

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

3

4 Authors

5 Frédéric Touzalin<sup>1,2</sup>, Eric J. Petit<sup>3</sup>, Emmanuelle Cam<sup>4</sup>, Claire Stagier<sup>1</sup>, Emma C. Teeling<sup>1</sup>, Sébastien  
6 J. Puechmaille<sup>5,6,7</sup>

7

8 <sup>1</sup>School of Biology and Environmental Science, Science Centre West, University College Dublin,  
9 Dublin, Ireland.

10 <sup>2</sup>Bretagne Vivante-SEPNB, Brest, France.

11 <sup>3</sup>DECOD (Ecosystem Dynamics and Sustainability), INRAE, Institut Agro, Ifremer, Rennes,  
12 France.

13 <sup>4</sup>Université de Bretagne occidentale, Brest, LEMAR, CNRS, IRD, Ifremer, F-29280 Plouzane,  
14 France.

15 <sup>5</sup>Zoological Institute and Museum, University of Greifswald, Greifswald, Germany.

16 <sup>6</sup>ISEM, Univ Montpellier, CNRS, IRD, Montpellier, France.

17 <sup>7</sup>Institut Universitaire de France, Paris, France

18

19

20

21

22 Correspondence

23 Frédéric Touzalin

24 Email: [fredtouzalin@gmail.com](mailto:fredtouzalin@gmail.com)

25

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

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, Arnason-Schwartz (AS), modelling framework. We explored **parameter bias** through  
38 simulations of a metapopulation system with different capture and survival rates. We also illustrated  
39 how mark loss can be easily estimated and accounted for using an empirical long-term (10 years)  
40 CMR dataset of bats, individually identified using both **PIT** tag technology as marks that can be  
41 lost, and multi-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 AS models. Ignoring  
47 such violations of model assumptions can have important implications for ecological inferences and  
48 conservation policies. In general, the use of permanent marks (e.g. genotype), should always be  
49 preferred when modelling population dynamics. If not possible, an alternative is to combine two  
50 independent types of temporary marks (e.g. PIT tags, bands).

51 5. Analysis of our empirical dataset on *Myotis myotis* bats has shown that tag loss is higher in  
52 juveniles than in adults during the first year after tagging. The tag loss rate can be reduced from  
53 28% to 19% in juveniles by using surgical glue to close the injection hole, while it did not change  
54 the tag loss rate in adults (~10%). Main bias appeared in survival rate in our metapopulation system,  
55 with up to 20% of underestimation of survival rate if tag loss is not accounted for. Such a bias can  
56 lead to misinterpretation of population dynamics trends and wrongly influence conservation  
57 policies.

58

59 KEYWORDS

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

## 62 **1 Introduction**

63 Capture-mark-recapture (CMR) methods have become a standard approach to estimate  
64 demographic rates of wild species thanks to the development of a range of different models.  
65 Accurately quantifying population dynamic parameters is critical to assess the state of populations,  
66 understand their dynamics, and ultimately make efficient management and conservation decisions.  
67 However, all CMR models make a number of assumptions of homogeneity (Johnson et al., 1986;  
68 Williams et al., 2002) that are prone to generate biases if violated. A widespread violation of CMR  
69 model assumptions, originally identified four decades ago (Nelson et al., 1980), is the loss of marks  
70 (see Supporting Information 1, Table S2). Mark loss has two consequences: (1) when mark  
71 shedding occurs it induces non-identifiability of these individuals (detection heterogeneity), which  
72 implies that they are considered either dead or out of the study area, despite being alive and present;  
73 (2) if these individuals are captured again, they will not be recognized and will be remarked as  
74 newly recruited individuals, known as “recycled” individuals (Malcolm-White et al., 2020). In open

75 population models, estimates of abundance in the Jolly-Seber (JS) model (Jolly, 1965; G. Seber,  
76 1965) or of survival in the Cormac-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber,  
77 1965) can be affected by mark loss (Arnason & Mills, 1981). Many statistical tools have been  
78 developed to remove the confounding effect of mark loss in these models (Arnason & Mills, 1981;  
79 Cowen & Schwarz, 2006; Robson & Regier, 1966; G. A. F. Seber & Felton, 1981). However, the  
80 multi-state models that have now undergone substantial development (Lebreton et al., 2009) have  
81 not received such attention and the effect of mark loss on state transition has not been studied.  
82 In multi-state models, if survival is state dependent, survival is the product of true survival and  
83 mark retention rate for individuals in a particular state (Lebreton et al., 1992; Lebreton et al., 2009).  
84 If the retention rate starts to drop below one without being considered in the model, while true  
85 survival remains constant, survival in a particular state is underestimated and becomes confounded  
86 with the probability of presence of the mark, even more if true survival is high, but it is not clear  
87 how state transitions are affected. Consider “1011”, a simple four occasions encounter history,  
88 where “1” implies the individual was caught and “0” not. If we note  $\phi_t$  the survival rate between  
89 occasion  $t$  and  $t+1$  and  $p_t$  the capture probability at occasion  $t$  (with  $q_t = 1 - p_t$ ), this encounter  
90 history occurs with probability  $\phi_1 q_2 \phi_2 p_3 \phi_3 p_4$ . This probability product can be broken down as  
91 follows: the individual survive between  $t_1$  and  $t_2$  ( $\phi_1$ ) but was not captured in  $t_2$  ( $q_2$ ) and survive  
92 between  $t_2$  and  $t_3$  ( $\phi_2$ ) and was captured in  $t_3$  ( $p_3$ ) and finally survive between  $t_3$  and  $t_4$  ( $\phi_3$ ) and was  
93 captured in  $t_4$  ( $p_4$ ). Now consider the individual can make a transition between 2 states, and its  
94 history becomes “1022”, with individual in state “1” at  $t_1$  and in state “2” at  $t_3$  and  $t_4$ . Two things  
95 might have happened at  $t_2$  when the individual was not detected: either it stayed in state 1 or it made  
96 a transition to state 2. This led us to introduce  $\psi^{i,j}$  the transition probability from state  $i$  to state  $j$  ( $i$   
97 and  $j$  in  $\{1,2\}$ ), conditional on survival. The new encounter history is now the sum of two  
98 components to account for the two possible his histories “1122” or “1222”, respectively:  
99  $\phi_1^{(1)} \psi^{(1,1)} q_2^{(1)} \phi_2^{(2)} \psi^{(1,2)} p_3^{(2)} \phi_3^{(2)} \psi^{(2,2)} p_4^{(2)} + \phi_1^{(1)} \psi^{(1,2)} q_2^{(2)} \phi_2^{(2)} \psi^{(2,2)} p_3^{(2)} \phi_3^{(2)} \psi^{(2,2)} p_4^{(2)}$ , with indices for state-

