Probability that an animal recaptured at occasion <i>i</i> (i.e. confirmed resident) is never recaptured again						

^aNothing is assumed about the capture probability of transients; for this reason, we monitor residency probability within the captured animals, not within all animals present.

 b Conditional probabilities: c=captured, f=never captured before, r=resident.

not change over time (Figure 2). In this example, r_t^F decreases, even though the actual proportion of transients remains constant (Figure 2). Consequently, if we fitted a model with the r_t^F parameter assumed constant over time (the simplest model) to estimate population growth and recruitment, it would result in an overestimation of both of these parameters (strong biases were confirmed by our simulations, not shown). Thus, we cannot use this approximative parametrization for the Pradel model, and instead we introduce a biologically more meaningful parametrization of residency probability relative to all individuals captured (r_t^C), and then re-condition this probability to newly captured individuals (r_t^F) , which is needed for the likelihood. When we rewrite the parameter r_t^F to the conditional notation (Table 1), we can easily apply Bayes rule to reverse the conditional probabilities, which gives an expression containing parameters r_t^C and ξ_t (see their conditional notations in Table 1):

$$r_t^F = p(r \mid f\&c) = \frac{p(f \mid r\&c) p(r \mid c)}{p(f \mid c)} = \frac{p(f \mid r\&c) p(r \mid c)}{p(f\&r \mid c) + p(f\&\neg r \mid c)} = \frac{\xi_t r_t^C}{\xi_t r_t^C + 1 - r_t^C}.$$
(4)

Equation 4 is graphically illustrated in Figure 2.



FIGURE 1 Schematic depiction of the model (including 'Model extension 2'), its parameters, and input data. Full arrows denote deterministic dependencies, and dashed arrows stochastic dependencies; the symbols are explained in Table 1. The CMR (capture-mark-recapture) data, which contain capture histories for every individual ('1' means that a given individual was captured during the respective occasion, '0' that it was not), are transformed into the input data for the model: two matrices, called m-arrays, $F_{i,t}$ (animals captured for the first time, i.e. a mixture of residents and transients) and $R_{i,t}$ (animals captured for second and subsequent times, i.e. confirmed residents). These matrices comprise the numbers of individuals captured at occasion *i* and next captured on each subsequent occasion *t*; 'n.r.' stands for 'never recaptured'. The figure shows an example of the m-array data format for three temporal occasions (k=3). The input data also includes a vector of numbers $F_{i,r}$, the row sums of matrix $F_{i,t}$ —that is, the numbers of animals captured for the first time at occasion *i*. The purpose of our model is to estimate primary model parameters (bottom row) by fitting the model on the input data. The dashed contours delimit the parts of the model corresponding to a traditional CJS model and its variant accounting for transients. The last column in the 'CMR data' table, the values $F_{i,i}$ (the diagonal of m-array *F*), and the parameter ω pertain to the 'Model extension 2'. Deletion of the parameters r^{C} , r^{F} and ω would lead to the original Pradel (1996) model.

Now, we are ready to define the likelihood. The enumeration of the probabilities of a first capture at a given occasion (f_t^*) is the most challenging part of the model, because these probabilities need to be conditioned to all animals captured during the study. We can start by enumerating the expected number of animals (both residents and transients) captured for the first time on occasion *t*:

$$N_t p_t \xi_t \frac{1}{r_t^F} = N_1 \left\{ \prod_{i=1}^{t-1} \lambda_i \right\} p_t \xi_t \frac{1}{r_t^F}.$$
(5)

This is the same step as in Pradel (1996), with the addition of division by r_t^F , to get the expected number of both residents and transients. Now, by normalizing these values to the sum of 1, we get probabilities f_t^* -in this process, absolute abundance N_1 cancels out:

$$f_{t}^{*} = \frac{f_{t}'}{\sum_{i=1}^{k} f_{i}'}; f_{t}' = \left\{ \prod_{i=1}^{t-1} \lambda_{i} \right\} p_{t} \xi_{t} \frac{1}{r_{t}^{F}}.$$
 (6)

