Titles: Mark loss can strongly bias demographic rates in multi-state models: a case study with simulated and empirical datasets

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Abstract

1. The development of methods for individual identification in wild species and the refinement of Capture-Mark-Recapture (CMR) models during the past decades has greatly improved the assessment of population demographic rates to answer ecological and conservation questions. In particular, multistate models, with their flexibility for the analysis of complex study systems, have become popular in the ecological community. However, despite the extensive use of these models, little attention has been paid to the effect of common violations of the CMR model assumptions, such as mark loss and the often-associated recycling of remarked individuals.

2. To explore this knowledge gap we used a wide range of simulation scenarios reflecting frequently encountered real case studies inspired from the survival rates of 700 vertebrates' species. We estimated the effects of mark loss and recycled individuals on parameter estimates using a multi-state Cormack-Jolly-Seber (MSCJS) framework. We explored parameter bias through simulations of a metapopulation system with different capture and survival rates. We also illustrated how mark loss can be easily estimated and accounted for using an empirical long-term (10 years) CMR dataset of bats, individually identified using both PIT tag technology as marks that can be lost, and multi-locus genotypes as 'permanent marks'.

3. The results from our simulated scenarios demonstrated that the occurrence of bias and the parameters concerned were highly dependent on the study system, and no general rules on parameter behaviour can be established *a priori*. The model structure and the interdependency among parameters make it challenging to predict how bias could affect estimates.

4. Our results highlight the need to assess the effect of mark loss when using MSCJS models. Ignoring such violations of model assumptions can have important implications for ecological inferences and conservation policies. In general, the use of permanent marks (e.g. genotype), should always be preferred when modelling of population dynamics and if not possible, combining two types of temporary marks (e.g. PIT tags, bands) should be considered.

KEYWORDS

Bayesian, bats, demographic rates, capture-mark-recapture, mark loss, *Myotis myotis*, multi-state Cormack-Jolly-Seber model, parameter bias.

1 Introduction

Capture-mark-recapture (CMR) methods have become a standard approach to estimate demographic rates of wild species thanks to the development of a range of different models. Accurately quantifying population dynamic parameters is critical to assess the state of populations, understand their dynamics, and ultimately make efficient management and conservation decisions. However, all CMR models make a number of assumptions of homogeneity (Johnson et al., 1986; Williams et al., 2002) that are prone to generate biases if violated. A widespread violation of CMR model assumptions, originally identified four decades ago (Nelson et al., 1980) is the loss of marks (see Supported Information 1, Table S2). Local survival is the product of true survival and mark retention rate for individual staying in the study area. If the retention rate starts to drop below one without being considered in the model, while true survival remains constant, then local survival is underestimated and becomes confused with the probability of presence of the mark, even more if true survival is high. Mark loss has two consequences: (1) when mark shedding occurs it induces non-identifiability of individuals, and individuals that have lost their mark may be considered either dead or out of the study area, despite being alive and present; (2) if such individuals are captured again, they will not be recognized and will be remarked as newly recruited individuals, which is called “recycling”.

Consider “1011”, a simple four occasions encounter history, where “*1*” implies the individual was caught and “*0*” not. If we note ϕ_t the survival rate between occasion t and $t+1$ and p_t the capture probability at occasion t (with $q_t = 1 - p_t$), this encounter history occurs with probability $\phi_1 q_2 \phi_2 p_3 \phi_3 p_4$. Now consider the individual can make a transition between 2 states, and its history

becomes “1022”, with individual in state “1” at t_1 and in state “2” at t_3 and t_4. If we define $\psi^{i,j}$ the transition probability from state *i* to state *j* (i and j in {1,2}), conditional on survival, the new encounter history occurs with probability $\phi_1^{(1)}\psi^{(1,1)}q_2^{(1)}\phi_2^{(2)}\psi^{(1,2)}p_3^{(2)}\phi_3^{(2)}\psi^{(2,2)}p_4^{(2)}$ + $\phi_1^{(1)}\psi^{(1,2)}q_2^{(2)}\phi_2^{(2)}\psi^{(2,2)}p_3^{(2)}\phi_3^{(2)}\psi^{(2,2)}p_4^{(2)}$, with indices for state-specific parameters noted in parentheses. If this individual loses its mark after its first capture and is remarked when recaptured at t_3, its encounter history becomes ‘two’ different histories from ‘two’ different individuals: one becoming “1000”, the second “0022”. In this case, survival and mark loss patterns are different, not only is survival underestimated (at least for the "first" history) but so are the transition probabilities, because there is no longer a change of state (the second history starts directly at state 2).

Many CMR studies, despite using different mark types, are affected by mark loss, the rate of which varies according to a myriad of factors, such as species (see Supported Information 1, Table S2), mark type (Smout et al., 2011a), sex (Conn et al., 2004), mass (Schwarz et al., 2012), size (Acolas et al., 2007), mark location (Kaemingk et al., 2011) or physiological stage (Besnard et al., 2007). Mark loss has previously been shown to produce negative bias in survival estimates and detection (Nichols et al., 1992; Nichols & Hines, 1993). Many statistical tools have been developed to remove the confounding effect of mark loss in single state models, (Robson & Regier, 1966; G. A. F. Seber & Felton, 1981). However, the effect of these violations has not been explored in the multi-state modelling framework.

