

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

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26 **Abstract**

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

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

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

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

51 KEYWORDS

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

54 **1 Introduction**

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

71 Consider “1011”, a simple four occasions encounter history, where “1” implies the individual was
72 caught and “0” not. If we note ϕ_t the survival rate between occasion t and $t+1$ and p_t the capture
73 probability at occasion t (with $q_t = 1 - p_t$), this encounter history occurs with probability
74 $\phi_1 q_2 \phi_3 p_3 \phi_4$. Now consider the individual can make a transition between 2 states, and its history

75 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
76 transition probability from state i to state j (i and j in $\{1,2\}$), conditional on survival, the new
77 encounter history occurs with probability $\phi_1^{(1)}\psi^{(1,1)}q_2^{(1)}\phi_2^{(2)}\psi^{(1,2)}p_3^{(2)}\phi_3^{(2)}\psi^{(2,2)}p_4^{(2)} +$
78 $\phi_1^{(1)}\psi^{(1,2)}q_2^{(2)}\phi_2^{(2)}\psi^{(2,2)}p_3^{(2)}\phi_3^{(2)}\psi^{(2,2)}p_4^{(2)}$, with indices for state-specific parameters noted in parentheses.
79 If this individual loses its mark after its first capture and is remarked when recaptured at t_3 , its
80 encounter history becomes ‘two’ different histories from ‘two’ different individuals: one becoming
81 “1000”, the second “0022”. In this case, survival and mark loss patterns are different, not only is
82 survival underestimated (at least for the “first” history) but so are the transition probabilities,
83 because there is no longer a change of state (the second history starts directly at state 2).
84 Many CMR studies, despite using different mark types, are affected by mark loss, the rate of which
85 varies according to a myriad of factors, such as species (see Supported Information 1, Table S2),
86 mark type (Smout et al., 2011a), sex (Conn et al., 2004), mass (Schwarz et al., 2012), size (Acolas
87 et al., 2007), mark location (Kaemingk et al., 2011) or physiological stage (Besnard et al., 2007).
88 Mark loss has previously been shown to produce negative bias in survival estimates and detection
89 (Nichols et al., 1992; Nichols & Hines, 1993). Many statistical tools have been developed to
90 remove the confounding effect of mark loss in single state models, (Robson & Regier, 1966; G. A.
91 F. Seber & Felton, 1981). However, the effect of these violations has not been explored in the multi-
92 state modelling framework.
93 Multi-state models were developed to deal with situations where the “state” (e.g. location,
94 behaviour, physiology, reproductive or social status) of an individual may affect its survival or
95 detection probability, and where the individual can change “state” during life (reviewed in Lebreton
96 et al., 2009). These models became popular and widely used because of their flexibility to address a
97 large range of study systems and biological questions, and because they can be used in a relatively
98 straightforward manner by biologists given the development of user-friendly software (e.g. Mark,
99 E-surge, Bugs). They are used to address many ecological and evolutionary hypotheses based on

100 variations in life history traits (state transitions) throughout an individual's life (Nichols & Kendall
101 (1995) see also Cam (2009) for an extensive discussion on the subject), or density dependence
102 effect (Schofield & Barker, 2008), co-evolution (Benkman et al., 2005), dispersal probability among
103 subpopulations or living areas (Hestbeck et al., 1991; Spendelow et al., 1995), disease prevalence in
104 wild populations (Jennelle et al., 2007). However, the literature dealing with the effect of mark loss
105 on multi-state model behaviour is scarce and much remains to be explored.