100 specific parameters noted in parentheses. But, if this individual loses its mark after its first capture  
101 **and is** remarked when recaptured at  $t_3$  and not recognized, its encounter history becomes ‘two’  
102 different histories from ‘two different’ individuals: one becoming “1000”, the second “0022”. In  
103 this case, survival and mark loss patterns are different. Not only is survival underestimated (at least  
104 for the "first" history), but so are the transition probabilities, because there is no longer a change of  
105 state (the second history starts directly at state 2).

106 **Many** CMR studies, ~~despite using different mark types~~, are affected by mark loss, the rate of which  
107 varies according to a myriad of factors, such as species (see **Supported** Information 1, Table S2),  
108 mark type (Smout et al., 2011a), sex (Conn et al., 2004), mass (Schwarz et al., 2012), size (Acolas  
109 et al., 2007), mark location (Kaemingk et al., 2011) or physiological stage (Besnard et al., 2007).  
110 Mark loss has previously been shown to produce negative bias in survival estimates and detection  
111 (Nichols et al., 1992; Nichols & Hines, 1993). Multi-state models were developed to deal with  
112 situations where the “state” (e.g. location, behaviour, physiology, reproductive or social status) of an  
113 individual may affect its survival or detection probability, and where the individual can change  
114 “state” during life (reviewed in Lebreton et al., 2009). These models became popular and widely  
115 used because of their flexibility to address a large range of study systems and biological questions,  
116 and because they can be used in a relatively straightforward manner by biologists given the  
117 development of user-friendly softwares (e.g. Mark (White & Burnham, 1999), WinBUGS (Lunn et  
118 al., 2000), JAGS (Plummer, 2003), E-SURGE (Choquet, et al., 2009), MultiBUGS (Goudie et al.,  
119 2020), NIMBLE (de Valpine et al., 2017), STAN (STAN Development Team, 2022)). They are used  
120 to address many ecological and evolutionary hypotheses based on variations in life history traits  
121 (state transitions) throughout an individual’s life (Nichols & Kendall, 1995; see also Cam 2009 for  
122 an extensive discussion on the subject), or density dependence effect (Schofield & Barker, 2008),  
123 co-evolution (Benkman et al., 2005), dispersal probability among subpopulations or living areas  
124 (Hestbeck et al., 1991; Spindel et al., 1995), disease prevalence in wild populations (Jennelle et

125 al., 2007). However, the literature dealing with the effect of mark loss on multi-state model  
126 behaviour is scarce and much remains to be explored (Seber & Schofield, 2019).  
127 To **address** this gap ~~in knowledge~~, we used simulation-based Arnason-Schwartz (AS) model  
128 approaches (Arnason, 1972, 1973; Schwarz et al., 1993) to investigate the impact of mark loss on  
129 estimates of model parameters within a Bayesian framework. Given the increasing use of such  
130 multi-states models, our goal is to assess the potential bias in the marginal posterior distributions of  
131 demographic parameter estimates using a metapopulation context, based on biologically realistic  
132 scenarios and if possible, provide comprehensive guidelines for both, ~~fieldwork~~ and data analyses.  
133 The AS model shares assumptions with the CJS model, particularly in relation to mark loss, but it  
134 assumes in addition that states are recorded without error. Similarly to CJS model, we predicted that  
135 the AS model would potentially **be subject to underestimation** of survival but also of transitions  
136 probabilities in case of tag loss and recycling (Nichols & Hines, 1993). As **transition probability is**  
137 conditional on survival and detection on state in our AS model, we expected errors in estimates to  
138 propagate to model parameters in different ways according to state transition rate.  
139 To illustrate our approach with an empirical example, we used our decade-long mark recapture  
140 dataset of PIT-tagged and genotyped greater mouse-eared bat (*Myotis myotis*), a taxonomic group  
141 particularly susceptible to PIT-tags loss (Freeland & Fry, 1995). We used **'genotype'** as an  
142 individual permanent mark to estimate bias between models accounting/**not accounting** for mark  
143 loss and recycling, **and** suggested recommendations for future studies.