Multi-state models were developed to deal with situations where the “state” (e.g. location, behaviour, physiology, reproductive or social status) of an individual may affect its survival or detection probability, and where the individual can change “state” during life (reviewed in Lebreton et al., 2009). These models became popular and widely used because of their flexibility to address a large range of study systems and biological questions, and because they can be used in a relatively straightforward manner by biologists given the development of user-friendly software (e.g. Mark, E-surge, Bugs). They are used to address many ecological and evolutionary hypotheses based on

variations in life history traits (state transitions) throughout an individual's life (Nichols & Kendall (1995) see also Cam (2009) for an extensive discussion on the subject), or density dependence effect (Schofield & Barker, 2008), co-evolution (Benkman et al., 2005), dispersal probability among subpopulations or living areas (Hestbeck et al., 1991; Spendelow et al., 1995), disease prevalence in wild populations (Jennelle et al., 2007). However, the literature dealing with the effect of mark loss on multi-state model behaviour is scarce and much remains to be explored.

To address this gap in knowledge, here we used simulation-based multi-state Cormack-Jolly-Seber (MSCJS) approaches to investigate the impact of mark loss on estimates of model parameters within a Bayesian framework. Given the increasing use of MSCJS models, our goal is to assess the potential bias in the marginal posterior distributions of demographic parameter estimates using a metapopulation context, based on biologically realistic scenarios and if possible, provide comprehensive guidelines for both, fieldwork and data analysis. The MSCJS model share assumptions with the CJS model (Cormack, 1964; Jolly, 1965; G. Seber, 1965), particularly in relation to mark loss. In addition, states are assumed to be recorded without error and survival, transition and observation probability must be the same for all individuals at a given occasion and state.

To illustrate our approach with an empirical example, we also used our decade-long mark recapture data set of PIT-tagged and genotyped Greater mouse-eared bat (*Myotis myotis*), a taxonomic group particularly susceptible to PIT-tags loss (Freeland & Fry, 1995). We used 'genotype' as an individual permanent mark to estimate bias between models accounting/not accounting for mark loss and recycling, and suggested recommendations for future studies. Similar to single state CJS models, we predicted that the MSCJS model would potentially be subject to underestimation of survival and overestimation of transitions in case of tag loss and recycling (Nichols & Hines, 1993). As transition probability is conditional on survival and detection on state in our MSCJS model, we expect errors in estimates to propagate to model parameters in different ways according to state

transition rate. We then hypothesised that posterior distributions of parameters are likely to be biased even in case of low survival and recapture rate.

2 Material and method

2.1 Data simulation

To quantify the potential bias induced by mark loss on parameter estimates in the MSCJS framework, we defined several scenarios corresponding to realistic situations inspired from the literature (Supporting Information 1). We considered a study period of 10 years, during which an individual can change state among 4 states (A, B, C, D), state 'D' being an absorbing state (without possibility to change when it is reached, e.g. permanent emigration), see Fig. 1.b. We considered two age classes: (1) individuals less than 1-year-old (hereafter ‘juveniles’); (2) individuals older than 1 year (hereafter ‘adults’). Sampling took place every year and state assignment can only be made one year after birth at the earliest. Consequently, all individuals were adults when detected the second time. When individuals are in state D they cannot be captured (nor marked), only resighted. We allowed stochastic annual variations in survival rate for each age class.

To set the most common values for survival parameters, we surveyed 700 species in six vertebrate classes- Actinopterygii, Chondrichthyes, Amphibia, Aves, Reptilia, and Mammalia. We used the existing database for tetrapods (Conde et al., 2019) and also compiled data from the literature for fish and bat species (Supporting Information 1, Table S1). The distribution of survival rates encompasses a large range of values (Supporting Information 1, Fig. S1). We observed a positive correlation between adult and juvenile survival for a subset of 143 species in which both rates were available (Supporting Information 1, Fig. S2). Based on these surveys, we defined 4 scenarios of study: (1) long-lived species with high detection; (2) long-lived species with low detection; (3) short-lived species with low detection; (4) short-lived species with high detection. Values of parameter simulated are reported in Table 1. and Fig 1.b and the complete simulation steps of the

MSCJS model between two-time intervals are displayed in Fig. 1.a. We considered two common ways of re-encountering individuals after marking: (1) recapture when individuals are physically caught again; (2) resighting, which is a passive way to detect individuals without handling them (e.g. using colour or alphanumeric rings or PIT-tags). This approach is motivated by the fact that in most studies, the probability of resighting is typically higher than the probability of recapture, therefore they can be differently affected by estimation biases. To investigate the effect of mark loss on the estimates of state transition probabilities, we simulated data using different transition probabilities between states (Fig. 1.b). Irrespective of their age, females were allowed to transition at each occasion between state A, B and C, at a permanent rate depending on the state they were before transition, but not in state D. Only juvenile males were able to transition to the D state, in different proportions depending on their initial state, while adult male never changed their state (Fig. 1.b). This sexual dissymmetry in transition is common in mammals (and other taxa) and allows us for example to distinguish permanent emigration (absorbing state) from other movements. At the first occasion, individuals in state A, B and C were composed of 40 juveniles (sex ratio 1:1) and 60 adults (80% females, 20% males); there was no individual in state D. On each subsequent occasion, 40 juveniles and 5 adults were marked in each state (A, B,C) except in state D, where it is not possible to recapture individuals but only to observe them.