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

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

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

127 **2 Material and method**

128 **2.1 Data simulation**

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

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

149 MSCJS model between two-time intervals are displayed in Fig. 1.a. We considered two common
150 ways of re-encountering individuals after marking: (1) recapture when individuals are physically
151 caught again; (2) resighting, which is a passive way to detect individuals without handling them
152 (e.g. using colour or alphanumeric rings or PIT-tags). This approach is motivated by the fact that in
153 most studies, the probability of resighting is typically higher than the probability of recapture,
154 therefore they can be differently affected by estimation biases. To investigate the effect of mark loss
155 on the estimates of state transition probabilities, we simulated data using different transition
156 probabilities between states (Fig. 1.b). Irrespective of their age, females were allowed to transition
157 at each occasion between state A, B and C, at a permanent rate depending on the state they were
158 before transition, but not in state D. Only juvenile males were able to transition to the D state, in
159 different proportions depending on their initial state, while adult male never changed their state
160 (Fig. 1.b). This sexual dissymmetry in transition is common in mammals (and other taxa) and
161 allows us for example to distinguish permanent emigration (absorbing state) from other movements.
162 At the first occasion, individuals in state A, B and C were composed of 40 juveniles (sex ratio 1:1)
163 and 60 adults (80% females, 20% males); there was no individual in state D. On each subsequent
164 occasion, 40 juveniles and 5 adults were marked in each state (A, B,C) except in state D, where it is
165 not possible to recapture individuals but only to observe them.
166 As mark shedding is often dependant on time since marking and occurs most frequently shortly
167 after marking in many species (in our case study; Fabrizio et al., 1999; Fokidis et al., 2006), for
168 each scenario, we investigated a range of mark loss rates commonly reported in the literature
169 (Supported Information 1, Table S2). We simulated three mark loss probabilities (0.05, 0.25, 0.4)
170 during the first year after marking and a constant 0.05 rate thereafter, which generated a diversity of
171 cases of mark loss and recycled individuals (Supported Information 2, Fig. S3). We simulated fifty
172 datasets for each of the 12 combination of parameters, and ran two MSCJS models: one with
173 recycled individuals, which mimicked the situation where it was not possible to identify individuals

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

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

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

181 **2.2 Data analysis**

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

192 **2.3 Real data analyses**

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

195 individuals were marked in 5 roosts: La Roche Bernard (47°31'N, 2°18'W), Férel (47°28'N,
196 2°20'W), Noyal-Muzillac (47°35'N, 2°27'W), Béganne (47°35'N, 2°14'W) and Limerzel (47°38'N,
197 2°21'W). The bats were individually tagged using PIT tags, ID-100C (Troven®), with a unique 10-
198 digit code. These small passive tags (2.12x11mm, 0.1gr) allowed identification from passive
199 readers. All individuals caught in roosts without PIT-tags were systematically tagged, which
200 included both, individuals who lost their tag and those which were never tagged before, and
201 genotyped as a second and permanent marking method. Genotypes were established from DNA
202 extracted from wing biopsies from all individuals tagged and from all males untagged caught during
203 swarming surveys (n=4,258 samples; details in Supporting Information 3, Fig. S1), as male capture
204 probability at roosts after birth was extremely low. A total of 16 microsatellite markers optimised
205 for *Myotis myotis* were used to establish individual genotypes (Foley et al., 2020). To minimize
206 genotyping errors, we analysed, when available, 2 different samples per individual and all samples
207 were genotyped and scored twice by two different people. We also performed genetic profile
208 comparisons to detect errors (Frantz et al., 2003; Puechmaille & Petit, 2007). We hypothesised that
209 the error rate of genotypes was low enough to be negligible and did not include this source of
210 uncertainty in the models. We also checked each winter for the presence of lost tags on the floor of
211 the roosts, which allowed us to identify, at least in part (66% compared to the genotype), the
212 individuals that lost their tag, with the rest of losses having occurred outside of the roosts. Most of
213 these tags were lost during the first year (Supporting Information 3, Fig. S2), which is confirmed by
214 the absence of their records from passive reading detectors. In total, 252 individuals out of 2,561
215 (~10%) were identified as having lost their tag at least once. From those individuals, 94 individuals
216 were recaptured and retagged a second time and three retagged a third time. As retagging occurred
217 during the last capture occasion for 13 individuals, ignoring tag loss led to the recycling of 81
218 individuals in total among the 94. To analyse these data, we fitted a multisite model (a special case
219 of multi-state models when states are sites and transition are movement between sites.), similar to

220 the MSCJS model used for simulated data (Supporting Information 3). Emigration from the five
221 studied subpopulations was assessed using capture and resighting data obtained between capture
222 occasions in swarming and wintering sites. We accounted for individual heterogeneity, including a
223 random effect in the estimation of survival probability, a widespread phenomenon in free
224 populations and a known source of bias in CMR models. (Gimenez et al., 2018).
225 We defined eight possible detection states which allowed us to estimate separately, capture and
226 resighting probabilities (see Supporting Information 3, Table S1). As empirical data suggested the
227 possible movement of individuals between all subpopulations and outside, we did not constrain
228 transition between subpopulations except for movement of juveniles from D toward A, B, C which
229 was not possible and therefore set to 0. In this study, we also tested the effect of surgical adhesive
230 (Vetbond®) after PIT-tag injection, in order to assess tag-loss reduction in comparison with self-
231 healing (Lebl & Ruf, 2010; van Harten et al., 2020). In this model, tag retention probabilities were
232 modelled like in the simulation study (eqn. 1), by accounting for time since marking (two discrete
233 classes: first year or subsequent years), individual age class (juvenile or adult), and the use of
234 surgical adhesive (yes or no) As per the simulated datasets, two models were run, a first one taking
235 into consideration tag loss and recycling, and a second model ignoring this information.