## 144 **2 Material and method**

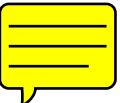

145 To quantify the potential bias induced by mark loss on parameter estimates in the AS framework,  
146 we defined several scenarios corresponding to representative situations inspired from the  
147 compilation of data from an existing database for tetrapods, the Demographic Species Knowledge  
148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

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


## 167 **2.1 Data generation**

168 For each scenario, we simulated data on a study period of 10 capture occasions (e.g. years), and  
169 between occasions the individuals can change state among 5 possible states : “A”, “B”, “C”, “D”  
170 and death. As death, state “D” was set as an absorbing state, without possibility to change when it is  
171 reached, which illustrated for example permanent emigration. At the first occasion, individuals in  
172 state “A”, “B” and “C” were composed of 40 juveniles (sex ratio 1:1) and 60 adults (80% females,  
173 20% males); there was no individual in state “D”. On each subsequent occasion, 40 juveniles and 5  
174 adults were marked in each state (“A”, “B”, “C”) except in state “D”, where it is not possible to

175 recapture individuals but only to observe them. This hypothetical system can be seen as 3 breeding  
176 sites (“A”, “B”, “C”) where capture and resighting occur each year, and a surrounding area (“D”),  
177 where only resighting is possible. **This sexual dissymmetry in transition** is common in mammals  
178 (and other taxa) and allows us for example to distinguish permanent emigration (absorbing state)  
179 from other movements. For each simulated scenario, all juveniles captured at one particular  
180 occasion are considered adult at the subsequent occasion. All scenarios shared the same data  
181 generation steps (Fig. 2). We began to simulate survival of individual  $i$  at occasion  $t$  with Bernoulli  
182 distribution:


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

183 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  
184 survival probability. We allowed stochastic variations in survival rate for each age class and  
185 occasion. If the individual survived, the state transition was simulated with Categorical distribution:


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

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



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

193 with  $ts_{i,t}$  a binary variable indicating the presence of the mark on individual  $i$  at occasion  $t$  and  $pr_{i,t}$   
 194 an age and time from marking dependant probability of retention (see Supported Information 2, Fig.  
 195 S2), which is the complement of mark loss probability  $ptl$  ( $ptl_{i,t} = 1 - pr_{i,t}$ ).  
 196 Finally, the detection process was simulated with Categorical distribution:

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

197 where  $pd_{i,t}$  was a state specific detection probability (Supported Information 2, section 1.2). We  
 198 considered two different and common ways of re-encountering individuals, physical capture, which  
 199 allowed either recycling (re-mark) or mark checking, and resighting which is a passive detection,  
 200 including only individuals that have retained their mark. This approach is motivated by the fact that  
 201 in most studies, the probability of resighting is typically higher than the probability of recapture,  
 202 therefore they can be differently affected by estimation biases. The probability of detection is  
 203 conditioned by the retention of the mark and was divided into 7 categories:

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

204 where  $pc_{i,t}$  was a state specific capture probability,  $pr_{i,t}$  a state specific resighting probability and  $pb$   
 205 the detection probability in state "D".

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


208 lived species with low detection rate; (3) short-lived species with low detection rate; (4) short-lived  
209 species with high detection rate. Values of parameter simulated are reported in Table 2. and Fig. 3.  
210 As mark shedding is often dependant on time since marking and occurs most frequently shortly  
211 after marking in many species (in our case study; Fabrizio et al., 1999; Fokidis et al., 2006;  
212 Kremers, 1988; Nichols & Hines, 1993), for each scenario, we investigated a range of mark loss  
213 rates commonly reported in the literature (Supported Information 1, Table S2). We simulated three  
214 mark loss probabilities, low ( $ptl = 0.05$ ), medium ( $ptl = 0.25$ ) and high ( $ptl = 0.4$ ), during the first  
215 year after marking and a constant 0.05 rate thereafter, which generated a diversity of cases of mark  
216 loss and recycled individuals (Supported Information 2, Fig. S2-3). This process allowed the  
217 generation of datasets that took into account mark loss in the presence of a second permanent mark.  
218 To generate datasets in which mark loss was not accounted for (no second permanent mark), we  
219 created recycled individual with the life history corresponding to the portion of life after mark loss  
220 and replaced the original life history from mark loss with zeros. For exemple, a life history “1111”  
221 of an individual that lost its mark between occasion 2 and 3 and is newly remarked at occasion 3,  
222 became two new histories: (1) “1100”, the first part of life before mark loss; (2) “0011”, a second  
223 individual, in fact the same but not recognised in the absence of a permanent mark, considered as  
224 newly recruited. Using this data generation process, we simulated 2 x 50 datasets for each of the 12  
225 combination of parameters (50 with and 50 without recycling), leading to a total of 1200 simulated  
226 datasets (Supported Information 2, Fig. S1). The computational codes for a fully reproducible  
227 example dataset are provided in the Supported Information 2.

