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, multi-state models, with their flexibility for the analysis of complex study systems, have become popular in the ecological community. We have addressed here the issue of mark loss and the often associated recycling of remarked individuals, which remains to be further explored in the context of the increasing use of these models.

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, Arnason-Schwartz (AS), modelling 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 AS 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 population dynamics. If not possible, an alternative is to combine two independent types of temporary marks (e.g. PIT tags, bands).

5. Analysis of our empirical dataset on *Moytis myotis* bats has shown that tag loss is higher in juveniles than in adults during the first year after tagging. The tag loss rate can be reduced from 28% to 19% in juveniles by using surgical glue to close the injection hole, while it did not change the tag loss rate in adults (~10%). Main bias appeared in survival rate in our metapopulation system, with up to 20% of underestimation of survival rate if tag loss is not accounted for. Such a bias can lead to misinterpretation of population dynamics trends and wrongly influence conservation policies.

KEYWORDS

Arnason-Schwarz model, Bayesian, bats, capture-mark-recapture, mark retention, *Myotis myotis*, multi-state, surgical glue.

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 Supporting Information 1, Table S2). Mark loss has two consequences: (1) when mark shedding occurs it induces non-identifiability of these individuals (detection heterogeneity), which implies that they are considered either dead or out of the study area, despite being alive and present; (2) if these individuals are captured again, they will not be recognized and will be remarked as newly recruited individuals, known as “recycled” individuals (Malcolm-White et al., 2020). In open

population models, estimates of abundance in the Jolly-Seber (JS) model (Jolly, 1965; G. Seber, 1965) or of survival in the Cormac-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) can be affected by mark loss (Arnason & Mills, 1981). Many statistical tools have been developed to remove the confounding effect of mark loss in these models (Arnason & Mills, 1981; Cowen & Schwarz, 2006; Robson & Regier, 1966; G. A. F. Seber & Felton, 1981). However, the multi-state models that have now undergone substantial development (Lebreton et al., 2009) have not received such attention and the effect of mark loss on state transition has not been studied.

In multi-state models, if survival is state dependent, survival is the product of true survival and mark retention rate for individuals in a particular state (Lebreton et al., 1992; Lebreton et al., 2009). If the retention rate starts to drop below one without being considered in the model, while true survival remains constant, survival in a particular state is underestimated and becomes confounded with the probability of presence of the mark, even more if true survival is high, but it is not clear how state transitions are affected. 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 $\phi_1 q_2 \phi_2 p_3 \phi_3 p_4$. This probability product can be broken down as follows: the individual survive between t_1 and t_2 (ϕ_1) but was not captured in t_2 (q_2) and survive between t_2 and t_3 (ϕ_2) and was captured in t_3 (p_3) and finally survive between t_3 and t_4 (ϕ_3) and was captured in t_4 (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. Two things might have happened at t_2 when the individual was not detected: either it stayed in state 1 or it made a transition to state 2. This led us to introduce $\psi^{i,j}$ the transition probability from state i to state j (i and j in {1,2}), conditional on survival. The new encounter history is now the sum of two components to account for the two possible his histories “1122” or “1222”, respectively: $\phi_1^{(1)}\psi^{(1,1)}q_2^{(1)}\phi_2^{(2)}\psi^{(1,2)}p_3^{(2)}\phi_3^{(2)}\psi^{(2,2)}p_4^{(2)} + \phi_1^{(1)}\psi^{(1,2)}q_2^{(2)}\phi_2^{(2)}\psi^{(2,2)}p_3^{(2)}\phi_3^{(2)}\psi^{(2,2)}p_4^{(2)}$, with indices for state-

specific parameters noted in parentheses. But, if this individual loses its mark after its first capture and is remarked when recaptured at t_3 and not recognized, 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). 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 softwares (e.g. Mark (White & Burnham, 1999), WinBUGS (Lunn et al., 2000), JAGS (Plummer, 2003), E-SURGE (Choquet, et al., 2009), MultiBUGS (Goudie et al., 2020), NIMBLE (de Valpine et al., 2017), STAN (STAN Development Team, 2022)). 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 (Seber & Schofield, 2019).

To address this gap in knowledge, we used simulation-based Arnason-Schwartz (AS) model approaches (Arnason, 1972, 1973; Schwarz et al., 1993) to investigate the impact of mark loss on estimates of model parameters within a Bayesian framework. Given the increasing use of such multi-states 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 analyses. The AS model shares assumptions with the CJS model, particularly in relation to mark loss, but it assumes in addition that states are recorded without error. Similarly to CJS model, we predicted that the AS model would potentially be subject to underestimation of survival but also of transitions probabilities in case of tag loss and recycling (Nichols & Hines, 1993). As transition probability is conditional on survival and detection on state in our AS model, we expected errors in estimates to propagate to model parameters in different ways according to state transition rate.

To illustrate our approach with an empirical example, we used our decade-long mark recapture dataset 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.

2 Material and method

To quantify the potential bias induced by mark loss on parameter estimates in the AS framework, we defined several scenarios corresponding to representative situations inspired from the compilation of data from an existing database for tetrapods, the Demographic Species Knowledge Index (Conde et al., 2019), and data from the literature for fish and bat species (Fig. 1, Supporting Information 1, Table S1). We limited the compilation of these survival data to published CMR

studies or data from controlled conditions, i.e. marked individuals of known fate (e.g. in zoos). Among the 700 species considered in six vertebrate classes: Actinopterygii, Chondrichthyes, Amphibia, Aves, Reptilia and Mammalia, the distribution of survival rates encompasses a large range of values (Fig. 1). The relationship between adult and juvenile survival, available for 143 species (Supporting Information 1, Fig. S1), shows that low adult survival is associated with low juvenile survival, whereas high adult survival can be associated with a wide range of juvenile survival. We decided to select values towards the extremes to limit the number of possible scenarios to explore. Two hypothetical populations, in which juvenile survival differed from adult survival, were then considered: the long-lived species with high survival rate in both age classes, (e.g. in large mammals) and the short-lived species with low survival rate in both age classes, (e.g. in amphibians). For each population, we explored cases where detection was high or low and tested for each case three different mark loss rates selected from the relevant literature (Supported Information 1, Table S2). We first present the generation of our simulated scenarios and second the two different models used to analyse these data: one model not accounting for mark loss; and one accounting for it, used as a reference model that better fits the data. Third, we describe the metrics used to assess the potential bias in the parameter estimates when not accounting for mark loss in the AS framework.

2.1 Data generation

For each scenario, we simulated data on a study period of 10 capture occasions (e.g. years), and between occasions the individuals can change state among 5 possible states : “A”, “B”, “C”, “D” and death. As death, state “D” was set as an absorbing state, without possibility to change when it is reached, which illustrated for example permanent emigration. 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. This hypothetical system can be seen as 3 breeding sites (“A”, “B”, ”C”) where capture and resighting occur each year, and a surrounding area (“D”), where only resighting is possible. 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. For each simulated scenario, all juveniles captured at one particular occasion are considered adult at the subsequent occasion. All scenarios shared the same data generation steps (Fig. 2). We began to simulate survival of individual *i* at occasion *t* with Bernoulli distribution:

$$A_{i,t+1} \sim \begin{cases} Bernouili(A_{i,t}\phi_{i,t}), \text{if } A_{i,t} = 1, \\ 0, \text{if } A_{i,t} = 0 \end{cases} \tag{1}$$

where $A_{i,t}$ = 1 if the individual *i* is alive at *t* or 0 if not, and $\Phi_{i,t}$ was a state, time and age specific survival probability. We allowed stochastic variations in survival rate for each age class and occasion. If the individual survived, the state transition was simulated with Categorical distribution:

$$s_{i,t} \sim \begin{cases} Categorical(\psi_{i,t}), \text{ if } A_{i,t} = 1, \\ dead, \text{ if } A_{i,t} = 0 \end{cases} \tag{2}$$

where $\psi_{i,t}$ was a state, sex and age specific transition probability. For all scenario, females, irrespective of their age, were allowed to transition at each occasion between state “A”, “B” and “C”, at a time constant rate depending on the state they were before transition, but not in state “D”. However, juvenile males were allowed to transition only to the “D” state, in different proportions depending on their initial state, while adult males never changed their state (Fig. 3 and Supported Information 2, section 1.2). After survival and transition, the mark loss/retention process was simulated with Bernoulli distribution:

$$ts_{i,t} \sim \begin{cases} Bernoulli(pr_{i,t}), \text{ if } ts_{i,t-1} = 1 \text{ and not capture at } t, \\ 1, \text{ if capture at } t \text{ (newly marked or recycled)}, \\ 0, \text{ if } ts_{i,t-1} = 0 \text{ and not capture at } t \end{cases} \tag{3}$$

with $ts_{i,t}$ a binary variable indicating the presence of the mark on individual *i* at occasion *t* and $pr_{i,t}$ an age and time from marking dependant probability of retention (see Supported Information 2, Fig. S2), which is the complement of mark loss probability *ptl* ($ptl_{i,t}$ = 1-$pr_{i,t}$).