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FIGURE 2 Example illustrating potential bias of the commonly used parametrization of residency/transiency as a proportion of newly captured animals (r_t^F) and the relationship of this parametrization with the more biologically meaningful parametrization as a proportion of all captured animals (r_t^F) and the relationship of this parametrization with the more biologically meaningful parametrization as a proportion of all captured animals (r_t^F) formally expressed by Equation 4. In this simple example, the number of residents and transients both remain constant over time ($\lambda_t = 1, r_t^C = 0.7$), and so do the seniority rate and the capture probability ($\gamma_t = 0.7, p_t = 0.4$). As the proportion of recaptured individuals increases, the number of newly captured residents (the shorter arrow) decreases. (The longer arrow refers to all newly captured individuals.) Consequently, the proportion of residents within the newly captured individuals (r_t^F) decreases, even though the real proportion of residents is constant. See Table 1 and Equation 4 for symbol explanations.

Thus, the first part of the likelihood—up to the first capture—can be expressed by applying these probabilities to $\mathbf{F}^* = (F_{1,*}, F_{2,*}, \dots, F_{k,*})$, a vector of row sums of matrix \mathbf{F} —that is, a vector whose *i*-th element is the number of animals captured for the first time at occasion *i* ($\sum \mathbf{F}^*$ gives the total number of animals captured during the study):

$$F^* \mid \sum F^* \sim \text{Multinomial} \left(\sum F^*, f^*_{1.k} \right).$$
 (7)

The remaining part of the likelihood (its second and third part combined, see $f_{i,t}$ and $r_{i,t}$ in Figure 1) is conditioned on the first capture and corresponds to a CJS model with transients (Pradel et al., 1997). Probabilities of the next recapture after first capture ($f_{i,t}$) are defined as:

$$f_{i,t} = r_i^F \phi_i \left\{ \prod_{j=i+1}^{t-1} \phi_j (1-p_j) \right\} p_t; \quad i < t \le k$$

$$f_{i,k+1} = 1 - \sum_{t=1}^k f_{i,t}.$$
(8)

The second part of the likelihood can thus be expressed by applying the above probabilities to each row *i* of the input m-array *F*:

$$\boldsymbol{F}_{i,1..k+1} \mid \boldsymbol{F}_{i,*} \sim \text{Multinomial} \left(\boldsymbol{F}_{i,*}, \boldsymbol{f}_{i,1..k+1} \right)$$
(9)

The third part of the likelihood corresponds to animals already caught twice, i.e. confirmed residents; thus, it is the plain CJS model:

$$r_{i,t} = \phi_i \left\{ \prod_{\substack{j=i+1\\k}}^{t-1} \phi_j (1-p_j) \right\} p_t; \quad i < t \le k$$

$$r_{i,k+1} = 1 - \sum_{t=1}^k r_{i,t}.$$
 (10)

Each row of m-array R has an independent multinomial distribution with the probabilities defined above. Therefore, the third part of the likelihood for the *i*-th row of R is:

$$\boldsymbol{R}_{i,2..k+1} \mid \boldsymbol{\Sigma}_{t} \boldsymbol{R}_{i,t} \sim \text{Multinomial} \left(\boldsymbol{\Sigma}_{t} \boldsymbol{R}_{i,t}, \boldsymbol{r}_{i,2..k+1} \right)$$
(11)

The overall likelihood is the product of the above-defined parts and can be expressed as $\mathcal{L}(F^*, F, R | \phi, \gamma, p, r^C, \omega)$.

4.1 | Model extension 1: Temporal changes in the study area

Our basic model described above, similarly to the original Pradel (1996) model, assumes a fixed study area. In many projects, though, notably those based on citizen science, the study area can change because it consists of multiple sites with temporal turnover; that is, some sites may be added later during the study, and some sites may be abandoned. In general, each site can have different temporal coverage. Since the likelihood is a product of multinomial likelihoods, which can be decomposed to the products of Bernoulli likelihoods for every single individual and state transition of our Markov model, it does not matter if and how the individual animals are grouped into sites. Thus, we can create separate input data (vector F* and m-arrays F and R) for each site and set the capture probability to zero for the site-time combinations where no monitoring has been done. All other parameters, including demographic ones, can (but do not have to) be fitted globally across all sites.