## 228 **2.2 Statistical models**


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

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

236 To estimate the state, time and age dependant survival  $\Phi$  for both model we used a Bernoulli  
237 distrib above eq. 1):


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

238 where  $A_{i,t}$  is the life status of individual  $i$  at time  $t$  and coefficient  $\alpha$  is a state effect,  $\beta$  a time effect,  $\delta$   
239 an age effect and  $\gamma$  a simultaneous effect of state, age and time. Transition and detection processes  
240 were estimated using the same distributions as described for data generation (see above eq. 2,4,5).  
241 The difference between the two models lied in the estimation of mark loss, which involved tracking  
242 the fate of marks (retained or lost) for each individual (*ModelA*). Several combination of single,  
243 double, and permanent marks have been used in the past to estimate mark loss (Laake et al., 2014).  
244 In *ModelA*, we considered a single mark loss approach, while the second mark is permanent, which  
245 allowed to identify if the non permanent mark was lost or retained at each capture occasion and  
246 resighting was conditional on mark retention (Eqn. 5). Using a statespace approach we built directly  
247 mark retention process in the model. While it is possible to model presence-absence of marks as  
248 states with a transition matrix (McMahon & White, 2009), or as a hidden Markov process for  
249 unobserved individuals for which we have no information if mark was retained or lost (Laake et al.,  
250 2014), we simply modelled mark retention process using a Bernoulli distribution with  $ts_{i,t}/ts_{i,t-1} \sim$   
251 Bernoulli( $pr_{i,t}$ ) if the individual was marked or retained its mark at t-1 ( $ts_{i,t-1} = 1$ ). Three retention  
252 probabilities ( $pr$ ) were estimated as a function of age and time since marking:

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


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

## 257 **2.3 Application on a bats dataset**

258 We used the simulations both to test general hypotheses about the effect of mark loss on multi-state  
259 model parameter estimates, but also to validate a parametrisation capable of estimating these  
260 parameters without bias. On this basis, we can accurately estimate the probability of mark loss in  
261 our own dataset, but also the relevance of using in the long term a permanent mark, i.e. the  
262 appropriateness of using double-marking to avoid estimation bias (Juillet et al., 2011). Our  
263 empirical dataset consisted of a 10-year study of CMR data on the greater-mouse eared bat (*Myotis*  
264 *myotis*) in Brittany (France; 2010-2019). A total of 2,561 individuals were marked in 5 maternity  
265 roosts: La Roche Bernard (47°31'N, 2°18'W), Férel (47°28'N, 2°20'W), Noyal-Muzillac (47°35'N,  
266 2°27'W), Béganne (47°35'N, 2°14'W) and Limerzel (47°38'N, 2°21'W). The bats were individually  
267 tagged using Passive Integrated Transponders (PIT) tags, ID-100C (Troven®), with a unique 10-  
268 digit code. These small tags (2.12x11mm, 0.1gr) allowed identification from passive readers. All  
269 individuals caught in roosts without PIT-tags were systematically tagged, which included both  
270 individuals who lost their tag and those which were never tagged before, and genotyped as a second  
271 and permanent marking method. Genotypes were established from DNA extracted from wing  
272 biopsies from all individuals tagged and from all males untagged caught during swarming surveys  
273 (n=4,258 samples; details in Supporting Information 3, Fig. S1), as male capture probability at  
274 roosts after birth was extremely low. A total of 16 microsatellite markers optimised for *Myotis*  
275 *myotis* were used to establish individual genotypes (Foley et al., 2020). To minimize genotyping  
276 errors, we analysed, when available, **2** different samples per individual and all samples were

277 genotyped and scored twice by two different people. We also performed genetic profile comparisons  
278 to detect errors (Frantz et al., 2003; Puechmaile & Petit, 2007). We hypothesised that the error rate  
279 of genotypes was low enough to be negligible and did not include this source of uncertainty in the  
280 models (Winiarski & McGarigal, 2016). We also checked each winter for the presence of lost tags  
281 on the floor of the maternity roosts, which allowed us to identify, at least in part (61.5% compared  
282 to the genotype), the individuals that lost their tag, with the rest of losses having occurred outside of  
283 the roosts. Most of these tags were lost during the first year (Supporting Information 3, Fig. S2),  
284 which is confirmed by the absence of their records from passive reading detectors. In total, 252  
285 individuals out of 2,561 (~10%) were identified as having lost their tag at least once. From those  
286 individuals, 94 individuals were recaptured and retagged a second time and three retagged a third  
287 time. As retagging took place during the last capture occasion for 13 individuals, ignoring tag loss  
288 for them led to the recycling of a total of 81 individuals out of 94. To analyse these data, we fitted a  
289 multisite model (where states are maternity roost and transition are movement between these sites),  
290 similar to the AS model used for simulated data (Supporting Information 3). We defined two age  
291 classes for survival, juveniles (individuals in their first year of life) and adults (individuals older  
292 than one year). In order to explore departures from the AS model assumptions, we performed  
293 goodness-of-fit tests on life history of the adult cohort, using R2ucare (Gimenez et al., 2018), an R  
294 package based on U-CARE (Choquet et al., 2009). Tests for transience and for memory showed  
295 minor overdispersion ( $\hat{c}_{3G.SR}=1.82$  and  $\hat{c}_{WBWA} = 1.96$  respectively). It was not possible to perform the  
296 other goodness-of-fit tests because the individual contingency tables had insufficient data to provide  
297 statistical values. We then retained our two-age class structure for survival modelling. Unmeasured  
298 individual survival heterogeneity was also modelled by including a normally distributed random  
299 effect in the estimation of survival probability, as other covariates do not capture the relevant  
300 variation. Indeed, individual heterogeneity plays a key role in population dynamics and evolution,  
301 and it is ubiquitous in wild population (Gimenez et al., 2018). Emigration from the five studied