Finally, the detection process was simulated with Categorical distribution:

$$z_{i,t} \sim \begin{cases} Categorical(pd_{i,t}), \text{ if } A_{i,t} = 1, \\ \text{not detected}, \text{ if } A_{i,t} = 0 \end{cases} \tag{4}$$

where $pd_{i,t}$ was a state specific detection probability (Supported Information 2, section 1.2). We considered two different and common ways of re-encountering individuals, physical capture, which allowed either recycling (re-mark) or mark checking, and resighting which is a passive detection, including only individuals that have retained their mark. 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. The probability of detection is conditioned by the retention of the mark and was divided into 7 categories:

$$pd_{i,t} = \begin{cases} pc_{i,t}(1 - ts_{i,t}p.r_{i,t}), \text{ if mark retained and caught in state "A","B" or "C"}, \\ (1 - pc_{i,t})ts_{i,t}p.r_{i,t}, \text{ if mark retained and resighted in state "A","B" or "C"}, \\ pc_{i,t}ts_{i,t}p.r_{i,t}, \text{ if mark retained and both caught and resighted in state "A","B" or "C"}, \\ pb, \text{ if mark retained and resighted in state "D"}, \\ 1 - pb, \text{ if mark retained and not resighted in state "D"}, \\ (1 - pc_{i,t})(1 - ts_{i,t}p.r_{i,t}), \text{ if undetected in state "A","B" or "C"}, \\ 0, \text{ if mark lost} \end{cases} \tag{5}$$

where $pc_{i,t}$ was a state specific capture probability, $p.r_{i,t}$ a state specific resighting probability and *pb* the detection probability in state "D".

Since we could expect more recycling when recapture rates is high and little recycling otherwise, we considered four scenarios (Table 1): (1) long-lived species with high detection rate; (2) long-

lived species with low detection rate; (3) short-lived species with low detection rate; (4) short-lived species with high detection rate. Values of parameter simulated are reported in Table 2. and Fig. 3. 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; Kremers, 1988; Nichols & Hines, 1993), 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, low (*ptl* = 0.05), medium (*ptl* = 0.25) and high (*ptl* = 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. S2-3). This process allowed the generation of datasets that took into account mark loss in the presence of a second permanent mark. To generate datasets in which mark loss was not accounted for (no second permanent mark), we created recycled individual with the life history corresponding to the portion of life after mark loss and replaced the original life history from mark loss with zeros. For exemple, a life history “1111” of an individual that lost its mark between occasion 2 and 3 and is newly remarked at occasion 3, became two new histories: (1) “1100”, the first part of life before mark loss; (2) “0011”, a second individual, in fact the same but not recognised in the absence of a permanent mark, considered as newly recruited. Using this data generation process, we simulated 2 x 50 datasets for each of the 12 combination of parameters (50 with and 50 without recycling), leading to a total of 1200 simulated datasets (Supported Information 2, Fig. S1). The computational codes for a fully reproducible example dataset are provided in the Supported Information 2.

2.2 Statistical models

As described, regardless of the scenario or parameter values used, two different datasets for which the permanent marking assumption is violated were simulated for each combination: one, where it is technically possible to identify individuals even after the loss of mark, thanks to a second permanent mark; the second, where recycling occurred due to absence of second permanent

marking (Supported Information 2, Fig. S3). We developed two AS models to analyse these data. *ModelA*, used for the first dataset, included the estimate of mark loss, while *ModelW*, for the second dataset, ignored mark loss (Supplementary Information 2).

To estimate the state, time and age dependant survival Φ for both model we used a Bernoulli distribution (see above eq. 1):

$$\begin{aligned} &p(A_{i,t+1}/A_{i,t}) \sim Bernoulli(A_{i,t}\phi_{i,t}), \\ &logit(\phi_{i,t}) = \alpha_{state_{i,t+1}} + \beta_{t+1} + \delta_{age_{i,t+1}} + \gamma_{state_{i,t+1},t+1,age_{i,t+1}} \end{aligned} \tag{6}$$

where $A_{i,t}$ is the life status of individual *i* at time *t* and coefficient α is a state effect, β a time effect, δ an age effect and γ a simultaneous effect of state, age and time. Transition and detection processes were estimated using the same distributions as described for data generation (see above eq. 2,4,5). The difference between the two models lied in the estimation of mark loss, which involved tracking the fate of marks (retained or lost) for each individual (*ModelA)*. Several combination of single, double, and permanent marks have been used in the past to estimate mark loss (Laake et al., 2014). In *ModelA*, we considered a single mark loss approach, while the second mark is permanent, which allowed to identify if the non permanent mark was lost or retained at each capture occasion and resighting was conditional on mark retention (Eqn. 5). Using a statespace approach we built directly mark retention process in the model. While it is possible to model presence-absence of marks as states with a transition matrix (McMahon & White, 2009), or as a hidden Markov process for unobserved individuals for which we have no information if mark was retained or lost (Laake et al., 2014), we simply modelled mark retention process using a Bernoulli distribution with $ts_{i,t}/ts_{i,t-1}$ ~ Bernoulli($pr_{i,t}$) if the individual was marked or retained its mark at t-1 ($ts_{i,t-1}$ = 1). Three retention probabilities (*pr*) were estimated as a function of age and time since marking:

$$pr = \begin{cases} pr_{juv.}, & \text{if marked when juvenile,} \\ pr_{adlt.,1}, & \text{at the first occasion after marking, if marked as an adult,} \\ pr_{adlt.,2}, & \text{for subsequent occasions (retained at list 2 occasions), if marked as an adult,} \end{cases} \tag{7}$$

When lost, a new mark was applied if the individual was recaptured, without change of identity in *modelA* contrary to *modelW,* where mark retention is not modelled and an individual that lost its mark was considered as newly recruited if recaptured. The priors used for each parameters are described in Supported Information 2 (section 1.6).

2.3 Application on a bats dataset

We used the simulations both to test general hypotheses about the effect of mark loss on multi-state model parameter estimates, but also to validate a parametrisation capable of estimating these parameters without bias. On this basis, we can accurately estimate the probability of mark loss in our own dataset, but also the relevance of using in the long term a permanent mark, i.e. the appropriateness of using double-marking to avoid estimation bias (Juillet et al., 2011). Our empirical dataset consisted of 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 maternity 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 Passive Integrated Transponders (PIT) tags, ID-100C (Troven®), with a unique 10-digit code. These small 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 (Winiarski & McGarigal, 2016). We also checked each winter for the presence of lost tags on the floor of the maternity roosts, which allowed us to identify, at least in part (61.5% 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 took place during the last capture occasion for 13 individuals, ignoring tag loss for them led to the recycling of a total of 81 individuals out of 94. To analyse these data, we fitted a multisite model (where states are maternity roost and transition are movement between these sites), similar to the AS model used for simulated data (Supporting Information 3). We defined two age classes for survival, juveniles (individuals in their first year of life) and adults (individuals older than one year). In order to explore departures from the AS model assumptions, we performed goodness-of-fit tests on life history of the adult cohort, using R2ucare (Gimenez et al., 2018), an R package based on U-CARE (Choquet et al., 2009). Tests for transience and for memory showed minor overdispersion ($\hat{c}_{3G.SR}$=1.82 and $\hat{c}_{WBWA}$ = 1.96 respectively). It was not possible to perform the other goodness-of-fit tests because the individual contingency tables had insufficient data to provide statistical values. We then retained our two-age class structure for survival modelling. Unmeasured individual survival heterogeneity was also modelled by including a normally distributed random effect in the estimation of survival probability, as other covariates do not capture the relevant variation. Indeed, individual heterogeneity plays a key role in population dynamics and evolution, and it is ubiquitous in wild population (Gimenez et al., 2018). Emigration from the five studied

subpopulations was assessed using capture and resighting data obtained between capture occasions at swarming and wintering sites.

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 outside the maternity roosts which was not possible (there was no tagging outside the 5 roosts) and therefore set to 0 (see Supporting Information 3, Fig. S3). 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 similarly to equation 7, by accounting for time since marking (two discrete classes: first year or subsequent years), individual age class (juvenile or adult), but also use of surgical adhesive (yes or no). As per the simulated datasets, two models were run on two datasets, a first one allowing tag loss estimation thanks to the genotyping (second permanent mark), and a second model ignoring this information on a transformed dataset including recycled individuals (following the same process as simulated data).

2.4 Estimation procedures and assessments

Despite a frequentist approach was possible for simulated data analyses (Lebreton et al., 2009), we chose a Bayesian approach to be consistent with the analysis of empirical data where these methods are more flexible in accounting for individual heterogeneity in survival (Gimenez, et al., 2018). Simulated and empirical data were analysed with JAGS (Kruschke, 2014; Plummer, 2003) through the jagsUI package (Kellner, 2016) from R 3.6.0 (R Core Team, 2019). We used four Monte Carlo Markov chains (MCMC) 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 denoted R-hat (Brooks & Gelman, 1998). Among the 1,200 simulations, some parameters showed R-hat values > 1.05, indicating convergence failure. Less than 0.4% of the estimated parameters for the model accounting for mark loss failed to converge (Supporting Information 2, Table S1), in particular coefficient γ (combined effect of state, time and age on survival probability) and $\gamma.c$ (combined effect of state and time on detection probability). The mean R-hat values of these parameters was less than 1.2 (Supporting Information 2, Fig. S4). For models not accounting for mark loss, 1.3% of the estimated parameters did not converge (Supporting Information 2, Table S2), in particular for scenario where either detection or both detection and survival were low (respectively scenario 2 and 3) and mark loss probability was set to 0.25 or 0.4. Again, in most case, parameters that failed to converge showed a mean R-hat value less than 1.2, only a few exceeded 1.5 (Supporting Information 2, Fig. S5). Of all the simulations, no convergence failures concerned the probability of mark loss. 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 was assumed 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 (for more details see Supporting Information 2, Fig. S76). 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. We also assessed parameter bias as the difference between the median of the posterior distribution and the true value simulated (median – truth). With the empirical data, the median of the posterior distribution of parameters from the model accounting for a secondary permanent mark was used as truth. Finally, precision (mean squared errors MSE = $bias^2$ + variance) of the parameter estimates was also calculated for the simulated data.