As mark shedding is often dependant on time since marking and occurs most frequently shortly after marking in many species (in our case study; Fabrizio et al., 1999; Fokidis et al., 2006), for each scenario, we investigated a range of mark loss rates commonly reported in the literature (Supported Information 1, Table S2). We simulated three mark loss probabilities (0.05, 0.25, 0.4) during the first year after marking and a constant 0.05 rate thereafter, which generated a diversity of cases of mark loss and recycled individuals (Supported Information 2,Fig. S3). We simulated fifty datasets for each of the 12 combination of parameters, and ran two MSCJS models: one with recycled individuals, which mimicked the situation where it was not possible to identify individuals

which have lost their mark; the second, accounting for mark loss, which mimicked situations where a permanent mark was used to identify individuals (i.e. no recycling possible). In this last model we only added to the previous model retention of mark as a Bernoulli process:

$$R_{i,t} \sim \begin{cases} Bernoulli(pr_1), \text{ if } i \text{ was juvenile and marked at } t-1, \\ Bernoulli(pr_2), \text{ if } i \text{ was adult and marked at } t-1, \\ Bernoulli(pr_3), \text{ if } i \text{ was adult and the mark was already present at } t-1, \\ 0, \text{ if } i \text{ had no mark at } t-1 \text{ and was not marked at } t-1, \end{cases} \quad \text{(eqn 1)}$$

with $R_{i,t}$ the retention rate of individual *i* at time *t* and pr_j the probability of retention *j* (*j* in {1,2,3}) that depend both of the age of the individual *i* and the status of the mark at time *t-1*. In total, 1,200 simulations were performed (Supported Information 2, Fig. S1). The computational codes for a fully reproducible example dataset are provided in the Supporting Information 2.

2.2 Data analysis

In the 600 simulated dataset, taking into account mark loss (without recycling), we identified individuals who lost their mark prior to running the model, and fitted a Bayesian MSCJS model, with priors and codes detailed in Supporting Information 2 (ModelA.jags). In the 600 simulated dataset, not accounting for tag loss, as individuals who lost their mark cannot be identified (i.e. recycled), we simply cut life histories each time mark loss occurred and added a new line into the dataset as a recycled individual. We then fitted a similar Bayesian MSCJS model, but removed the part concerning mark loss estimation (Supporting Information 2, ModelW.jags). The model codes and the initial values used for parameter estimation are provided in Supporting Information 2. All prior distributions used for the model without recycling were the same as those used for the model with recycled individuals.

2.3 Real data analyses

To illustrate the simulations, we analysed an empirical dataset from a 10-year study of CMR data on the Greater-mouse eared bat (*Myotis myotis*) in Brittany (France; 2010-2019). A total of 2,561

individuals were marked in 5 roosts: La Roche Bernard (47˚31’N, 2˚18’W), Férel (47˚28’N, 2˚20’W), Noyal-Muzillac (47˚35’N, 2˚27’W), Béganne (47˚35’N, 2˚14’W) and Limerzel (47˚38’N, 2˚21’W). The bats were individually tagged using PIT tags, ID-100C (Troven®), with a unique 10-digit code. These small passive tags (2.12x11mm, 0.1gr) allowed identification from passive readers. All individuals caught in roosts without PIT-tags were systematically tagged, which included both, individuals who lost their tag and those which were never tagged before, and genotyped as a second and permanent marking method. Genotypes were established from DNA extracted from wing biopsies from all individuals tagged and from all males untagged caught during swarming surveys (n=4,258 samples; details in Supporting Information 3, Fig. S1), as male capture probability at roosts after birth was extremely low. A total of 16 microsatellite markers optimised for *Myotis myotis* were used to establish individual genotypes (Foley et al., 2020). To minimize genotyping errors, we analysed, when available, 2 different samples per individual and all samples were genotyped and scored twice by two different people. We also performed genetic profile comparisons to detect errors (Frantz et al., 2003; Puechmaille & Petit, 2007). We hypothesised that the error rate of genotypes was low enough to be negligible and did not include this source of uncertainty in the models. We also checked each winter for the presence of lost tags on the floor of the roosts, which allowed us to identify, at least in part (66% compared to the genotype), the individuals that lost their tag, with the rest of losses having occurred outside of the roosts. Most of these tags were lost during the first year (Supporting Information 3, Fig. S2), which is confirmed by the absence of their records from passive reading detectors. In total, 252 individuals out of 2,561 (~10%) were identified as having lost their tag at least once. From those individuals, 94 individuals were recaptured and retagged a second time and three retagged a third time. As retagging occurred during the last capture occasion for 13 individuals, ignoring tag loss led to the recycling of 81 individuals in total among the 94. To analyse these data, we fitted a multisite model (a special case of multi-state models when states are sites and transition are movement between sites.), similar to

the MSCJS model used for simulated data (Supporting Information 3). Emigration from the five studied subpopulations was assessed using capture and resighting data obtained between capture occasions in swarming and wintering sites. We accounted for individual heterogeneity, including a random effect in the estimation of survival probability, a widespread phenomenon in free populations and a known source of bias in CMR models. (Gimenez et al., 2018).

We defined eight possible detection states which allowed us to estimate separately, capture and resighting probabilities (see Supporting Information 3, Table S1). As empirical data suggested the possible movement of individuals between all subpopulations and outside, we did not constrain transition between subpopulations except for movement of juveniles from D toward A, B, C which was not possible and therefore set to 0. In this study, we also tested the effect of surgical adhesive (Vetbond®) after PIT-tag injection, in order to assess tag-loss reduction in comparison with self-healing (Lebl & Ruf, 2010; van Harten et al., 2020). In this model, tag retention probabilities were modelled like in the simulation study (eqn. 1), by accounting for time since marking (two discrete classes: first year or subsequent years), individual age class (juvenile or adult), and the use of surgical adhesive (yes or no) As per the simulated datasets, two models were run, a first one taking into consideration tag loss and recycling, and a second model ignoring this information.