302 subpopulations was assessed using capture and resighting data obtained between capture occasions  
303 at swarming and wintering sites.  
304 We defined eight possible detection states which allowed us to estimate separately, capture and  
305 resighting probabilities (see Supporting Information 3, Table S1). As empirical data suggested the  
306 possible movement of individuals between all subpopulations and outside, we did not constrain  
307 transition between subpopulations except for movement of juveniles from outside the maternity  
308 roosts which was not possible (there was no tagging outside the 5 roosts) and therefore set to 0 (see  
309 Supporting Information 3, Fig. S3). In this study, we also tested the effect of surgical adhesive  
310 (Vetbond®) after PIT-tag injection, in order to assess tag-loss reduction in comparison with self-  
311 healing (Lebl & Ruf, 2010; van Harten et al., 2020). In this model, tag retention probabilities were  
312 modelled similarly to [equation 7](#), by accounting for time since marking (two discrete classes: first  
313 year or subsequent years), individual age class (juvenile or adult), but also use of surgical adhesive  
314 (yes or no). As per the simulated datasets, two models were run on two datasets, a first one allowing  
315 tag loss estimation thanks to the genotyping (second permanent mark), and a second model ignoring  
316 this information on a transformed dataset including recycled individuals (following the same  
317 process as simulated data).

## 318 **2.4 Estimation procedures and assessments**

319 Despite a frequentist approach was possible for simulated data analyses (Lebreton et al., 2009), we  
320 chose a Bayesian approach to be consistent with the analysis of empirical data where these methods  
321 are more flexible in accounting for individual heterogeneity in survival (Gimenez, et al., 2018).  
322 Simulated and empirical data were analysed with JAGS (Kruschke, 2014; Plummer, 2003) through  
323 the jagsUI package (Kellner, 2016) from R 3.6.0 (R Core Team, 2019). We used four Monte Carlo  
324 Markov chains (MCMC) with 150,000 iterations each and drew samples from posterior  
325 distributions after discarding the first 50,000 iterations (burn-in). We retained every twentieth  
326 iteration generating 20,000 samples from the posterior distribution for each parameter. Chain

327 convergence was assessed with the Gelman-Rubin statistic denoted  $R\text{-hat}$  (Brooks & Gelman,  
328 1998). Among the 1,200 simulations, some parameters showed  $R\text{-hat}$  values  $> 1.05$ , indicating  
329 convergence failure. Less than 0.4% of the estimated parameters for the model accounting for mark  
330 loss failed to converge (Supporting Information 2, Table S1), in particular coefficient  $\gamma$  (combined  
331 effect of state, time and age on survival probability) and  $\gamma.c$  (combined effect of state and time on  
332 detection probability). The mean  $R\text{-hat}$  values of these parameters was less than 1.2 (Supporting  
333 Information 2, Fig. S4). For models not accounting for mark loss, 1.3% of the estimated parameters  
334 did not converge (Supporting Information 2, Table S2), in particular for scenario where either  
335 detection or both detection and survival were low (respectively scenario 2 and 3) and mark loss  
336 probability was set to 0.25 or 0.4. Again, in most case, parameters that failed to converge showed a  
337 mean  $R\text{-hat}$  value less than 1.2, only a few exceeded 1.5 (Supporting Information 2, Fig. S5). Of all  
338 the simulations, no convergence failures concerned the probability of mark loss. To avoid  
339 prohibitively long computing time, we did not attempt to increase the number of iterations to  
340 achieve the complete convergence of MCMC chains for these parameters in the simulations  
341 concerned. Our results are based on 50 simulated datasets per scenario, and it was assumed that lack  
342 of convergence for these few parameters has no substantial influence on our results.

343 For assessing bias in parameter estimates when mark loss or recycling is not accounted for, we  
344 computed the Earth Mover Distance (EMD), using the  $EMD-L_1$  algorithm (Ling & Okada, 2007), a  
345 distance function that quantifies the difference between two distributions. This metric measures the  
346 minimum cost of turning, point by point, a distribution into another. We also estimated a ROPE  
347 (Region Of Practical Equivalence, Kruschke, 2018) for each scenario to assess the degree of  
348 difference between distribution represented by the EMD metric. To define this ROPE for each  
349 scenario, we randomly built 1,000 pairs of models from the 50 simulations and calculated the  
350 associated 1,000 EMDs from the posterior distributions of the estimated parameters (for more  
351 details see Supporting Information 2, Fig. S76). The obtained distributions of EMD represented

352 variations expected for inferences obtained from simulations initiated with the same parameter  
353 values. The ROPE was then defined between 0 and the upper value of the 80% highest posterior  
354 density interval (hdi) from the distribution of these EMD. Finally, the proportion of EMD for each  
355 simulated case outside the ROPE was computed, giving a direct indication of bias, the higher this  
356 proportion, the higher the bias. Comparisons of EMD between the models that did and did not  
357 account for tag loss and recycling to their respective ROPE is a way to illustrate cases in which not  
358 accounting for tag loss leads to estimates that substantially differ from estimates obtained when  
359 accounting for tag loss. We also assessed parameter bias as the difference between the median of the  
360 posterior distribution and the true value simulated (median – truth). With the empirical data, the  
361 median of the posterior distribution of parameters from the model accounting for a secondary  
362 permanent mark was used as truth. Finally, precision (mean squared errors  $MSE = bias^2 + variance$ )  
363 of the parameter estimates was also calculated for the simulated data.