236 **2.4 Computation details**

237 We used JAGS (Plummer, 2003) with the jagsUI package (Kellner, 2016) from R 3.6.0 (R Core
238 Team, 2019) for analyses of simulated and empirical datasets. We used four MCMC chains with
239 150,000 iterations each and drew samples from posterior distributions after discarding the first
240 50,000 iterations (burn-in). We retained every twentieth iteration generating 20,000 samples from
241 the posterior distribution for each parameter. Chain convergence was assessed with the Gelman-
242 Rubin statistic (Brooks & Gelman, 1998). Among 1,200 simulations, some showed R-hat values >
243 1.1, indicating a convergence failure. Convergence problems concerned few parameters and the
244 corresponding R-hat values were still low. To avoid prohibitively long computing time, we did not

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

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

268 **3 Results**

269 **3.1 Simulation results**

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

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

292 **3.2 Bat metapopulation**

293 Most of the estimated parameters (survival, capture, resighting and state transition probabilities)
294 show both negative and positive biases, with no clear pattern, but **no** substantial bias appeared in the
295 model not accounting for tag loss and recycling compared to the model taking them into account
296 (Supporting Information 3, Fig. S4-S11). Larger biases appeared in survival estimates, with the
297 estimated median survival difference between the two models reaching values greater than 0.2
298 (Supplementary Information 3, Fig. S4-S5), which could profoundly affect the results of studies
299 interested in evaluating the effect of annual covariates (e.g., climate variables) on survival
300 probability. The estimated tag loss probability was high for juveniles but substantially reduced by
301 the use of surgical glue (Fig. 4), decreasing by one third from 0.28 (90%hdi [0.23,0.33]) to 0.19
302 (90%hdi [0.16,0.22]). However, in adults the use of surgical glue did not affect tag loss rate, with an
303 overlap of 69% of the probability distributions. The adult tag loss rate was around 0.1 which is two
304 times less than in juveniles when surgical glue was used. Considering the period following one-year
305 post-tagging, the probability of tag loss when surgical glue was used is higher (median 0.03, 90%
306 hdi [0.02, 0.04]) versus not used (median 0.02, 90%hdi [0.01, 0.02]). This difference is in fact an
307 artefact due to a lack of search for lost tags on the ground of the colonies in the first year of the
308 study (Supplementary Information 3, part 3 and Fig. S12). Other parameter estimates can be found
309 in Supporting Information 3, part 2.6.

310 **4 Discussion**

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

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

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

341 Preliminary studies with multiple marks could also be considered when possible (Smout et al.,
342 2011b). This would allow CMR study design to be optimised prior to the study being conducted and
343 hence limit biases from the onset.

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

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

365 1995). Here we confirmed that PIT-tag shedding can be reduced in the short term by the use of
366 surgical adhesive (Lebl & Ruf, 2010; van Harten et al., 2020).

367 As illustrated, surgical adhesive is not sufficient to reduce tag loss to zero, and the use of a
368 permanent mark (e.g. genotype) is required, for all or part of the population studied (Laake et al.,
369 2014). Similar situations, where permanent marks should be considered, arise when marks
370 deteriorate and become unreadable, equivalent to an increase of mark loss with time, like neck
371 collars or ear tags (Conn et al., 2004; Diefenbach & Alt, 1998). In this case, we expect a decrease in
372 accuracy of model parameter estimates for the duration of the study, and further supports the use of
373 permanent marks for CMR studies.

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

383

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393

394 **Author contribution**

395 F.T. designed the project with the other co-authors. E.C.T., F.T. and BV acquired the funding.
396 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
397 the fieldwork. E.C.T., E.J.P., F.T. and S.J.P. collected samples. S.J.P. & F.T. supervised the
398 microsatellite genotyping. C.S. generated the genotypes. F.T. and E.C. developed the R scripts for
399 simulating and analysing data with help of E.J.P. and S.J.P. F.T. led the writing of the manuscript
400 and all authors contributed to manuscript revisions and gave final approval for publication.