3 Results

3.1 Simulation results

The number of mark lost and individuals recycled increased in scenarios with higher survival, detection and mark loss rate (Supported Information 2, Fig. S3). As expected, for an equivalent rate of mark loss, the proportion of individuals recycled relative to the number of marks lost was higher when the recapture rate was high (i.e. in scenario 1 and 4). Irrespective of scenarios, no estimation bias appeared on demographic parameters when mark loss was set to 0.05 (Supporting Information 2, Fig. S28-S31). The number of parameters for which estimates were biased increased with the rate of mark loss, but the magnitude was not consistent across the simulated scenarios. In particular, some adult and juvenile survival showed substantial underestimation in scenario 1 (Fig. 4 & 5). The probability of remaining in the same state was also underestimated among juveniles, and therefore their probability of transitioning to another state was overestimated (Fig. 4 & 6). The resighting

probability was underestimated in all state but B (Fig. 4 & 6). The state transition biases were particularly high for transitions to absorbing states as it is the case in our simulations for juveniles who transit to the "D" state (Supporting Information 2, Fig. S57-S71). For simulations with a mark loss rate of 0.4, scenarios 1 and 4, that share both high recapture probabilities, showed underestimates of adult survival in the early years of the study only (Supporting Information 2, Fig. S21-S22 and S27). Juvenile survival was less biased, nevertheless moderate underestimations occurred for high mark loss rate in particular for state A and B in scenario 1 and 4 (Supporting Information 2, Fig. S21-S22 and S27). Lack of precision in the estimate of juvenile survival was also observed for model not accounting for tag loss when mark loss rate was high. Resighting probability showed substantial bias, with underestimates mainly in state “A” and “C” (Fig. 4 and 7.a), as well as lack of precision for all scenarios and mark loss rates (Supporting Information 2, Fig. S28-S49). However, recapture, our second component of detection, showed little bias except during the second capture occasion for state “A” and “C” in scenario 1 when mark loss rate was 0.25 and scenario 1 and 4 when mark loss rate was 0.4. This came along with a decrease in the precision of the latter parameter at high mark loss. A large percentage of the transition probabilities estimates were biased when mark loss and recycling were ignored (Fig. 6.b-e), with in general an underestimate of the probability to remain in the same state and, as a corollary, an overestimates of the probability of changing state, with a decrease in precision mainly at high mark loss rate (Supporting Information 2, Fig. S50-S71). Overestimations occurred in juvenile males except from state “C”, where transition rate to state “D” was the highest (0.9). For females, when mark loss was set at a high level, the same pattern was observed in states "A" and "B", from which states transitions were set at a low level. On the contrary, for 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. S67-S70).

3.2 Bat metapopulation

Most of the estimated parameters (survival, capture, resighting and state transition probabilities) showed both negative and positive biases, with no clear pattern (Fig. 7, Supporting Information 3, Fig. S4-S11). Larger biases were apparent in survival estimates, with underestimation of median survival reaching over 0.26 in juveniles (Fig. 7a) and 0.21 in adults (Fig. 7b). Emigration, i.e., movement outside ("Out") the maternity sites studied, was overestimated by an average of 0.05 throughout the study (Fig. 7b). The probability of recapture was overestimated and underestimated by up to 0.1, depending on occasion and roost (Fig. 7c). The estimated bias in the other parameters was small (Fig. 7 d and e). The estimated tag loss probability was high for juveniles but substantially reduced by the use of surgical glue (Fig. 8), decreasing by one third from 0.28 (90%hdi [0.23,0.33]) to 0.19 (90%hdi [0.16,0.22]). 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 may be in fact an artefact due to a lack of search for lost tags on the ground of the maternity roost 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

Mark loss as a violation of CMR model assumptions, has been the subject of numerous studies and model developments. Most work has focused on survival, birth or population size estimates in the framework of Jolly-Seber models (Arnason & Mills, 1981; Malcolm-White et al., 2020; Schwarz et al., 2012; Smout et al., 2011a), recovery models (Kremers, 1988; Robson & Regier, 1966), CJS models (Laake et al., 2014; Nelson et al., 1980), and integrated population model (Riecke et al.,

2019). However, for AS models, few developments have been proposed to account for mark loss (Besnard et al., 2007; Conn et al., 2004; Johnson et al., 2016), all used a similar approach, implicitly modelling mark status or using an adjustment factor (Nishizawa et al., 2018). Furthermore, we found no exploratory studies on the effect of mark loss in parameter estimates. Here, we fill this gap by exploring both the effect of mark loss and recycled individuals on parameter estimates using simulations, and by modelling the state of the mark (retained or lost) as an intendant Bernoulli process. In particular, this allow us to explore how mark loss can affect state transition of individual states when capture and survival probabilities varied over time, survival varied also among age classes and mark loss processes depended 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 are 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 the 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. In particular, the probability to stay in the same state is underestimated when transition from this state is low but become overestimated for high transition probabilities. Severity of bias can also vary over time, with bias in survival and recapture decreasing with time as in our simulated datasets. This is partly due to the mark loss pattern we chose, stressing 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 (not investigated here), we would expect an increase of bias with time.

The combination of the simulation and empirical study results 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 patterns can be. In our simulation, although we intended to cover demographic variations classically observed across vertebrates, they have not been carried out under the immense range of parameters combinations that can be encountered in nature. 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., 2011a). This would allow CMR study design to be optimised prior to the study being conducted and hence limit biases from the onset.

AS models have been preliminary developed to estimate movement between sites, recruitment, dispersal, 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 if transitions are movements) or to change state (e.g. emigration) 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 JS model for abundance estimates, where mark loss and recycling is prone to generate serious biases (Malcolm-White et al., 2020). The loss of the mark remains largely unconsidered despite an increasing use of AS 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, ideally independent in loss or where dependence in loss is taken into account (Laake et al., 2014; McMahon & White, 2009; Schwarz et al., 2012), 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 avoid potential bias in estimations of 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 in the short term can be reduced 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 additional data (e.g. evidence of tag loss) or 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. A recent study, that assess tag loss on Gould's wattled bats (*Chalinolobus gouldii*), over a relatively short period of 13-14 months, showed that tag shedding was low (2.7%) and generalised these results to all insectivorous bats (van Harten et al., 2020). Our study proves that this generalisation is partly wrong, and rather suggests that it is difficult to generalise such a conclusion and that the pattern of mark loss is highly species dependent, among other parameters. 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. 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., and S.J.P supervised the fieldwork. E.C.T., E.J.P., F.T. and S.J.P. collected samples. S.J.P. & F.T. supervised the microsatelite 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, are accessible on Zenodo (https://zenodo.org/record/6453953).

References

Acolas, M. L., Roussel, J. M., Lebel, J. M., & Bagliniere, J. L. (2007). Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile brown trout (*Salmo trutta*). *Fisheries Research*, *86*(2–3), 280–284. https://doi.org/10.1016/j.fishres.2007.05.011

Arnason, A. N. (1972). Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Population Ecology*, *13*(2), 97–113. https://doi.org/10.1007/BF02521971

Arnason, A. N. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology*, *15*(2), 1–8. https://doi.org/10.1007/BF02510705

Arnason, A. N., & Mills, K. H. (1981). Bias and Loss of Precision Due to Tag Loss in Jolly–Seber Estimates for Mark–Recapture Experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(9), 1077–1095. https://doi.org/10.1139/f81-148

Benkman, C. W., Colquitt, J. S., Gould, W. R., Fetz, T., Keenan, P. C., & Santisteban, L. (2005). Can Selection by an Ectoparasite Drive a Population of Red Crossbills from Its Adaptive Peak? *Evolution*, *59*(9), 2025–2032. https://doi.org/10.1111/j.0014-3820.2005.tb01071.x

Besnard, A., Piry, S., Berthier, K., Lebreton, J.-D., & Streiff, R. (2007). Modeling survival and mark loss in molting animals: Recapture, dead recoveries, and exuvia recoveries. *Ecology*, *88*(2), 289–295. https://doi.org/10.1890/05-0811

Brooks, S., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.2307/1390675

Cam, E. (2009). Contribution of Capture-Mark-Recapture Modeling to Studies of Evolution by Natural Selection. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.), *Modeling Demographic Processes In Marked Populations* (pp. 83–129). Springer US. https://doi.org/10.1007/978-0-387-78151-8_5

Cam, E., Monnat, J.-Y. M., & Royle, A. (2004). Dispersal and individual quality in a long lived species. *Oikos*, *106*(2), 386–398. https://doi.org/10.1111/j.0030-1299.2003.13097.x

Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., & Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography*, *32*(6), 1071–1074.