## 364 **3 Results**

### 365 **3.1 Simulation results**



366 The number of mark lost and individuals recycled increased in scenarios with higher survival,  
367 detection and mark loss rate (Supported Information 2, Fig. S3). As expected, for an equivalent rate  
368 of mark loss, the proportion of individuals recycled relative to the number of marks lost was higher  
369 when the recapture rate was high (i.e. in scenario 1 and 4). Irrespective of scenarios, no estimation  
370 bias appeared on demographic parameters when mark loss was set to 0.05 (Supporting Information  
371 2, Fig. S28-S31). The number of parameters for which estimates were biased increased with the rate  
372 of mark loss, but the magnitude was not consistent across the simulated scenarios. In particular,  
373 some adult and juvenile survival showed substantial underestimation in scenario 1 (Fig. 4 & 5). The  
374 probability of remaining in the same state was also underestimated among juveniles, and therefore  
375 their probability of transitioning to another state was overestimated (Fig. 4 & 6). The resighting



376 probability was underestimated in all state but B (Fig. 4 & 6). The state transition biases were  
377 particularly high for transitions to absorbing states as it is the case in our simulations for juveniles  
378 who transit to the "D" state (Supporting Information 2, Fig. S57-S71). For simulations with a mark  
379 loss rate of 0.4, scenarios 1 and 4, that share both high recapture probabilities, showed  
380 underestimates of adult survival in the early years of the study only (Supporting Information 2, Fig.  
381 S21-S22 and S27). Juvenile survival was less biased, nevertheless moderate underestimations  
382 occurred for high mark loss rate in particular for state A and B in scenario 1 and 4 (Supporting  
383 Information 2, Fig. S21-S22 and S27). Lack of precision in the estimate of juvenile survival was  
384 also observed for model not accounting for tag loss when mark loss rate was high. Resighting  
385 probability showed substantial bias, with underestimates mainly in state "A" and "C" (Fig. 4 and  
386 7.a), as well as lack of precision for all scenarios and mark loss rates (Supporting Information 2,  
387 Fig. S28-S49). However, recapture, our second component of detection, showed little bias except  
388 during the second capture occasion for state "A" and "C" in scenario 1 when mark loss rate was  
389 0.25 and scenario 1 and 4 when mark loss rate was 0.4. This came along with a decrease in the  
390 precision of the latter parameter at high mark loss. A large percentage of the transition probabilities  
391 estimates were biased when mark loss and recycling were ignored (Fig. 6.b-e), with in general an  
392 underestimate of the probability to remain in the same state and, as a corollary, an overestimates of  
393 the probability of changing state, with a decrease in precision mainly at high mark loss rate  
394 (Supporting Information 2, Fig. S50-S71). Overestimations occurred in juvenile males except from  
395 state "C", where transition rate to state "D" was the highest (0.9). For females, when mark loss was  
396 set at a high level, the same pattern was observed in states "A" and "B", from which states  
397 transitions were set at a low level. On the contrary, for transition from state "C" to "B" (set high =  
398 0.4), we observed an underestimation of the transition probability and an overestimation of the  
399 probability to remain in state "C" with scenarios set with low detection rates (scenario 2 and 3,  
400 Supporting Information 2, Fig. S67-S70).

## 401 **3.2 Bat metapopulation**

402 Most of the estimated parameters (survival, capture, resighting and state transition probabilities)  
403 showed both negative and positive biases, with no clear pattern (Fig. 7, Supporting Information 3,  
404 Fig. S4-S11). Larger biases were apparent in survival estimates, with underestimation of median  
405 survival reaching over 0.26 in juveniles (Fig. 7a) and 0.21 in adults (Fig. 7b). Emigration, i.e.,  
406 movement outside ("Out") the maternity sites studied, was overestimated by an average of 0.05  
407 throughout the study (Fig. 7b). The probability of recapture was overestimated and underestimated  
408 by up to 0.1, depending on occasion and roost (Fig. 7c). The estimated bias in the other parameters  
409 was small (Fig. 7d and e). The estimated tag loss probability was high for juveniles but  
410 substantially reduced by the use of surgical glue (Fig. 8), decreasing by one third from 0.28  
411 (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  
412 tag loss rate, with an overlap of 69% of the probability distributions. The adult tag loss rate was  
413 around 0.1 which is two times less than in juveniles when surgical glue was used. Considering the  
414 period following one-year post-tagging, the probability of tag loss when surgical glue was used is  
415 higher (median 0.03, 90%hdi [0.02, 0.04]) versus not used (median 0.02, 90%hdi [0.01, 0.02]). This  
416 difference may be in fact an artefact due to a lack of search for lost tags on the ground of the  
417 maternity roost in the first year of the study (Supplementary Information 3, part 3 and Fig. S12).  
418 Other parameter estimates can be found in Supporting Information 3, part 2.6.