2.4 Computation details

We used JAGS (Plummer, 2003) with the jagsUI package (Kellner, 2016) from R 3.6.0 (R Core Team, 2019) for analyses of simulated and empirical datasets. We used four MCMC chains with 150,000 iterations each and drew samples from posterior distributions after discarding the first 50,000 iterations (burn-in). We retained every twentieth iteration generating 20,000 samples from the posterior distribution for each parameter. Chain convergence was assessed with the Gelman-Rubin statistic (Brooks & Gelman, 1998). Among 1,200 simulations, some showed R-hat values > 1.1, indicating a convergence failure. Converge problems concerned few parameters and the corresponding R-hat values were still low. To avoid prohibitively long computing time, we did not

attempt to increase the number of iterations to achieve the complete convergence of MCMC chains for these parameters in the simulations concerned. Our results are based on 50 simulated datasets per scenario, and it is expected that lack of convergence for these few parameters has no substantial influence on our results.

For assessing bias in parameter estimates when mark loss or recycling is not accounted for, we computed the Earth Mover Distance (EMD), using the EMD-L_1 algorithm (Ling & Okada, 2007), a distance function that quantifies the difference between two distributions. This metric measures the minimum cost of turning, point by point, a distribution into another. We also estimated a ROPE (Region Of Practical Equivalence, Kruschke, 2018) for each scenario to assess the degree of difference between distribution represented by the EMD metric. To define this ROPE for each scenario, we randomly built 1,000 pairs of models from the 50 simulations and calculated the associated 1,000 EMDs from the posterior distributions of the estimated parameters (Supporting Information 2, Fig. S43). The obtained distributions of EMD represented variations expected for inferences obtained from simulations initiated with the same parameter values. The ROPE was then defined between 0 and the upper value of the 80% highest posterior density interval (hdi) from the distribution of these EMD. Finally, the proportion of EMD for each simulated case outside the ROPE was computed, giving a direct indication of bias, the higher this proportion, the higher the bias. Comparisons of EMD between the models that did and did not account for tag loss and recycling to their respective ROPE is a way to illustrate cases in which not accounting for tag loss leads to estimates that substantially differ from estimates obtained when accounting for tag loss. However, it is not a way to estimate absolute bias. This is not a problem when the model that accounts for tag loss correctly recovers simulated parameter values, which was the case for most parameters in most situations.

3 Results

3.1 Simulation results

Mark loss and recycling increase in scenarios with higher survival, recapture and mark loss rate (Supported Information 2, Fig. S3). However, the estimates from the model accounting for mark loss and recycling did not show major departures from the simulated values in any scenario (Supporting Information 2, Fig. S3-S42). Irrespective of scenarios, little to no estimation bias appeared when tag loss was set to 0.05, only resighting probability showed some underestimations. The number of parameters whose estimates were biased increased with increasing mark loss rate, but the extent was scenario-dependent (Fig. 2 & 3). In particular, Adult survival showed substantial underestimation (Fig. 2.b) in scenario 1 for all state but “D”, but bias decreased with time (Supporting Information 2, Fig. S7-S14). For scenario 4, moderate underestimates in adult survival were also observed during the first study year. Juvenile survival and capture probabilities were less biased, nevertheless moderate underestimations occurred for high mark loss rate (Supporting Information 2, Fig. S11-S14 and S23-S26).

Resighting probability showed substantial bias, with underestimates mainly in state A and C, for all scenarios and mark loss rates (Fig. 3.a). A large percentage of the transition probabilities estimates were also biased when mark loss and recycling were ignored (Fig. 3.b-e), with in general an underestimates of the probability to remain in the same state and, as a corollary, an overestimates of the probability of changing of state (Supporting Information 2, Fig. S27-S37). Overestimations occurred in juvenile males except from state C, where transition rate was the highest (0.9). For females, the same pattern was observed in state A and B for which transition rates were low. On the contrary, for state transition from state C to B (set high = 0.4), we observed an underestimation of the transition probability and an overestimation of the probability to remain in state C with scenarios set with low detection rates (scenario 2 and 3, Supporting Information 2, Fig. S36-S37).

3.2 Bat metapopulation

Most of the estimated parameters (survival, capture, resighting and state transition probabilities) show both negative and positive biases, with no clear pattern, but no substantial bias appeared in the model not accounting for tag loss and recycling compared to the model taking them into account (Supporting Information 3, Fig. S4-S11). Larger biases appeared in survival estimates, with the estimated median survival difference between the two models reaching values greater than 0.2 (Supplementary Information 3, Fig. S4-S5), which could profoundly affect the results of studies interested in evaluating the effect of annual covariates (e.g., climate variables) on survival probability. The estimated tag loss probability was high for juveniles but substantially reduced by the use of surgical glue (Fig. 4), decreasing by one third from 0.28 (90%hdi [0.23,0.33]) to 0.19 (90%hdi [0.16,0.22]). However, in adults the use of surgical glue did not affect tag loss rate, with an overlap of 69% of the probability distributions. The adult tag loss rate was around 0.1 which is two times less than in juveniles when surgical glue was used. Considering the period following one-year post-tagging, the probability of tag loss when surgical glue was used is higher (median 0.03, 90% hdi [0.02, 0.04]) versus not used (median 0.02, 90%hdi [0.01, 0.02]). This difference is in fact an artefact due to a lack of search for lost tags on the ground of the colonies in the first year of the study (Supplementary Information 3, part 3 and Fig. S12). Other parameter estimates can be found in Supporting Information 3, part 2.6.