Choquet, R., Rouan, L., & Pradel, R. (2009). Program E-Surge: A Software Application for Fitting Multievent Models. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.), *Modeling Demographic Processes In Marked Populations* (Vol. 3, pp. 845–865). Springer US. https://doi.org/10.1007/978-0-387-78151-8_39

Conde, D. A., Staerk, J., Colchero, F., da Silva, R., Schöley, J., Baden, H. M., Jouvet, L., Fa, J. E., Syed, H., Jongejans, E., Meiri, S., Gaillard, J.-M., Chamberlain, S., Wilcken, J., Jones, O. R., Dahlgren, J. P., Steiner, U. K., Bland, L. M., Gomez-Mestre, I., … Vaupel, J. W. (2019). Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences*, *116*(19), 9658–9664. https://doi.org/10.1073/pnas.1816367116

Conn, P. B., Kendall, W. L., & Samuel, M. D. (2004). A General Model for the Analysis of Mark-Resight, Mark-Recapture, and Band-Recovery Data under Tag Loss. *Biometrics*, *60*(4), 900–909. https://doi.org/10.1111/j.0006-341X.2004.00245.x

Cormack, R. (1964). Estimates of Survival from Sighting of Marked Animals. *Biometrika*, *51*(3–4), 429–438. https://doi.org/10.2307/2334149

Cowen, L., & Schwarz, C. J. (2006). The Jolly–Seber Model with Tag Loss. *Biometrics*, *62*(3), 699–705. https://doi.org/10.1111/j.1541-0420.2006.00523.x

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming With Models: Writing Statistical Algorithms for General Model Structures With NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2), 403–413. https://doi.org/10.1080/10618600.2016.1172487

Diefenbach, D. R., & Alt, G. L. (1998). Modeling and Evaluation of Ear Tag Loss in Black Bears. *The Journal of Wildlife Management*, *62*(4), 1292–1300. https://doi.org/10.2307/3801993

Fabrizio, M. C., Nichols, J. D., Hines, J., Swanson, B. L., & Schram, S. T. (1999). Modeling data from double-tagging experiments to estimate heterogeneous rates of tag shedding in lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(8), 1409–1419. https://doi.org/10.1139/F99-069

Fokidis, H. B., Robertson, C., & Risch, T. S. (2006). Keeping tabs: Are redundant marking systems needed for rodents? *Wildlife Society Bulletin*, *34*(3), 764–771. https://doi.org/10.2193/0091-7648(2006)34[764:KTARMS]2.0.CO;2

Foley, N. M., Petit, E. J., Brazier, T., Finarelli, J. A., Hughes, G. M., Touzalin, F., Puechmaille, S. J., & Teeling, E. C. (2020). Drivers of longitudinal telomere dynamics in a long-lived bat species, *Myotis myotis*. *Molecular Ecology*, *29*(16), 2963–2977. https://doi.org/10.1111/mec.15395

Frantz, A. C., Pope, L. C., Carpenter, P. J., Roper, T. J., Wilson, G. J., Delahay, R. J., & Burke, T. (2003). Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. *Molecular Ecology*, *12*(6), 1649–1661. https://doi.org/10.1046/j.1365-294x.2003.01848.x

Freeland, W. J., & Fry, K. (1995). Suitability of passive integrated transponder tags for marking live animals for trade. *Wildlife Research*, *22*(6), 767–773. https://doi.org/10.1071/WR9950767

Gimenez, O., Cam, E., & Gaillard, J.-M. (2018). Individual heterogeneity and capture–recapture models: What, why and how? *Oikos*, *127*(5), 664–686. https://doi.org/10.1111/oik.04532

Gimenez, O., Lebreton, J.-D., Choquet, R., & Pradel, R. (2018). R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models. *Methods in Ecology and Evolution*, *9*(7), 1749–1754. https://doi.org/10.1111/2041-210X.13014

Goudie, R. J. B., Turner, R. M., De Angelis, D., & Thomas, A. (2020). MultiBUGS: A Parallel Implementation of the BUGS Modelling Framework for Faster Bayesian Inference. *Journal of Statistical Software*, *95*, 7. https://doi.org/10.18637/jss.v095.i07

Hestbeck, J. B., Nichols, J. D., & Malecki, R. A. (1991). Estimates of Movement and Site Fidelity Using Mark-Resight Data of Wintering Canada Geese. *Ecology*, *72*(2), 523–533. https://doi.org/10.2307/2937193

Horton, G. E., Letcher, B. H., & Kendall, W. L. (2011). A Multistate Capture–Recapture Modeling Strategy to Separate True Survival from Permanent Emigration for a Passive Integrated Transponder Tagged Population of Stream Fish. *Transactions of the American Fisheries Society*, *140*(2), 320–333. https://doi.org/10.1080/00028487.2011.567861

Huntsman, B. M., Venarsky, M. P., Abadi, F., Huryn, A. D., Kuhajda, B. R., Cox, C. L., & Benstead, J. P. (2020). Evolutionary history and sex are significant drivers of crayfish demography in resource-limited cave ecosystems. *Evolutionary Ecology*, *34*(2), 235–255. https://doi.org/10.1007/s10682-019-10029-w

Jennelle, C. S., Cooch, E. G., Conroy, M. J., & Senar, J. C. (2007). State-specific detection probabilities and disease prevalence. *Ecological Applications*, *17*(1), 154–167. https://doi.org/10.1890/1051-0761(2007)017[0154:SDPADP]2.0.CO;2

Johnson, D. H., Burnham, K. P., & Nichols, J. D. (1986). The role of heterogeneity in animal population dynamics. *Proceedings of the International Biometrics Conference*, *13*, 5.3.1-5.3.15.

Johnson, D. S., Laake, J. L., Melin, S. R., & DeLong, R. L. (2016). Multivariate State Hidden Markov Models for Mark-Recapture Data. *Statistical Science*, *31*(2), 233–244. https://doi.org/10.1214/15-STS542

Jolly, G. (1965). Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. *Biometrika*, *52*, 225–247. https://doi.org/10.2307/2333826

Juillet, C., Choquet, R., Gauthier, G., & Pradel, R. (2011). A Capture–Recapture Model with Double-Marking, Live and Dead Encounters, and Heterogeneity of Reporting Due to Auxiliary Mark Loss. *Journal of Agricultural, Biological, and Environmental Statistics*, *16*(1), 88–104. https://doi.org/10.1007/s13253-010-0035-5

Kaemingk, M. A., Weber, M. J., McKenna, P. R., & Brown, M. L. (2011). Effect of Passive Integrated Transponder Tag Implantation Site on Tag Retention, Growth, and Survival of Two Sizes of Juvenile Bluegills and Yellow Perch. *North American Journal of Fisheries Management*, *31*(4), 726–732. https://doi.org/10.1080/02755947.2011.611863

Kellner, K. (2016). *JagsUI: A Wrapper Around "rjags" to Streamline "JAGS" Analyses*. https://CRAN.R-project.org/package=jagsUI

Kremers, W. K. (1988). Estimation of survival rates from a mark-recapture study with tag loss. *Biometrics*, *44*(1), 117–130. JSTOR. https://doi.org/10.2307/2531900

Kruschke, J. (2014). *Doing Bayesian Data Analysis: A Tutorial with R, JAGS, and Stan* (2 edition). Academic Press.

Kruschke, J. K. (2018). Rejecting or Accepting Parameter Values in Bayesian Estimation. *Advances in Methods and Practices in Psychological Science*, *1*(2), 270–280. https://doi.org/10.1177/2515245918771304

Laake, J. L., Johnson, D. S., Diefenbach, D. R., & Ternent, M. A. (2014). Hidden Markov Model for Dependent Mark Loss and Survival Estimation. *Journal of Agricultural Biological and Environmental Statistics*, *19*(4), 524–540. https://doi.org/10.1007/s13253-014-0190-1

Lebl, K., & Ruf, T. (2010). An easy way to reduce PIT-tag loss in rodents. *Ecological Research*, *25*(1), 251–253. https://doi.org/10.1007/s11284-009-0629-y

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals—a unified approach with case-studies. *Ecological Monographs*, *62*(1), 67–118.