## 419 **4 Discussion**

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

425 2019). However, for AS models, few developments have been proposed to account for mark loss  
426 (Besnard et al., 2007; Conn et al., 2004; Johnson et al., 2016), all used a similar approach, implicitly  
427 modelling mark status or using an adjustment factor (Nishizawa et al., 2018). Furthermore, we  
428 found no exploratory studies on the effect of mark loss in parameter estimates. Here, we fill this gap  
429 by exploring both the effect of mark loss and recycled individuals on parameter estimates using  
430 simulations, and by modelling the state of the mark (retained or lost) as an intendant Bernoulli  
431 process. In particular, this allow us to explore how mark loss can affect state transition of individual  
432 states when capture and survival probabilities varied over time, survival varied also among age  
433 classes and mark loss processes depended on time since marking.

434 We showed that not only survival, but capture, resighting and state transition probabilities estimates  
435 can be substantially affected by this violation of CMR model assumptions. Survival is mainly  
436 underestimated in cases where capture and detection are high. This trend is accentuated when  
437 survival is also high, which moderates previous studies suggesting that biases mainly occur in  
438 species with both high survival rates, catchability and mark loss (Diefenbach & Alt, 1998). Our  
439 simulation results confirmed that the inaccuracy of model estimates is positively linked to the rate  
440 of mark loss, but can also occur when tag loss rate is low (5%) and can be independent of survival  
441 and capture rates. Indeed, in datasets with few recycled individuals, i.e. with low survival and  
442 capture rates, transition and resighting probabilities can be severely biased if mark loss is high. This  
443 suggests that results from studies where survival and capture are low should also be interpreted with  
444 caution if mark loss is suspected but not taken into consideration. In particular, the probability to  
445 stay in the same state is underestimated when transition from this state is low but become  
446 overestimated for high transition probabilities. Severity of bias can also vary over time, with bias in  
447 survival and recapture decreasing with time as in our simulated datasets. This is partly due to the  
448 mark loss pattern we chose, stressing the fact that, even in studies conducted over short periods,

449 parameters can be substantially biased. In cases where mark loss increases with time since marking  
450 (not investigated here), we would expect an increase of bias with time.

451 The combination of the simulation and empirical study results highlight how the complexity and  
452 interdependence of parameters can compound or counteract estimation biases in the absence of  
453 mark loss modelling. While the simulations showed some global rules on the direction of the biases,  
454 the real example showed instead how unexpected the bias patterns can be. In our simulation,  
455 although we intended to cover demographic variations classically observed across vertebrates, they  
456 have not been carried out under the immense range of parameters combinations that can be  
457 encountered in nature. Most study systems and monitoring methods have their own specificities and  
458 *a priori* prediction of bias without simulating them can be misleading. The propagation of  
459 uncertainty in parameter estimates due to mark loss is still challenging to predict and increases with  
460 system complexity. Therefore, prior to planning a CMR study, we advocate that  
461 researchers/managers run simulations to evaluate in which conditions (i.e. under which parameters  
462 combination) their study would provide reliable estimates of the parameters of interest (e.g.  
463 demographic, state transition). Preliminary studies with multiple marks could also be considered  
464 when possible (Smout et al., 2011a). This would allow CMR study design to be optimised prior to  
465 the study being conducted and hence limit biases from the onset.

466 AS models have been preliminary developed to estimate movement between sites, recruitment,  
467 dispersal, temporary or permanent emigration (Lebreton et al., 2003, 2009; Schaub et al., 2004).  
468 Our simulation results suggest that state transition probabilities are sensitive to mark loss, even at  
469 low rates, e.g. the probability to stay in the same state (philopatry if transitions are movements) or  
470 to change state (e.g. emigration) showed both under and overestimations. These parameters are  
471 often of central interest in many studies to answer ecological and demographic questions and are  
472 used for management and conservation purposes (Cam et al., 2004; Horton et al., 2011). Although  
473 the loss of marks is regularly reported for a wide variety of tags and taxa, it is only marginally

474 considered in studies interested in estimates of population dynamics parameters (Nelson et al.,  
475 1980; Ostrand et al., 2012; Smout et al., 2011b; Tavecchia et al., 2012). Most model developments  
476 to account for mark loss have focussed on the JS model for abundance estimates, where mark loss  
477 and recycling is prone to generate serious biases (Malcolm-White et al., 2020). The loss of the mark  
478 remains largely unconsidered despite an increasing use of AS models in ecology, demography,  
479 management and conservation (Huntsman et al., 2020; Melnychuk et al., 2017). In light of our  
480 study, we recommend the use of permanent or double temporary marks, ideally independent in loss  
481 or where dependence in loss is taken into account (Laake et al., 2014; McMahon & White, 2009;  
482 Schwarz et al., 2012), as any analysis of CMR data is potentially affected by this violation of model  
483 assumption (Riecke et al., 2019).

484 Despite the fact that PIT tags are suitable in an increasing number of studies and allow the  
485 collection of data without physically re-capturing individuals, our case study highlights the  
486 importance of a second marking method to avoid potential bias in estimations of demographic rates.  
487 Tag loss has long been known in small mammal species, in particular those that fly or glide  
488 (Freeland & Fry, 1995). Here we confirmed that PIT-tag shedding in the short term can be reduced  
489 by the use of surgical adhesive (Lebl & Ruf, 2010; van Harten et al., 2020).