4 Discussion

We used simulations to assess the effect of mark loss and recycled individuals on parameter estimates in the MSCJS model, where capture and survival probabilities vary over time, survival also varies among age classes and mark loss processes depend on time since marking. We showed that not only survival, but capture, resighting and state transition probabilities estimates can be substantially affected by this violation of CMR model assumptions. Survival is mainly

underestimated in cases where capture and detection is high, this trend is accentuated when survival is also high, which moderates previous studies suggesting that biases mainly occur in species with both high survival rates, catchability and mark loss (Diefenbach & Alt, 1998). Our simulation results confirmed that inaccuracy of model estimates is positively linked to the rate of mark loss, but can also occur when tag loss rate is low (5%) and can be independent of survival and capture rates. Indeed, in datasets with few recycled individuals, i.e. with low survival and capture rates, transition and resighting probabilities can be severely biased if mark loss is high. This suggests that results from studies where survival and capture are low should also be interpreted with caution if mark loss is suspected but not taken into consideration. Severity of bias can also vary over time, with bias in survival decreasing with time as in our simulated datasets. This is partly due to the mark loss pattern we chose and stresses the fact that, even in studies conducted over short periods, parameters can be substantially biased. In cases where mark loss increases with time since marking, we would expect an increase of bias with time.

The simulation and the empirical study results together highlight how the complexity and interdependence of parameters can compound or counteract estimation biases in the absence of mark loss modelling. While the simulations showed some global rules on the direction of the biases, the real example showed instead how unexpected the bias pattern can be. Although we tried to cover in our simulation demographic variations classically observed across vertebrates, they have not been carried out under the immense range of parameters combinations that can be encountered. Most study systems and monitoring methods have their own specificities and *a priori* prediction of bias without simulating them can be misleading. The propagation of uncertainty in parameter estimates due to mark loss is still challenging to predict and increases with system complexity. Therefore, prior to planning a CMR study, we advocate that researchers/managers run simulations to evaluate in which conditions (i.e. under which parameters combination) their study would provide reliable estimates of the parameters of interest (e.g. demographic, state transition).

Preliminary studies with multiple marks could also be considered when possible (Smout et al., 2011b). This would allow CMR study design to be optimised prior to the study being conducted and hence limit biases from the onset.

MSCJS models have been partly developed to estimate movement between sites, recruitment, dispersion, temporary or permanent emigration (Lebreton et al., 2003, 2009; Schaub et al., 2004). Our simulation results suggest that state transition probabilities are sensitive to mark loss, even at low rates, e.g. the probability to stay in the same state (philopatry) or to change state showed both under and overestimations. These parameters are often of central interest in many studies to answer ecological and demographic questions and are used for management and conservation purposes (Cam et al., 2004; Horton et al., 2011). Although the loss of marks is regularly reported for a wide variety of tags and taxa, it is only marginally considered in studies interested in estimates of population dynamics parameters (Nelson et al., 1980; Ostrand et al., 2012; Smout et al., 2011b; Tavecchia et al., 2012). Most model developments to account for mark loss have focussed on the Jolly-Seber model (Jolly, 1965; G. Seber, 1965) for abundance estimates, where mark loss and recycling are prone to generate serious biases (Malcolm-White et al., 2020). The loss of the mark remains largely unconsidered despite an increasing use of MSCJS models in ecology, demography, management and conservation (Huntsman et al., 2020; Melnychuk et al., 2017). In light of our study, we recommend the use of permanent or double temporary marks, where dependence in loss is taken into account (Laake et al., 2014; McMahon & White, 2009), as any analysis of CMR data is potentially affected by this violation of model assumption (Riecke et al., 2019).

Despite the fact that PIT tags are suitable in an increasing number of studies and allow the collection of data without physically re-capturing individuals, our case study highlights the importance of a second marking method to estimate potential bias in demographic rates. Tag loss has long been known in small mammal species, in particular those that fly or glide (Freeland & Fry,

1995). Here we confirmed that PIT-tag shedding can be reduced in the short term by the use of surgical adhesive (Lebl & Ruf, 2010; van Harten et al., 2020).

As illustrated, surgical adhesive is not sufficient to reduce tag loss to zero, and the use of a permanent mark (e.g. genotype) is required, for all or part of the population studied (Laake et al., 2014). Similar situations, where permanent marks should be considered, arise when marks deteriorate and become unreadable, equivalent to an increase of mark loss with time, like neck collars or ear tags (Conn et al., 2004; Diefenbach & Alt, 1998). In this case, we expect a decrease in accuracy of model parameter estimates for the duration of the study, and further supports the use of permanent marks for CMR studies.

Mark loss is typically not considered from ecological and management perspectives except when researchers are interested in understanding factors influencing mark failures or in improving their marking methods. Our results highlight the need to assess the effect of mark loss each time mark failure is suspected, to avoid spurious conclusions about the dynamics of their studied species. In our experience and according to the literature, PIT-tags are prone to being shed regardless of the studied taxa, often in the short but sometimes in the long term. Mark loss should therefore be carefully considered in all CMR analyses and possibly also in other studies using similar datasets, and should be explicitly modelled when necessary for more accurate estimations of population dynamics.