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4.2 | Model extension 2: Confirmation of residency status within the first capture occasion

In our basic model described above, an animal is considered a confirmed resident when it is captured for a second time. However, in the CMR schemes where each temporal occasion consists of several sampling sub-occasions (e.g. repeated sampling events during the same breeding season), it may also be reasonable to confirm residency status by a second capture that happens in a subsequent sub-occasion still within the occasion of the first capture (see Cave et al., 2010; Johnston et al., 2016; and our case study below). For this purpose, we can extend the model to use the information about the number of animals recaptured within the occasion of the first capture (the values $F_{i,i}$, the diagonal of F, see Table 1), and then, by introducing new parameter ω (see Table 1), we can extend the Equation 8 to also include the corresponding probabilities $f_{i,i}$:

$$f_{i,i} = r_i^F \omega$$

$$f_{i,t} = r_i^F (1 - \omega) \phi_i \left\{ \prod_{j=i+1}^{t-1} \phi_j (1 - p_j) \right\} p_t; \quad i < t \le k$$

$$f_{i,k+1} = 1 - \sum_{t=1}^k f_{i,t}.$$
(12)

Note that this is the only way the information from sampling suboccasions is used to further inform our model, in contrast to the socalled 'robust design' which explicitly operates with all the data from individual sub-occasions (see Cooch & White, 2017). Additionally, if the residency status of a newly captured individual can also be confirmed by, for example, some cues signalizing breeding, then this information can be supplied to the model as a 'recapture' within the occasion of the first capture.

4.3 | Model implementation

The models were written in BUGS language and fitted in the Bayesian environment using Nimble (de Valpine et al., 2017), using three parallel chains with 200,000 iterations, disposing the first 80,000 as burn-in and using only every 40th iteration. We used uniform priors for probabilities and standard deviations, and a flat normal for the slopes. Derived parameters (recruitment and population growth) were calculated post hoc on the Markov Chain Monte Carlo (MCMC) samples of the primary model parameters (survival and seniority) to ensure the proper propagation of the uncertainty of estimates. To verify the validity of our implementation, we performed a simulation study (Appendix A), which shows that the model provides unbiased estimates of the demographic parameters. The calculations were done in R (R Core Team, 2020). Extensively commented code is available at https://github.com/ telenskyt/pradel_tr_paper/, with implementations of basic as well extended model in BUGS language for both Nimble and JAGS (Plummer, 2003), along with simple examples.

5 | GRAPHICAL PRESENTATION OF MODEL RESULTS

Our model can estimate all four demographic rates defined in the section 'Model assumptions and notation'—population growth, survival, recruitment and seniority. These demographic rates compose a twodimensional space, since they are all determined by any two of these. Thus, we can conveniently plot the whole situation in a single 2-D graph, which we hereafter call the 'talon plot' (Figure 3a), with three axes:

- survival and recruitment, representing the two primary demographic parameters, correspond to two major orthogonal axes;
- population growth as their sum is oriented as a vertical axis.

The vertical orientation of the population growth axis emphasizes its central importance, as well as the fact that it is the sum of two principally independent (although not necessarily uncorrelated) components.



FIGURE 3 Talon plots depicting the relationships between survival, recruitment and population growth rate. (a) Survival ϕ and recruitment *b* are the two major orthogonal axes, while population growth λ is their sum and thus corresponds to the vertical axis. The right–left tilt, that is, the polar angle between the recruitment axis and the dashed line connecting a given point with the graph origin, corresponds to seniority γ (i.e. the proportion of survival in the population growth); $\gamma = 1/(1 + 1/\tan(\text{angle}))$. (b) Survival and recruitment may be negatively correlated, suggesting a strong and immediate regulation of population growth, with high recruitment compensating for low survival and vice versa. (c) Alternatively, survival may be positively correlated with recruitment, suggesting that common factors simultaneously affect both parameters. The points correspond to different temporal occasions; the horizontal dashed line corresponds to population growth=1. This plot clearly and comprehensively summarizes the relationships among demographic rates, namely:

- The contribution of survival to population growth at each of those data points—i.e. seniority—corresponds to the right-to-left tilt, that is, the polar angle from the recruitment axis (the angle between the recruitment axis and an imaginary line connecting a given point with the graph origin). The more this line is tilted to the left, the higher the proportion of survival in the population growth; and vice versa, the more it is tilted to the right, the higher the proportion of recruitment.
- Contributions of survival and recruitment at different levels of population growth—a comparison of the positions of the data points shows what happens at temporal occasions with lower (or higher) population growth rates: that is, whether they are related to lower (or higher) survival or recruitment.
- 3. The variability of survival and recruitment and their relationship with population growth shows which of these vital rates is more correlated with population growth.
- 4. Correlation between survival and recruitment where two basic scenarios (sensu Julliard, 2004) can be described (see Figure 3b,c): (i) survival and recruitment are negatively correlated (points spread horizontally), indicating that high survival can limit the recruitment of new individuals or low survival can be compensated for by high recruitment; (ii) survival and recruitment are positively correlated (points spread vertically), indicating that both survival and recruitment can be affected by a common factor (e.g. winter weather affecting the survival of both adults and juveniles).

We provide a standalone R package 'talonplot' (https://github. com/telenskyt/talonplot/), which allows to render the talon plot from any model estimating survival and recruitment.

6 | CASE STUDY: CONSTANT EFFORT SITES MIST-NETTING SCHEME IN THE CZECH REPUBLIC

Here, we show an example of the application of our model to CMR data collected by the Constant Effort Sites (CES) programme in the Czech Republic. CES is a bird ringing scheme performed in multiple European countries and is based on the standardized mist-netting protocol conducted by skilled volunteers with constant effort at each site (Robinson et al., 2009). In the Czech Republic, data are collected annually, covering 50 sites since 2004 (Telenský et al., 2020). Each site is visited nine times every year in ca. 10-day intervals covering the advanced breeding season (May–July).

For the model, the time unit (occasion) used to evaluate bird demography is a year. At each site, the data from all nine visits in a given year are taken as if they come from a single occasion, with one exception: we track whether the bird was captured during multiple visits in the year of the first capture (the $F_{i,i}$ counts), which is an additional confirmation of its residency status in its inaugural year (see

'Model extension 2'). We used the procedure described in 'Model extension 1' to handle the different temporal coverage of the sites. We modelled the p_t and ω parameters as constant over time with a random site effect; residency probability r_t^C is modelled as a linear function of year. For each species, we ran two models: one without the discrimination of habitat types at different sites, and one with demographic rates and residency probability defined separately for two different habitat types: wet (reedbeds, wet scrub) and dry (dry scrub); each site was represented by one of these habitat types. For each species, we then selected the better performing model according to Watanabe-Akaike Information Criterion (Watanabe, 2010). The correlations of the demographic rates were calculated on the MCMC posterior samples, providing a posterior distribution of the correlation coefficients (Kéry & Schaub, 2012). This way, the uncertainty of the estimates of the demographic rates is properly propagated to the uncertainty of the correlation coefficient. As a measure of density, we also calculated the adult population index in year t. The index was set to 1 in the first year, and for subsequent years calculated as a product of $\lambda_1 \lambda_2 \dots \lambda_{t-1}$. The 95% confidence ellipses of every single data point (year) in the 'talon' plot were calculated from the MCMC samples of survival and recruitment, using the R package car (Fox & Weisberg, 2019).