Lebreton, J.-D., Hines, J. E., Pradel, R., Nichols, J. D., & Spendelow, J. A. (2003). Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos*, *101*(2), 253–264. https://doi.org/10.1034/j.1600-0706.2003.11848.x

Lebreton, J.-D., Nichols, J. D., Barker, R. J., Pradel, R., & Spendelow, J. A. (2009). Chapter 3 Modeling Individual Animal Histories with Multistate Capture–Recapture Models. In Hal Caswell (Ed.), *Advances in Ecological Research: Vol. Volume 41* (pp. 87–173). Academic Press. http://www.sciencedirect.com/science/article/pii/S0065250409004036

Ling, H., & Okada, K. (2007). An Efficient Earth Mover's Distance Algorithm for Robust Histogram Comparison. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *29*(5), 840–853. https://doi.org/10.1109/TPAMI.2007.1058

Lunn, D. J., Thomas, A., Best, N., & Spiegelhalter, D. (2000). WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, *10*(4), 325–337. https://doi.org/10.1023/A:1008929526011

Malcolm-White, E., McMahon, C. R., & Cowen, L. L. E. (2020). Complete tag loss in capture–recapture studies affects abundance estimates: An elephant seal case study. *Ecology and Evolution*, *10*(5), 2377–2384. https://doi.org/10.1002/ece3.6052

McMahon, C. R., & White, G. C. (2009). Tag loss probabilities are not independent: Assessing and quantifying the assumption of independent tag transition probabilities from direct observations. *Journal of Experimental Marine Biology and Ecology*, *372*(1–2), 36–42. https://doi.org/10.1016/j.jembe.2009.02.006

Melnychuk, M. C., Dunton, K. J., Jordaan, A., McKown, K. A., & Frisk, M. G. (2017). Informing conservation strategies for the endangered Atlantic sturgeon using acoustic telemetry and multi-state mark-recapture models. *Journal of Applied Ecology*, *54*(3), 914–925. https://doi.org/10.1111/1365-2664.12799

Nelson, L. J., Anderson, D. R., & Burnham, K. P. (1980). The effect of band loss on estimates of annual survival. In *Journal of Field Ornithology* (Vol. 51, Issue 1, p. 9).

Nichols, J. D., Bart, J., Limpert, R. J., Sladen, W. J. L., & Hines, J. E. (1992). Annual Survival Rates of Adult and Immature Eastern Population Tundra Swans. *The Journal of Wildlife Management*, *56*(3), 485–494. https://doi.org/10.2307/3808863

Nichols, J. D., & Hines, J. E. (1993). Survival rate estimation in the presence of tag loss using joint analysis of capture-recapture and resighting data. In *Marked Individuals in the Study of Bird Population* (Birkhauser Verlag, pp. 229–243). https://pubs.er.usgs.gov/publication/5210628

Nichols, J. D., & Kendall, W. L. (1995). The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics*, *22*(5–6), 835–846. https://doi.org/10.1080/02664769524658

Nishizawa, H., Joseph, J., Chew, V. Y.-C., Liew, H.-C., & Chan, E.-H. (2018). Assessing tag loss and survival probabilities in green turtles (*Chelonia mydas*) nesting in Malaysia. *Journal of the Marine Biological Association of the United Kingdom*, *98*(4), 961–972. https://doi.org/10.1017/S0025315417000224

Ostrand, K. G., Zydlewski, G. B., Gale, W. L., & Zydlewski, J. D. (2012). Long Term Retention, Survival, Growth, and Physiological Indicators of Juvenile Salmonids Marked with Passive Integrated Transponder Tags. In J. R. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. G. Mesa, & Q. Phelps (Eds.), *Advances in Fish Tagging and Marking Technology* (Vol. 76, pp. 135–145). Amer Fisheries Soc.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, 1–10.

Puechmaille, S. J., & Petit, E. J. (2007). Empirical evaluation of non-invasive capture–mark–recapture estimation of population size based on a single sampling session. *Journal of Applied Ecology*, *44*(4), 843–852. https://doi.org/10.1111/j.1365-2664.2007.01321.x

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Riecke, T. V., Williams, P. J., Behnke, T. L., Gibson, D., Leach, A. G., Sedinger, B. S., Street, P. A., & Sedinger, J. S. (2019). Integrated population models: Model assumptions and inference.

Methods in Ecology and Evolution, *10*(7), 1072–1082. https://doi.org/10.1111/2041-210X.13195

Robson, D. S., & Regier, H. A. (1966). Estimates of Tag Loss from Recoveries of Fish Tagged and Permanently Marked. *Transactions of the American Fisheries Society*, *95*(1), 56–59. https://doi.org/10.1577/1548-8659(1966)95[56:EOTLFR]2.0.CO;2

Schaub, M., Gimenez, O., Schmidt, B. R., & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology*, *85*(8), 2107–2113.

Schofield, M. R., & Barker, R. J. (2008). A Unified Capture-Recapture Framework. *Journal of Agricultural Biological and Environmental Statistics*, *13*(4), 458–477. https://doi.org/10.1198/108571108X383465

Schwarz, C. J., Schweigert, J. F., & Arnason, A. N. (1993). Estimating Migration Rates Using Tag-Recovery Data. *Biometrics*, *49*(1), 177–193. https://doi.org/10.2307/2532612

Schwarz, L. K., Hindell, M. A., McMahon, C. R., & Costa, D. P. (2012). The implications of assuming independent tag loss in southern elephant seals. *Ecosphere*, *3*(9), art81. https://doi.org/10.1890/ES12-00132.1

Seber, G. (1965). A Note on Multiple-Recapture Census. *Biometrika*, *52*, 249–260.

Seber, G. A. F., & Felton, R. (1981). Tag loss and the Petersen mark-recapture experiment. *Biometrika*, *68*(1), 211–219. https://doi.org/10.1093/biomet/68.1.211

Seber, G. A. F., & Schofield, M. R. (2019). Tagging Methods and Tag Loss. In G. A. F. Seber & M. R. Schofield (Eds.), *Capture-Recapture: Parameter Estimation for Open Animal Populations* (pp. 13–37). Springer International Publishing. https://doi.org/10.1007/978-3-030-18187-1_2

Smout, S., King, R., & Pomeroy, P. (2011a). Estimating demographic parameters for capture-recapture data in the presence of multiple mark types. *Environmental and Ecological Statistics*, *18*(2), 331–347. https://doi.org/10.1007/s10651-010-0135-y

Smout, S., King, R., & Pomeroy, P. (2011b). Integrating heterogeneity of detection and mark loss to estimate survival and transience in UK grey seal colonies. *Journal of Applied Ecology*, *48*(2), 364–372. https://doi.org/10.1111/j.1365-2664.2010.01913.x

Spendelow, J. A., Nichols, J. D., Nisbet, I. C. T., Hays, H., Cormons, G. D., Burger, J., Safina, C., Hines, J. E., & Gochfeld, M. (1995). Estimating Annual Survival and Movement Rates of Adults within a Metapopulation of Roseate Terns. *Ecology*, *76*(8), 2415–2428. https://doi.org/10.2307/2265817

STAN Development Team. (2022). *Stan Modeling Language Users Guide and Reference Manual, 2.31*. http://mc-stan.org/

Tavecchia, G., Adrover, J., Navarro, A. M., & Pradel, R. (2012). Modelling mortality causes in longitudinal data in the presence of tag loss: Application to raptor poisoning and electrocution. *Journal of Applied Ecology*, *49*(1), 297–305. https://doi.org/10.1111/j.1365-2664.2011.02074.x

van Harten, E., Reardon, T., Holz, P. H., Lawrence, R., Prowse, T. A. A., & Lumsden, L. F. (2020). Recovery of southern bent-winged bats (*Miniopterus orianae bassanii*) after PIT-tagging and the use of surgical adhesive. *Australian Mammalogy*, *42*(2), 216–219. https://doi.org/10.1071/AM19024

White, G., & Burnham, K. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, *46*(S), 120–139.

Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and Management of Animal Populations* (1 edition). Academic Press.

Winiarski, K. J., & McGarigal, K. (2016). Effects of Photo and Genotype-Based Misidentification Error on Estimates of Survival, Detection and State Transition using Multistate Survival Models. *PLOS ONE*, *11*(1), e0145640. https://doi.org/10.1371/journal.pone.0145640

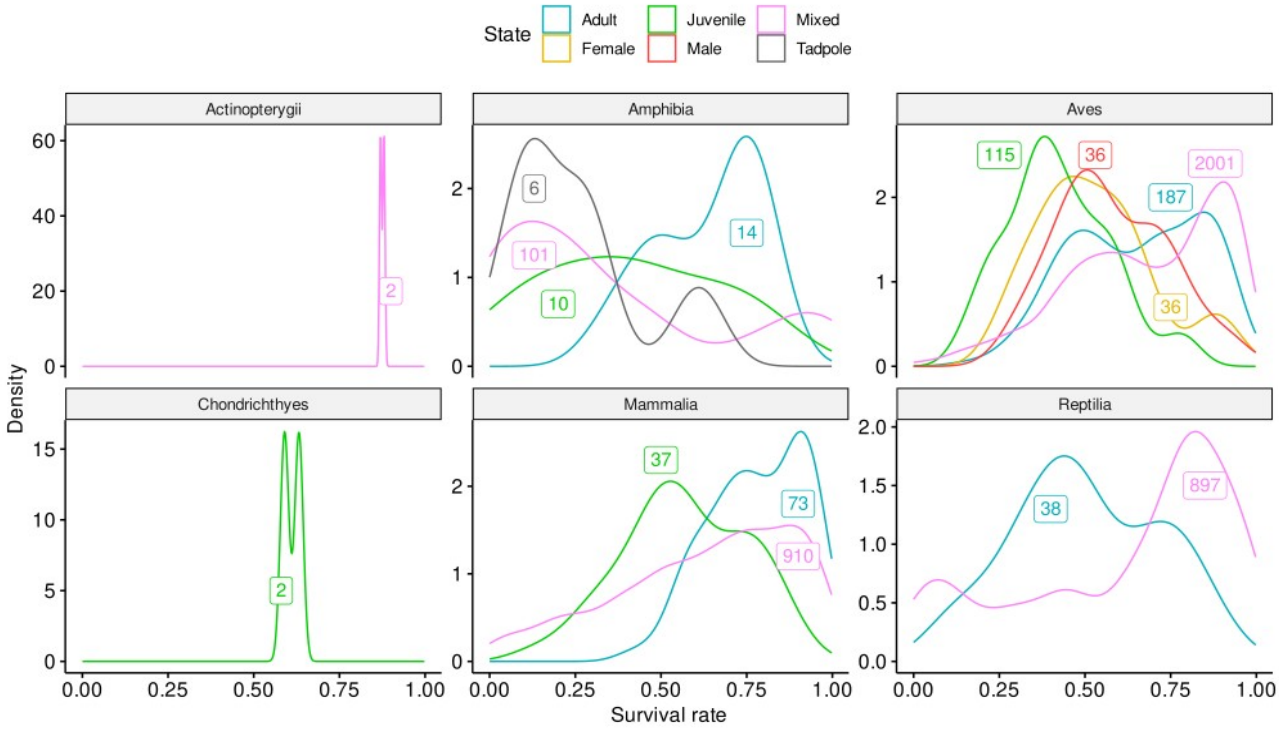

Figure 1: Density of probability of survival across age class and taxa for 700 species. Sample size are indicated by labels, with colour corresponding to the state of individual sampled.