401

402 **Data accessibility**

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

405

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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
p_{cA}	Capture probability in state A	~ 0.65 [U(0.6-0.7)]	~ 0.15 [U(0.6-0.7)-0.5]
p_{cB}	Capture probability in state B	~ 0.75 [U(0.7-0.8)]	~ 0.25 [U(0.7-0.8)-0.5]
p_{cC}	Capture probability in state C	~ 0.7 [U(0.65-0.75)]	~ 0.2 [U(0.65-0.75)-0.5]
p_{cD}	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.

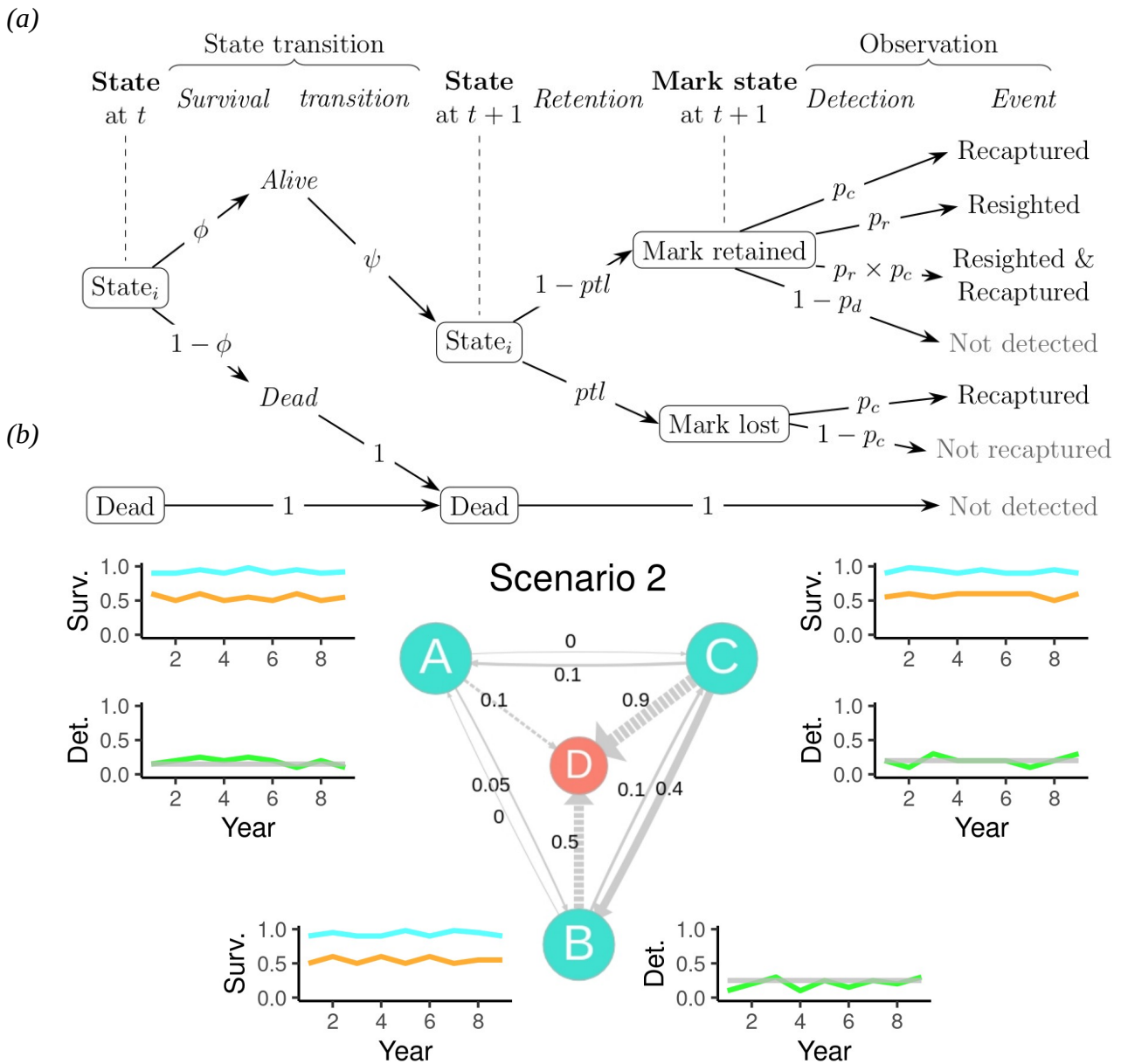
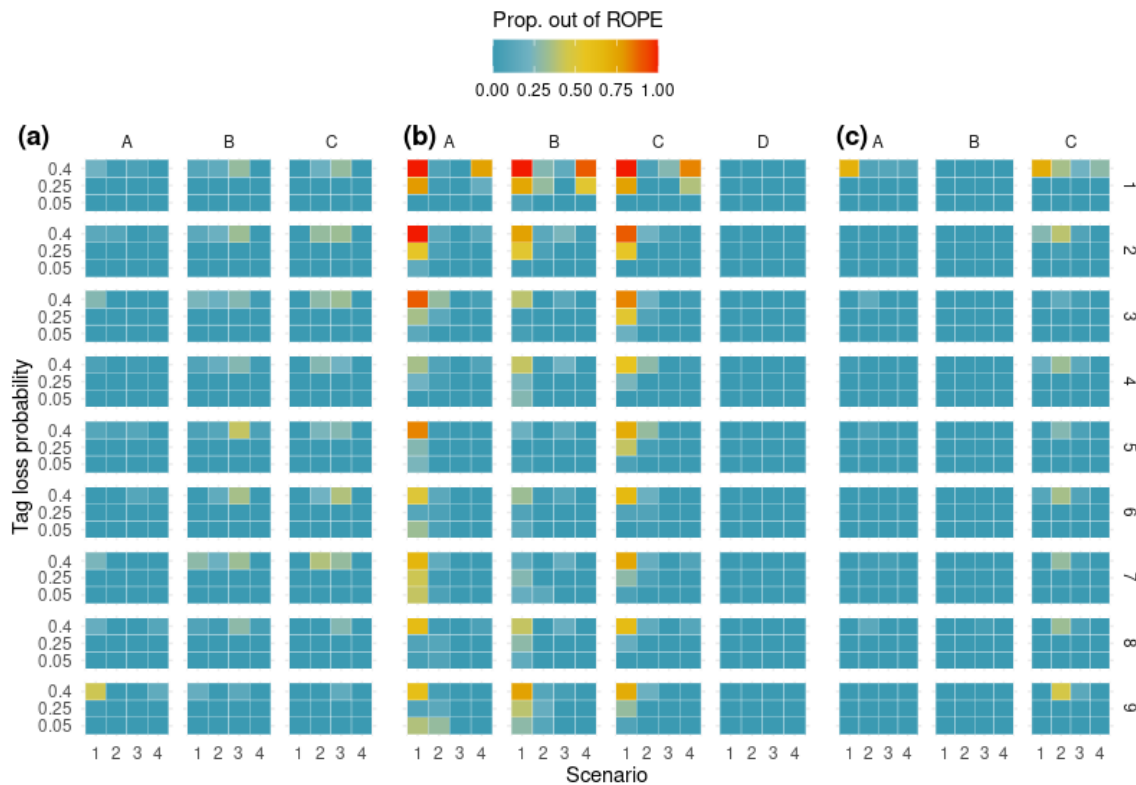