For illustration, we show two species that represent the two scenarios (see Figure 3b,c) differing in their relationships among demographic rates: the Great Tit (*Parus major*) represents species with a negative relationship between survival and recruitment, while the Common Reed Warbler (*Acrocephalus scirpaceus*) represents species with a positive relationship (Figure 4, Table 2). Selected models were not habitat specific for these species. Population growth was correlated with recruitment in both species, while with survival only in the Eurasian Reed Warbler (Figure 4, Table 2). Population growth and recruitment were density dependent in both species; survival was density dependent only in the Reed Warbler (Table 2). The mean proportion of residents was much higher in the Great Tit (0.860) than in the Reed Warbler (0.480). See Table 2 for correlations between the respective demographic parameters estimated by the model.

In addition, we illustrate the possibility of studying temporal trends of residence/transience in two other species, where the best models were habitat specific. In the Garden Warbler (*Sylvia borin*), the proportion of residents is significantly declining in dry habitats and significantly increasing in wet habitats (Figure 5). In the Common Blackbird (*Turdus merula*), the proportion of resident individuals is larger in dry habitats than in wet habitats (Figure 5).

7 | DISCUSSION

In studies of animal demography, residents are usually the main focus whereas transient individuals act as noise in the data. Yet, the presence of transient individuals is very common in many taxa (Oro & Doak, 2020), and the bias they produce in demographic rates may be substantial (Orgeret et al., 2014). The well-known and widely



FIGURE 4 Talon plots for the Great Tit (*Parus major*) and Eurasian Reed Warbler (*Acrocephalus scirpaceus*) from the Czech Constant Effort Sites capture-mark-recapture programme, representing the two scenarios theoretically introduced in Figure 3b,c: negative (Great Tit) and positive (Eurasian Reed Warbler) correlations between survival and recruitment. Black points correspond to mean estimates for each year, with 95% confidence ellipses; the tiny grey dots represent the MCMC samples. The horizontal dashed line corresponds to population growth = 1.

	Parus major			Acrocephalus scirpaceus		
	Mean	2.5%	97.5%	Mean	2.5%	97.5%
$mean(\gamma_t)$	0.456	0.176	0.806	0.491	0.390	0.611
$cor(\phi_t, b_t)$	-0.416	-0.746	0.040	0.296	-0.056	0.618
$\operatorname{cor}(\lambda_t, \phi_t)$	0.336	-0.094	0.701	0.709	0.476	0.869
$\operatorname{cor}(\lambda_t, b_t)$	0.691	0.361	0.894	0.877	0.756	0.950
$cor(\lambda_t, density_t)$	-0.390	-0.677	-0.160	-0.735	-0.823	-0.635
$cor(\phi_t, density_t)$	-0.052	-0.403	0.293	-0.533	-0.752	-0.265
$cor(b_t, density_t)$	-0.338	-0.599	-0.057	-0.638	-0.785	-0.449
$mean(r_t^C)$	0.860	0.693	0.992	0.480	0.459	0.501
Temporal slope of r_t^C	0.396	-0.907	1.996	0.077	0.013	0.143

TABLE 2 Summary of demographic parameters and derived quantities for two avian species (the Great Tit *Parus major*, n = 2007 individuals, and Eurasian Reed Warbler *Acrocephalus scirpaceus*, n = 14,379individuals) with capture-mark-recapture data from the Constant Effort Sites programme in the Czech Republic. Each quantity is presented by a mean value and 95% confidence interval. cor denotes the Pearson correlation coefficient of the two given parameters; density_t is an index of the resident adult population (l_t from Table 1), representing the population density of the species. See Table 1 for symbol definitions.

used original Pradel (1996) temporal symmetry model for CMR data to estimate survival, recruitment and population growth was designed for resident individuals only, but some studies have used it on data with transient individuals, while being aware of the risk of bias in survival and recruitment estimates (Giroux et al., 2021; Rodrigues et al., 2021; Tenan et al., 2014). Another study reported poor model fit (Sasso et al., 2006). Here, we have resolved these issues by developing an extension of the Pradel model that takes into account both transient individuals and temporal changes in the study area. We introduce a novel, biologically meaningful parametrization of residency/transiency as a proportion of all individuals captured, as opposed to the usual parametrization as a proportion of newly captured individuals. We also propose a specific graphic representation (talon plot) for the outputs of our modified model.