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Author contribution

F.T. designed the project with the other co-authors. E.C.T., F.T. and BV acquired the funding. E.C.T., E.J.P., S.J.P. and E.C. supervised the project. E.C.T., F.T., E.J.P., S.J.P and BV supervised the fieldwork. E.C.T., E.J.P., F.T. and S.J.P. collected samples. S.J.P. & F.T. supervised the microsatellite genotyping. C.S. generated the genotypes. F.T. and E.C. developed the R scripts for simulating and analysing data with help of E.J.P. and S.J.P. F.T. led the writing of the manuscript and all authors contributed to manuscript revisions and gave final approval for publication.

Data accessibility

R scripts for simulating the data, and analysing the data with JAGS, will be archived at the Dryad Digital Repository.

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Parameter	Definition	Value	
		Long-live	Short-live
$\phi_{ad.}$	Adultes survival in state A, B, C	∼0.92 [logit(N(2.5,0.3))]	∼0.62 [logit(N(2.5,0.3)-0.3))]
$\phi_{ad.}$	Adultes survival in state D	∼0.81 [logit(N(1.5,0.3))]	∼0.51 [logit(N(1.5,0.3)-0.3))]
$\phi_{juv.}$	Juveniles survival in state A, B, C	∼0.55 [logit(N(0.2,0.3))]	∼0.35 [logit(N(0.2,0.3)-0.2))]
		High	Low
pc_A	Capture probability in state A	∼0.65 [U(0.6-0.7)]	∼0.15 [U(0.6-0.7)-0.5]
pc_B	Capture probability in state B	∼0.75 [U(0.7-0.8)]	∼0.25 [U(0.7-0.8)-0.5]
pc_C	Capture probability in state C	∼0.7 [U(0.65-0.75)]	∼0.2 [U(0.65-0.75)-0.5]
pc_D	Capture probability in state D	0	0
p_A	Resighting probability in state A	0.85	0.35
p_B	Resighting probability in state B	0.95	0.45
p_C	Resighting probability in state C	0.9	0.4
p_D	Resighting probability in state D	0.7	0.2

Table1: Parameter values used to simulate the 4 scenarios. For random values generated, the corresponding distribution is indicated in brackets (N=Normal distribution; U=Univariate distribution). For transition values between states see Fig. 1.b.