Scenario	Survival	Detection
Scenario 1	Long-lived (high survival)	High detection rate (capture & resighting)
Scenario 2	Long-lived (high survival)	Low detection rate (capture & resighting)
Scenario 3	Short-lived (low survival)	Low detection rate (capture & resighting)
Scenario 4	Short-lived (low survival)	High detection rate (capture & resighting)

Table 1: Summary of the characteristics of each simulated scenario.

Parameter	Definition	Value	
		Long-lived species	Short-lived species
$\phi_{ad.}$	Adult survival in state "A", "B", "C"	logit(N(2.5,0.3)) [0.92]	logit(N(2.5,0.3)-0.3)) [0.62]
$\phi_{ad.}$	Adult survival in state "D"	logit(N(1.5,0.3)) [0.81]	logit(N(1.5,0.3)-0.3)) [0.51]
$\phi_{juv.}$	Juvenile survival in state "A", "B", "C"	logit(N(0.2,0.3)) [0.55]	logit(N(0.2,0.3)-0.2)) [0.35]
$\phi_{juv.}$	Juvenile survival in state "D"	NA	NA
		High	Low
pc_A	Capture probability in state "A"	U(0.6,0.7) [0.65]	U(0.6,0.7)-0.5 [0.15]
pc_B	Capture probability in state "B"	U(0.7,0.8) [0.75]	U(0.7,0.8)-0.5 [0.25]
pc_C	Capture probability in state "C"	U(0.65,0.75) [0.7]	U(0.65,0.75)-0.5 [0.2]
pc_D	Capture probability in state "D"	0	0
$p.r_A$	Resighting probability in state "A"	0.85	0.35
$p.r_B$	Resighting probability in state "B"	0.95	0.45
$p.r_C$	Resighting probability in state "C"	0.9	0.4
$p.r_D$	Resighting probability in state "D"	0.7	0.2

Table 2: Parameter values used to simulate the 4 scenarios. For random values generated, the corresponding distribution is indicated with N (a, b) the normal distribution with mean a and variance b, and U(a,b) the uniform distribution with lower bound a and upper bound b. The square brackets show mean values on the probability scale. To simulate survival for short-lived species, we used the same distribution on as long-lived species but subtract generated values by 0.3 for adults and 0.2 for juveniles. In the same way, we obtained the low values of probability of capture and re-sighting by subtracting 0.5 from the high values. The probability of capture in state "D" is set to 0, as no capture is possible when individuals are in this state. For the transition values between states see Fig. 3.

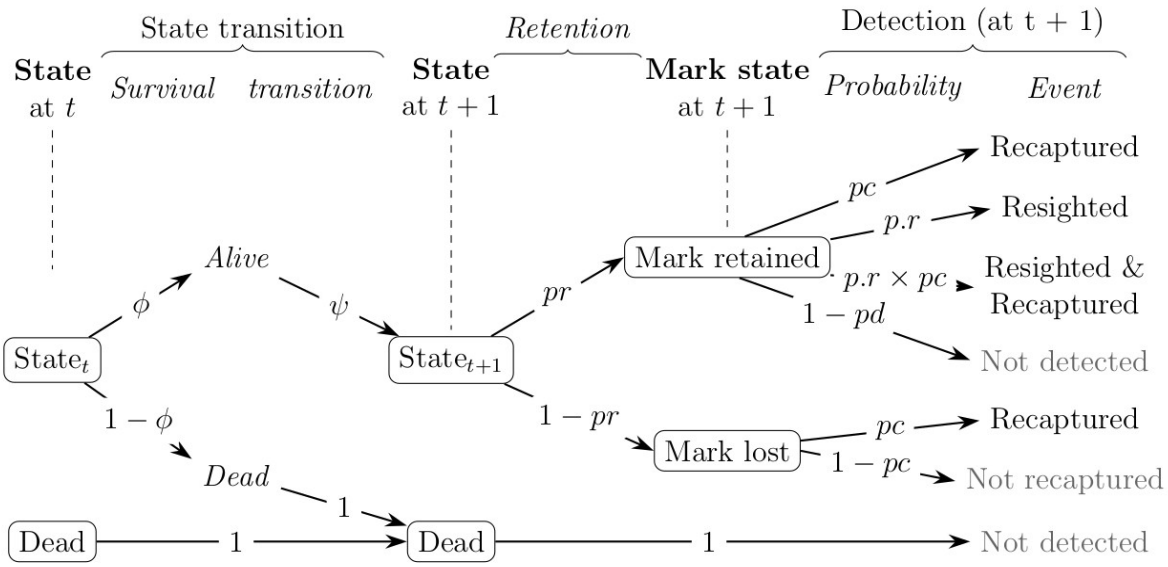

*Figure 2: The possible fates of an individual between occasion t and t+1. We first consider the state transition process: if the individual dies between occasions, it can only remain dead and can no longer be detected, both with probability 1 (absorbing state). The individual can, however, survive between occasions with probability φ (depending on time and state at t) and can then change state with probability ψ (see Fig. 1). Second, the mark retention process: if it survives between occasions, then the individual can retain its mark with probability pr (depending on age and time since marking) or lose its mark with probability ptl = 1-pr. Thirdly, the detection process: if this individual has lost his mark between occasions, he may possibly be recaptured with a probability pc (depending on time and state at t+1) and if this happens, he is marked again before being released. However, if the mark is retained, other events may occur: the individual may also be captured with probability pc, but it may also be resighted with probability p.r (depending on the state at t+1), or both with probability pc*p.r, or finally not be detected at all with probability 1-pd = (1-pc)*(1-p.r).*

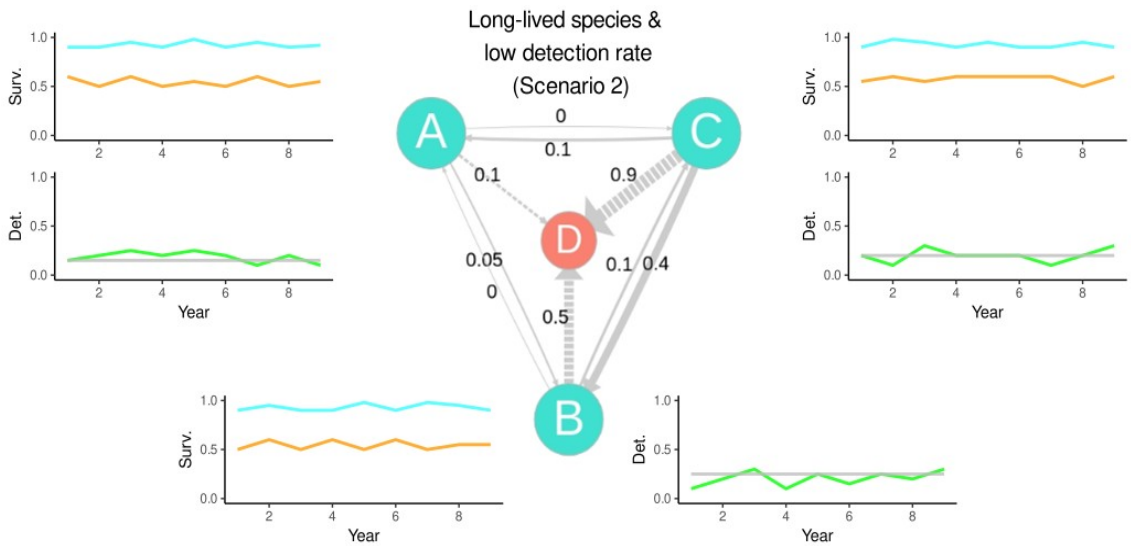

Figure 3: Schematic description of parameter values used to simulate data under scenario 2 (long-lived species with low detection). Central graph: solid arrows correspond to possible transitions of females and dashed arrows to those of males. The size of the arrows is proportional to the probability of transition indicated next to them, all were kept constant over time. Peripheral graph: simulated survival (Surv.) and detection (Det.) probabilities were displayed for states "A", "B" and "C". The light blue lines correspond to adult survival, the orange lines to juvenile survival and the green lines to the probability of capture, which are derived from Normal and Uniform distribution and therefore fluctuate over the years (see Table 1). The grey lines correspond to the probability of resighting, they differed between state but were set constant in time.