Prior to our study, the usual solution for estimating survival, recruitment and population growth from CMR data while accounting for transients was to estimate survival and seniority separately in two independent CJS models accounting for transients (Pradel et al., 1997) and then post hoc derive population growth and recruitment (Labonne & Gaudin, 2005). However, the proper propagation of uncertainty is impossible in this case, since the estimates of demographic parameters come from separate models. Our extended Pradel model allows to estimate all the demographic rates in a single model, providing not only their confidence intervals but also their joint error distributions. This, especially in combination with MCMC model fitting, allows for a full propagation of the uncertainty of the primary model parameter estimates to the uncertainty of any function calculated from these parameters (Kéry & Schaub, 2012). We demonstrated this in a case study on the simple correlations of vital rates. The full propagation of the uncertainty of the estimates can be applied to a whole range of more advanced follow-up analyses, for example sensitivity analyses (Caswell, 2019), transient perturbation analyses (Stott, 2016) and transient life table response experiment-LTRE

FIGURE 5 Temporal trend in proportion of resident individuals in dry (left) and wet (right) habitats in two species (Garden Warbler *Sylvia borin* and Eurasian Blackbird *Turdus merula*) in the Czech Constant Effort Sites programme. The shaded areas show 95% CI. The temporal slopes (linear on the logit scale) are reported as mean estimates with 95% CI in parentheses, with posterior probability that the slope is greater or smaller than zero.



(Koons et al., 2017). The joint error distribution provided by our model is also a necessary input for some analyses (e.g. the transient LTRE), and plays a crucial role in the uncertainty propagation, since the error covariance between the vital rate estimates is not negligible—there is always a strong negative correlation between the posterior samples of survival and recruitment estimates for a given year, as can be observed on the shape and orientation of the confidence ellipses in Figure 4.

The primary purpose of our model is the decomposition of population growth into survival and recruitment. The talon plot proposed for the visualization of these vital rates contains a single point for each temporal occasion. The polar angle of a given point from the recruitment axis directly corresponds to the seniority parameter-the proportion of survival in the population growth in that temporal occasion. Seniority thus shows us the balance between the contributions of survival and recruitment to population growth at every single temporal occasion (on an absolute scale; not to be confused with the contributions of variation in these vital rates to the variation of population growth). The overall position of a given species on this gradient can be interpreted as a position along the fast-slow continuum of life history strategies. This can be illustrated by mean seniority values for a long-lived seabird, Blue-footed Booby (Sula nebouxii)-0.818 (Ancona et al., 2017), in contrast to small passerines such as the Great Tit and Common Reed Warbler-0.456, 0.491 (our study), or a small rodent, Brush Mouse (Peromyscus boylii)-0.06 (Polyakov et al., 2021; monthly rates recalculated to annual).

Another important feature of these demographic rates that can be observed in the talon plot is the correlation between survival and recruitment (Figure 3b,c). In our case study, the Common Reed Warbler had a positive correlation between these rates, while the rates correlated negatively in the Great Tit. The negative correlation may indicate a compensatory mechanism, in which higher survival limits recruitment, and low survival is compensated for by high recruitment. This could be due to, for example, limited nesting possibilities in this cavity-nesting species. In contrast, a positive correlation may be due to an interannually varying factor that simultaneously affects both survival and recruitment (for instance climatic conditions in African wintering grounds, see Telenský et al., 2020).

Accounting for transiency in our extended Pradel model introduced the possibility of parametrizing residency (i.e. 1 minus transiency) as a proportion of all individuals captured, an option that is not available in CJS models. The transiency parameter in the form used in CJS models, that is, relative to the number of newly captured individuals (Cave et al., 2010; Johnston et al., 2016; Pradel et al., 1997), is not easy to interpret biologically, since it is prone to bias when compared over time (see Figure 2 for a more detailed explanation; see also Oro et al., 2004). While this parametrization was acceptable in survival CJS models (unless one needed to interpret the transience parameter), it could not be used in the Pradel model since it would result in a large bias in estimated population growth and recruitment. In contrast, our new parametrization of residency/transiency relative to all birds captured not only allows