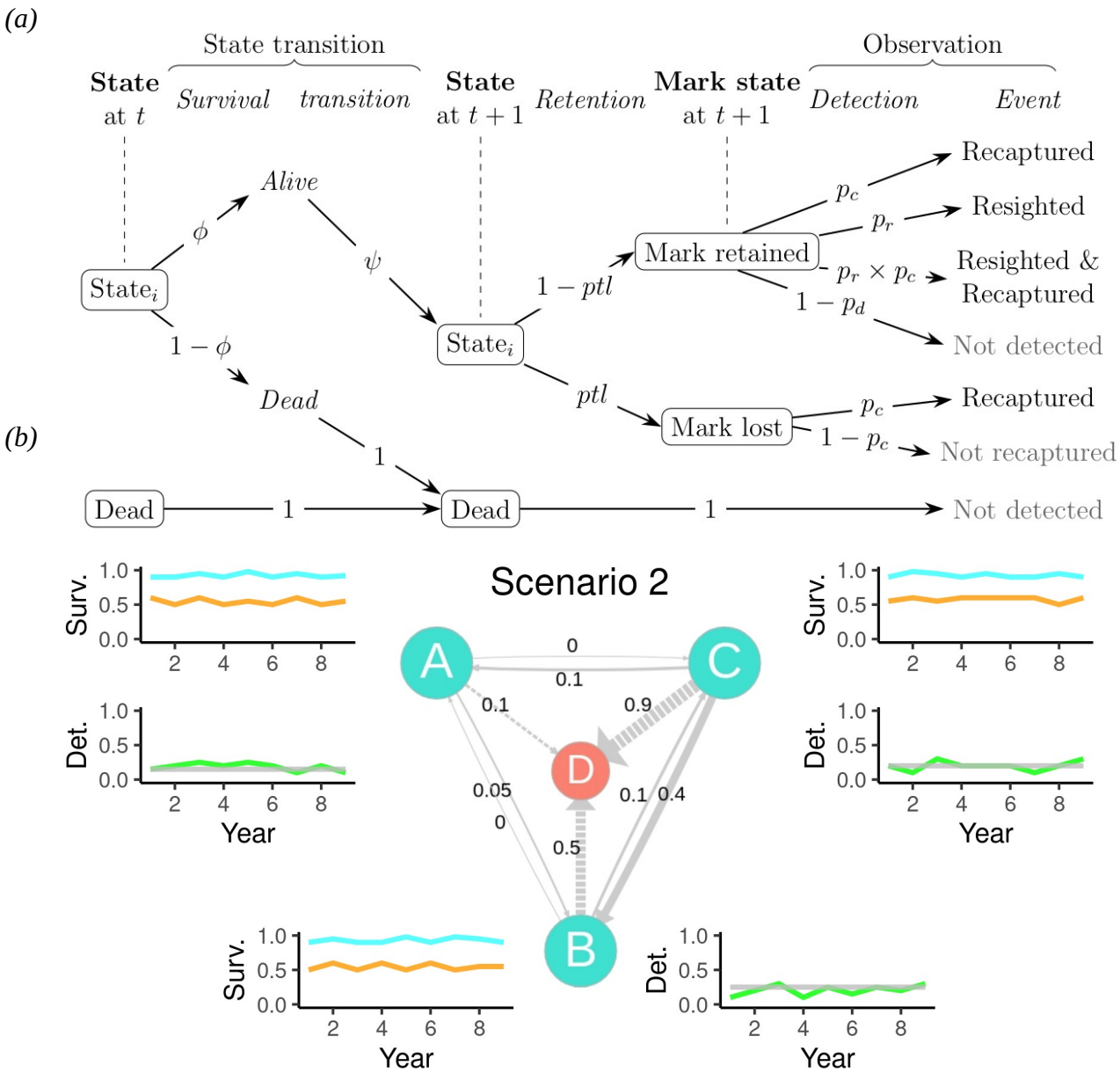

Figure 1: Multistate capture-mark-recapture model. Panel (a) illustrate the fate of individuals captured and realised at t or dead at t. From t to t+1 dead individuals stay dead and cannot be detected (absorbing sate), while released individuals can change state. Arrows indicate the possible paths, first in the state-transition, second in the mark retention process and third in the observation steps. Indices on arrows indicate corresponding probabilities. ϕ is the survival probability (time- and state-dependant), ψ is the state transition indicated in panel (b) where plain arrows correspond to females' possible transitions and dotted arrows to males. ptl is the probability to lose the mark (dependent on age and time from marking). p_c is the capture probability (time- and state-dependant), p_r is the resighting probability (state-dependant), and the detection probability equal $(1-p_c)(1-p_r)$. Only juvenile males can reach state D and can be re-observed but not recaptured. On panel (b), simulated survival (Surv.) and detection (Det.) rates were displayed for states A, B and C according to scenario 2 (long-lived species with low detection). Blue lines correspond to adult survival, orange line to juvenile survival, grey line to resighting probability and green line to capture probability.

407

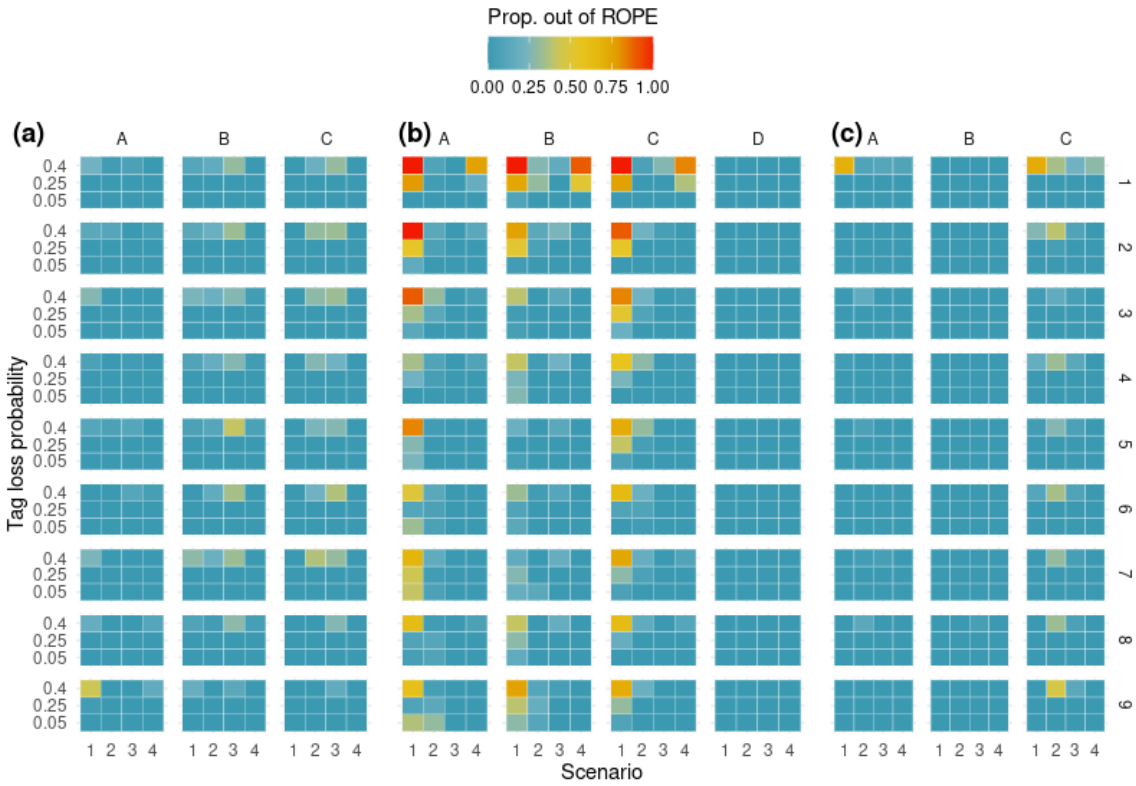

Figure 2: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between the model accounting for tag loss and recycling and the model ignoring them. Each tile represents annual (right axis) juvenile survival (a), adult survival (b) and capture probability (c) for each scenario and tag loss probabilities.