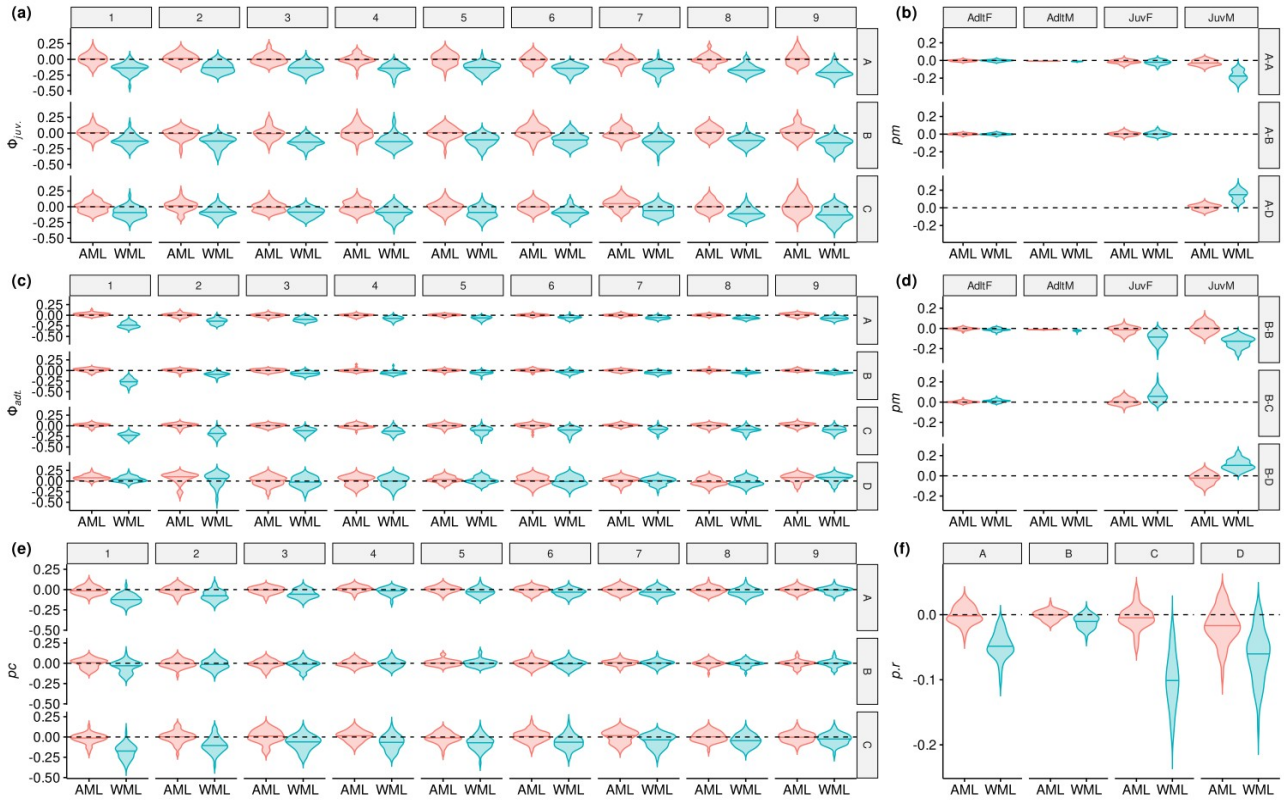

Figure 4: Comparison of bias for estimates of juvenile (a) and adult (c) survival, transition (b and d), capture (e) and resighting (f) probabilities between model accounting for mark loss (AML) or not (WML). All violin plots show the distribution of bias over 50 simulations from scenario 1 (long-lived species and high detection probabilities), with a simulated probability of mark loss of 0.4. The median of each simulated distribution is shown with a horizontal line. The numbers 1 to 9 are the recapture opportunities, the letters from A to D represent the different states, AdtF the adult females, AdtM the adult males, JuvF the juvenile females and JuvM the juvenile males.

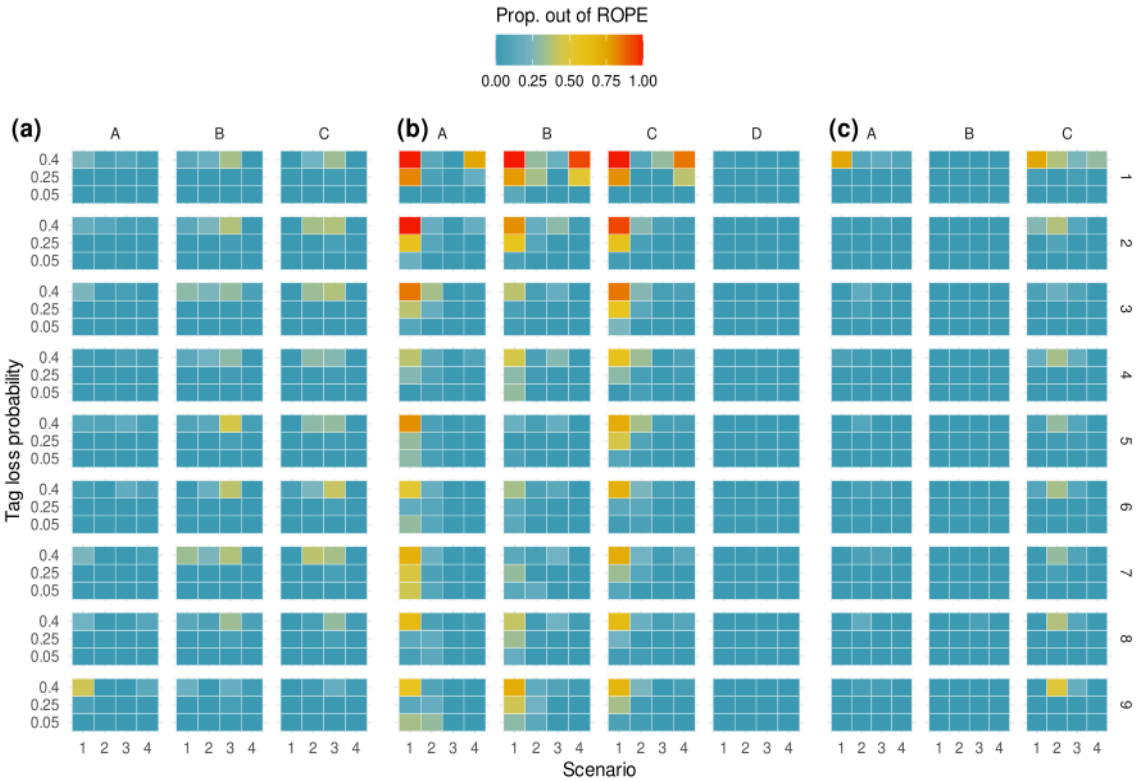

Figure 5: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between the model accounting for tag loss and recycling (ModelA) and the model ignoring them (ModelW). The ROPE corresponds to the interval including 80% hdi of the posterior density distribution of the "true value" of a parameter which was estimated with ModelA. Each tile represents annual (right axis) juvenile survival (a), adult survival (b) and capture probability (c) for each scenario (y axis) and tag loss probabilities (x axis). The scenarios indicated at the bottom are: (1) long-lived species and high detection rate; (2) long-lived species and low detection rate; (3) short-lived species and low detection rate; (4) short-lived species and high detection rate. At the top of each panel, A, B, C and D correspond to the states.