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the demographic rates as well as transience in a single model provides joint error distributions of the estimates, and thus allows the proper propagation of the uncertainty of the estimates in a whole range of follow-up analyses. Our model can be further extended in many different directions-for instance, one could build a so-called 'robust design' (Cooch & White, 2017) model variant allowing a trap response to be accounted for, or to study additional demographic parameters such as temporary emigration. Thus, our modification of the Pradel model described here can be the foundation for a wide range of demographic analyses. AUTHOR CONTRIBUTIONS Tomáš Telenský conceived the idea, designed and implemented the model, analysed the data and led writing. Petr Klvaňa coordinated data collection and validated the data. David Storch and Jiří Reif contributed to writing and supervised the work of Tomáš Telenský. Jiří Reif acquired funding. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and extensively commented code used in this paper are openly available at https://github.com/telenskyt/pradel_tr_paper/ under a CC-BY licence. We provide basic as well as extended model implementations in Nimble and JAGS, along with simple examples and code for all analyses and figures. We provide a standalone R package 'talonplot' (https://github.com/telenskyt/talonplot/), which allows to render the talon plot from any model estimating survival and recruitment. Both repositories are also archived at Zenodo (https://zenodo.org/badge/latestdoi/716883624, https://zenodo. org/badge/latestdoi/716840715).

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raphy of residents, but also is biologically more meaningful, since it corresponds to the actual ratio of residents/transients in the population. Some previous studies have done post hoc calculations to get the same parameter in CJS models using an approximative formula (Jessopp et al., 2006; Pradel et al., 1997), or worked around it by combining the results of two CJS models, one with modified capture histories (Oro et al., 2004). However, to our knowledge, our study is the first to implement this parameter directly into the model. It should again be noted that this could not have been implemented in the CJS model since integrating this parametrization into our model requires the seniority parameter.

one to properly filter out the transience as a 'noise' in the demog-

Our novel, biologically more plausible parametrization of residency/transiency opens a whole avenue for studying transience as an ecological phenomenon, for example by testing its temporal trends or relating it to various covariates such as habitat types. We briefly demonstrated these possibilities in our case study. The Garden Warbler showed a decreasing proportion of residents over time in dry habitats and increasing in wet habitats. As decreasing residency and increasing transiency might be a consequence of deteriorating habitat quality (Oro & Doak, 2020), this pattern could be related to the frequent droughts that have occurred in our study area over the last decade, which could have led Garden Warblers to move to wetter habitats.

Some studies that use CMR data only for the estimation of survival argue that the Pradel model has a disadvantage in the need for the extra assumption of equal capture probability of both newly captured and recaptured individuals (Ahrestani et al., 2017). While this is true, it is worth noting that this assumption is often made anyway, whether explicitly or not. For example, estimating recruitment in the timereversed CJS model relies on this assumption as well, and so does any inference about population sizes and population growth, since these pool the newly captured and recaptured individuals together. Any attempt to biologically interpret transience in a survival-only CJS model, for example by scaling the transience to all individuals captured (Jessopp et al., 2006; Pradel et al., 1997), also requires this assumption. Nevertheless, as in the original Pradel model, the assumption that a resident individual has an equal probability of a first capture and subsequent recaptures is also essential in our model. Its violation, for example due to a trap response or heterogeneity in capture probability, would lead to the same biases as in the original Pradel model (Hines & Nichols, 2002). Our model can be further extended to tackle these biases using the same modifications as have been done for the original Pradel model (see e.g. Pradel et al., 2010).

In conclusion, we have developed an extension of the Pradel model to account for transience and to allow for temporal changes in the study area. These changes make this model accessible to CMR data sets collected over large areas, such as long-term citizen science projects like CES in Europe and MAPS (Monitoring of Avian Productivity and Survivorship) in North America. We have introduced a biologically meaningful parametrization of transience, which allows to test hypotheses directly within a single model and to study the ecological context of this phenomenon. Estimating all

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article. **Appendix A.** Test of the model on simulated data.

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