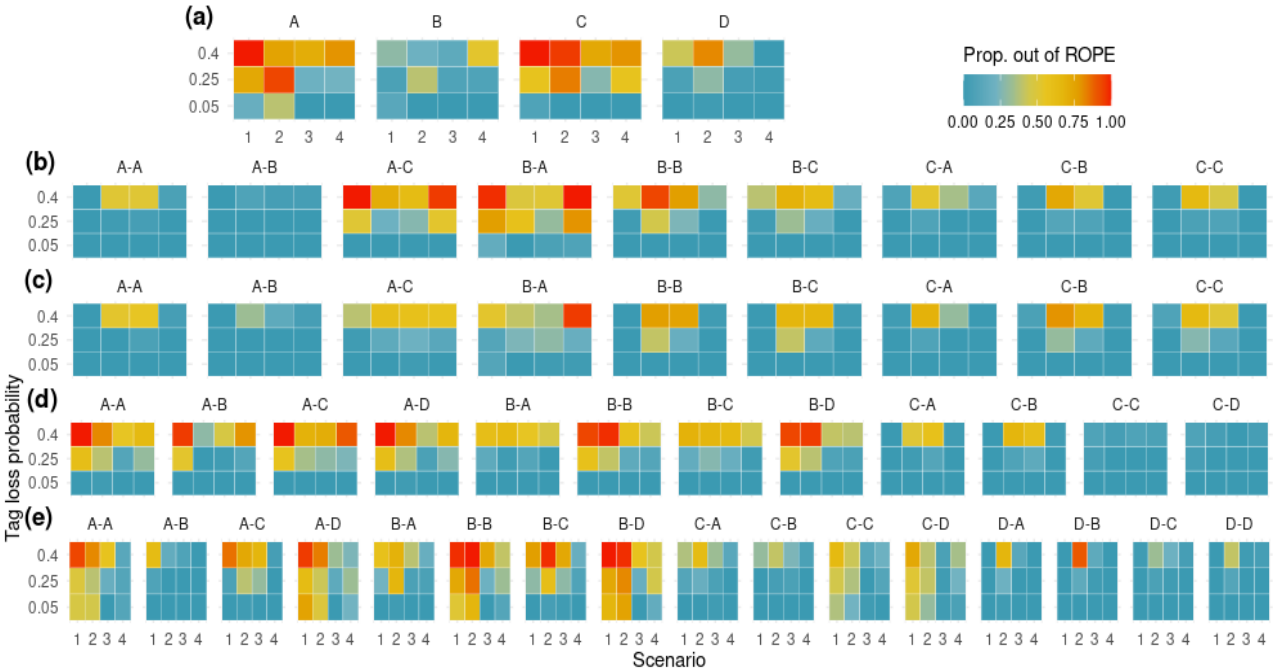

Figure 3: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between model accounting for tag loss and recycling and the model ignoring them for each simulated cases. Each tile represents resighting probability (a) and movement probabilities between subpopulations (direction, "from-to", are indicated above each tile-plot) of juvenile female (b), adult female (c), juvenile male (d) and adult male (e) for each scenario and tag loss probabilities.

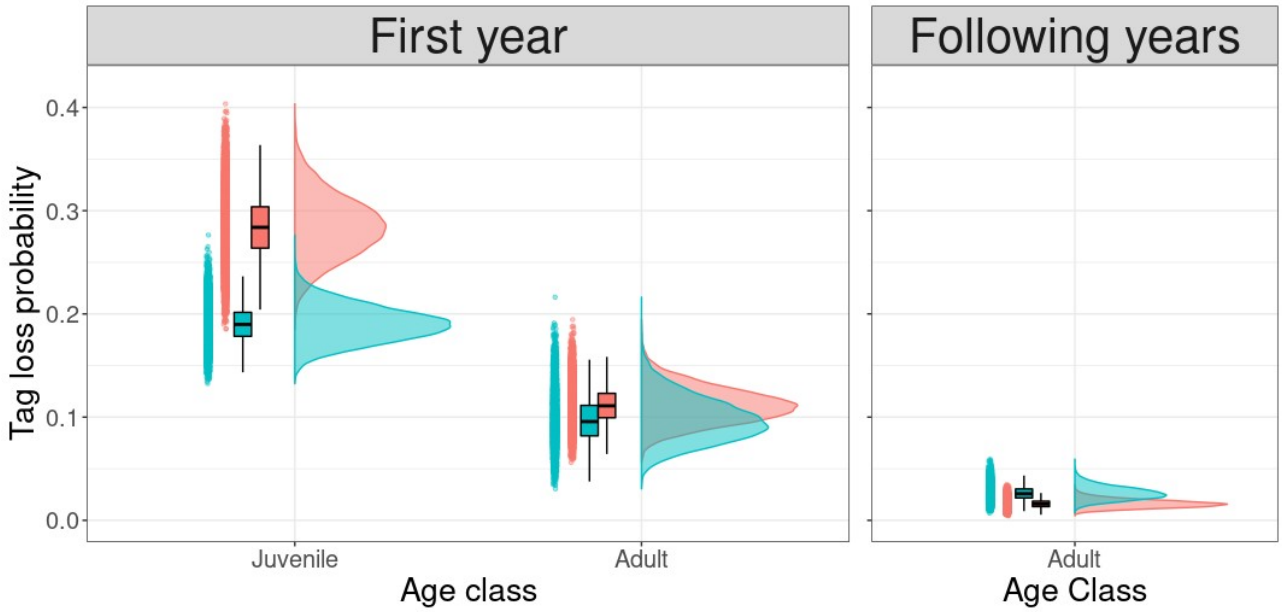

Figure 4: Posterior distribution of the tag loss probabilities according to age classes and time after marking in the Myotis myotis *dataset. Left panel correspond to tag shedding rate during the year following the tag injection and the right panel for the following years (constant in time). In blue, distribution if surgical adhesive was used after tag injection and in red, without surgical adhesive.*

444