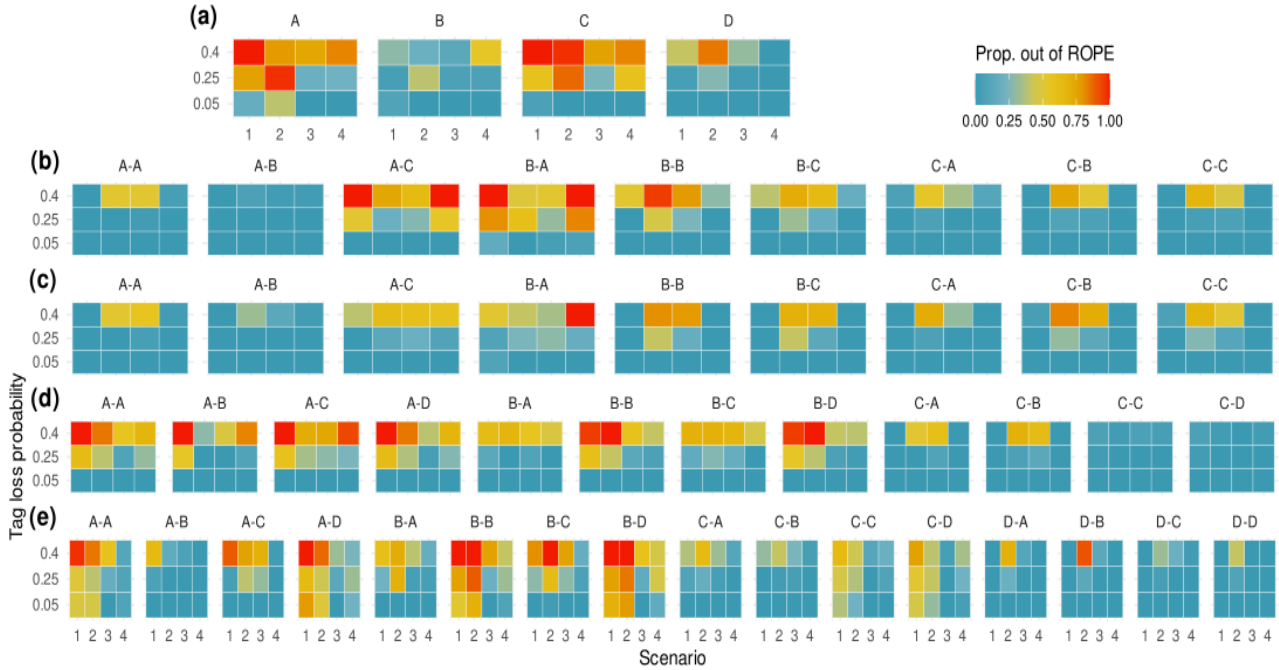

Figure 6: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between model accounting for tag loss and recycling (ModelA) and the model ignoring them (ModelW) for each simulated cases. The ROPE corresponds to the interval including 80% hdi of the posterior density distribution of the "true value" of a parameter which was estimated with ModelA. Each tile represents resighting probability (a) and transition probabilities between subpopulations (direction, "from-to", are indicated above each tile-plot, e.g "A-B" correspond to state transition from A to B) of juvenile female (b), adult female (c), juvenile male (d) and adult male (e) for each scenario and tag loss probabilities. The scenario are indicated at the bottom: (1) long-lived species and high detection rate; (2) long-lived species and low detection rate; (3) short-lived species and low detection rate; (4) short-lived species and high detection rate. At the top of each panel, A, B, C and D correspond to the states.

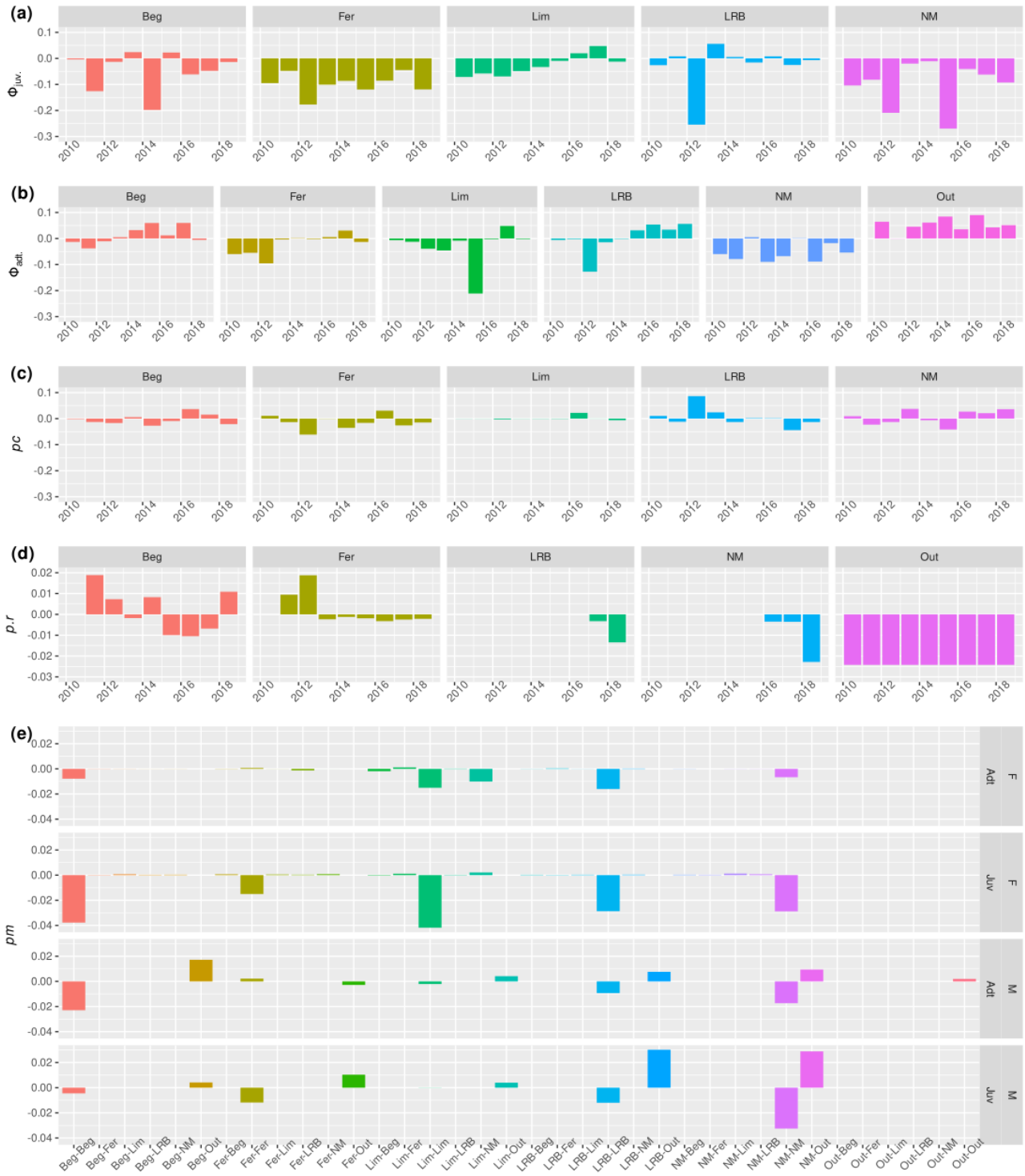

Figure 7: Differences in the medians of the posterior distributions of juvenile (a) and adult (b) survival, capture (c) resighting (d) and transition (e) probabilities between the model accounting for tag-loss and the model ignoring it, both estimated from the empirical data. Colonies are abbreviated: Beg = Beganne; Fer = Férel; LIM = Limerzel; LRB = La Roche Bernard; NM = Noyal-Muzillac. Movements between sites are indicated on x axis with direction "from-to". Movements (e) are specified by age (Adt. = Adulte, Juv. = juvenile) and sex classes (M = male, F = Female), indicated on the right side of the plot (e).

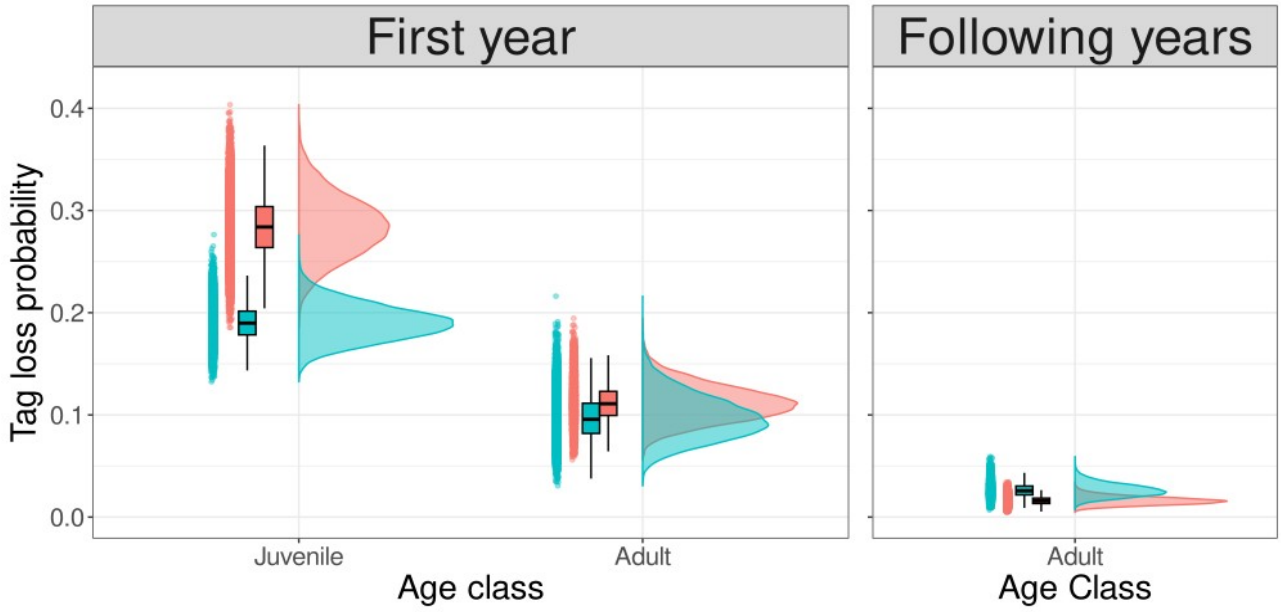

Figure 8: Posterior distribution of the tag loss probabilities according to age classes and time after marking in the Myotis myotis dataset. Left panel correspond to tag shedding rate during the year following the tag injection and the right panel for the following years (constant in time). In blue, distribution if surgical adhesive was used after tag injection and in red, without surgical adhesive.