Figure 1: Multistate capture-mark-recapture model. Panel (a) illustrate the fate of individuals captured and realised at t or dead at t . From t to $t+1$ dead individuals stay dead and cannot be detected (absorbing state), while released individuals can change state. Arrows indicate the possible paths, 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.

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

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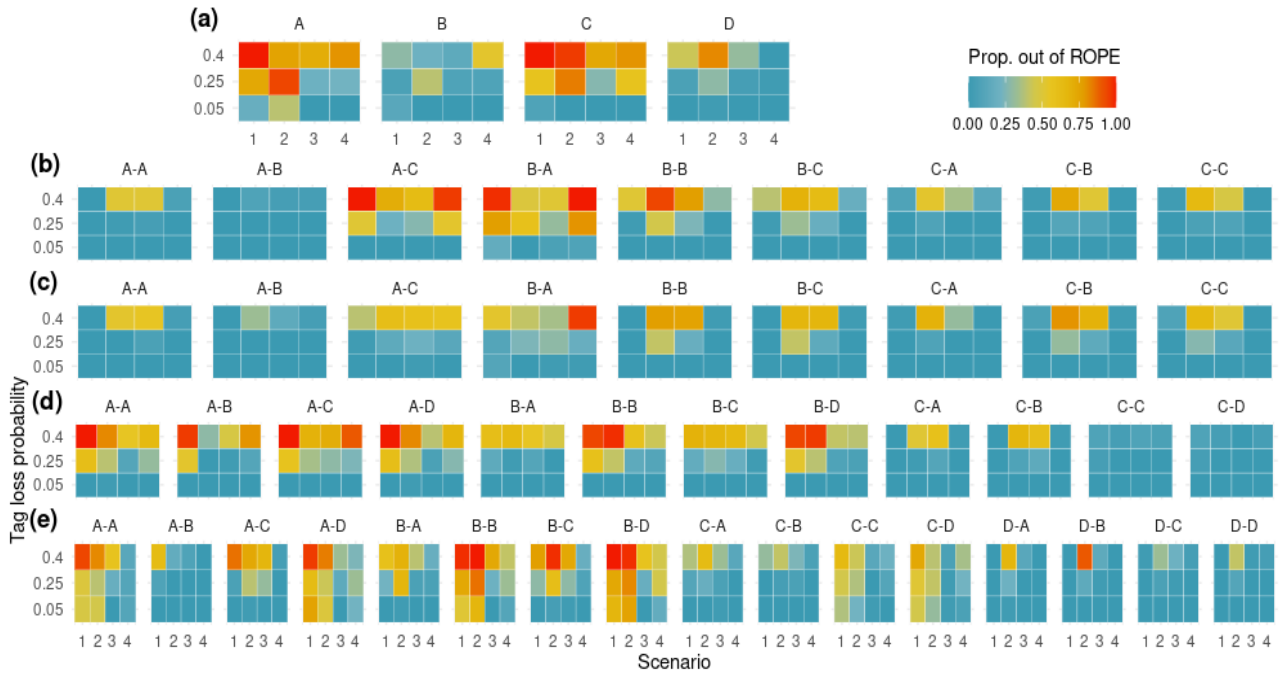


Figure 3: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between model accounting for tag loss and recycling and the model ignoring them for each simulated cases. Each tile represents resighting 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.

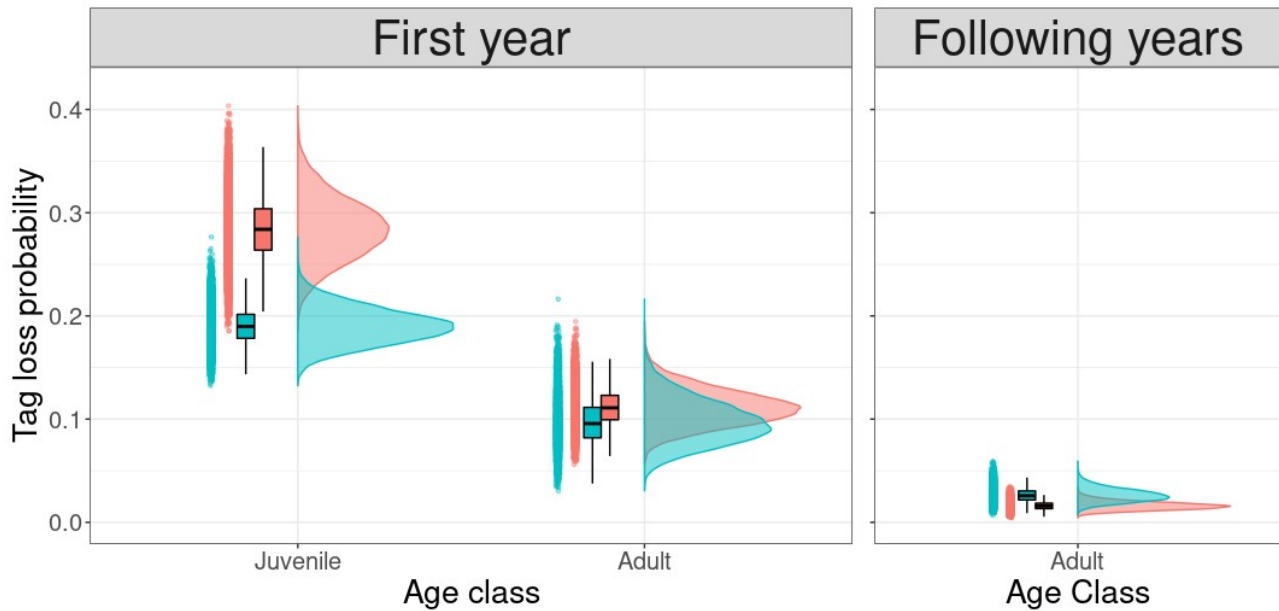


Figure 4: Posterior distribution of the tag loss probabilities according to age classes and time after marking in the *Myotis myotis* dataset. Left panel correspond to tag shedding rate during the year following the tag injection and the right panel for the following years (constant in time). In blue,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