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

497 Mark loss is typically not considered from ecological and management perspectives except when  
498 researchers are interested in understanding factors influencing mark failures or in improving their

499 marking methods. Our results highlight the need to assess the effect of mark loss each time mark  
500 failure is suspected, to avoid spurious conclusions about the dynamics of their studied species. In  
501 our experience and according to the literature, PIT-tags are prone to being shed regardless of the  
502 studied taxa, often in the short but sometimes in the long term. A recent study, that assess tag loss on  
503 Gould's wattled bats (*Chalinolobus gouldii*), over a relatively short period of 13-14 months, showed  
504 that tag shedding was low (2.7%) and generalised these results to all insectivorous bats (van Harten  
505 et al., 2020). Our study proves that this generalisation is partly wrong, and rather suggests that it is  
506 difficult to generalise such a conclusion and that the pattern of mark loss is highly species  
507 dependent, among other parameters. Mark loss should therefore be carefully considered in all CMR  
508 analyses and possibly also in other studies using similar datasets, and should be explicitly modelled  
509 when necessary for more accurate estimations of population dynamics.

510

## 511 **Acknowledgements**

512 This project was funded by an Irish Research Council Postdoctoral Fellowship Grant  
513 GOIPD/2018/256 awarded to F.T., a European Research Council Research Grant ERC-2012-  
514 StG311000 and an Irish Research Council Laureate Award awarded to E.C.T. The French field  
515 study was supported by the European Regional Development Fund EU000141 and a Contrat Nature  
516 grant awarded to Bretagne Vivante (BV). S.J.P. was supported by a Junior chair from the Institut  
517 Universitaire de France. We would like to thank the volunteers of BV for assistance in the  
518 fieldwork. Sampling was carried out in accordance with the French ethical and sampling guidelines  
519 issued in 3 successive permits delivered by the Préfet du Morbihan (Brittany) awarded to E.J.P., F.T.  
520 and S.J.P. for the period 2010–2020.

521

## 522 **Author contribution**

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

529

### 530 **Data accessibility**

531 R scripts for simulating the data, and analysing the data with JAGS, are accessible on Zenodo  
532 (<https://zenodo.org/record/6453953>).

533

### 534 **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](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](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](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](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., & Terner, 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., & Spendelov, 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., & Spendelov, 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](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](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>

- Spendelov, 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>

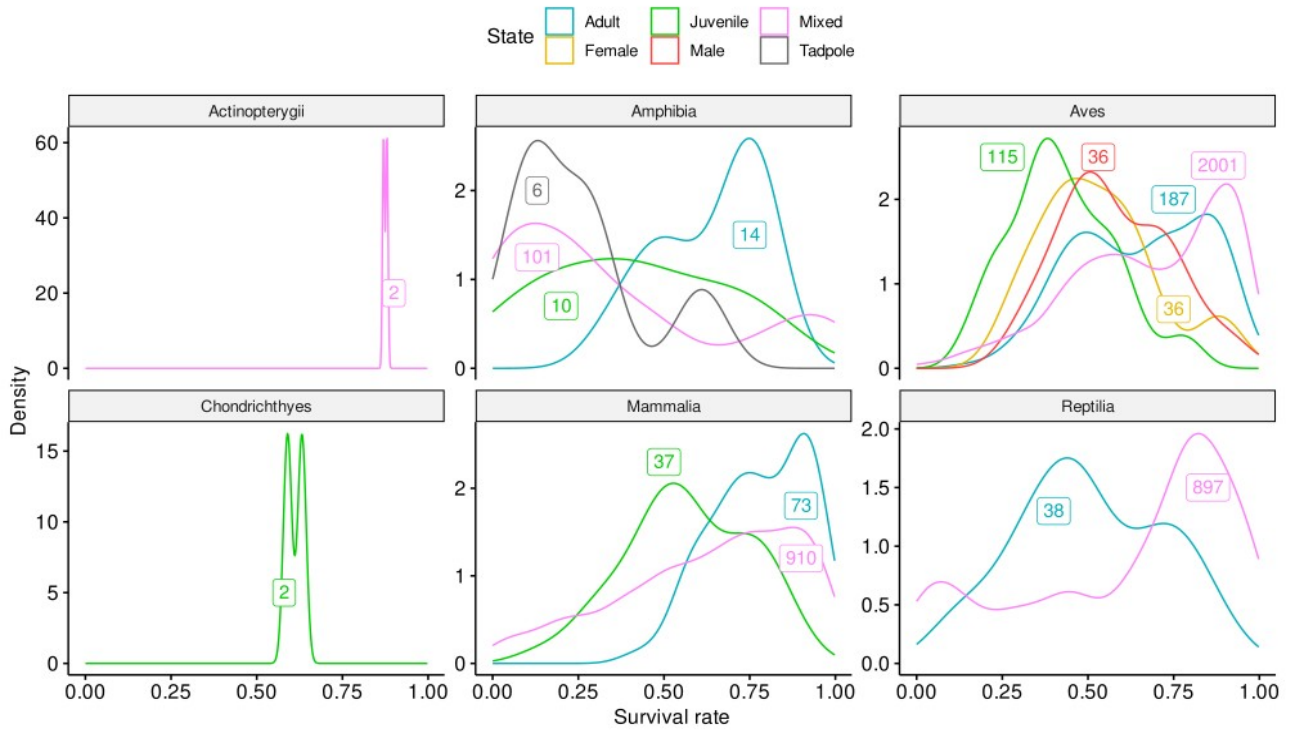


Figure 1: Density of probability of survival across age class and taxa for 700 species. Sample size are indicated by labels, with colour corresponding to the state of individual sampled.

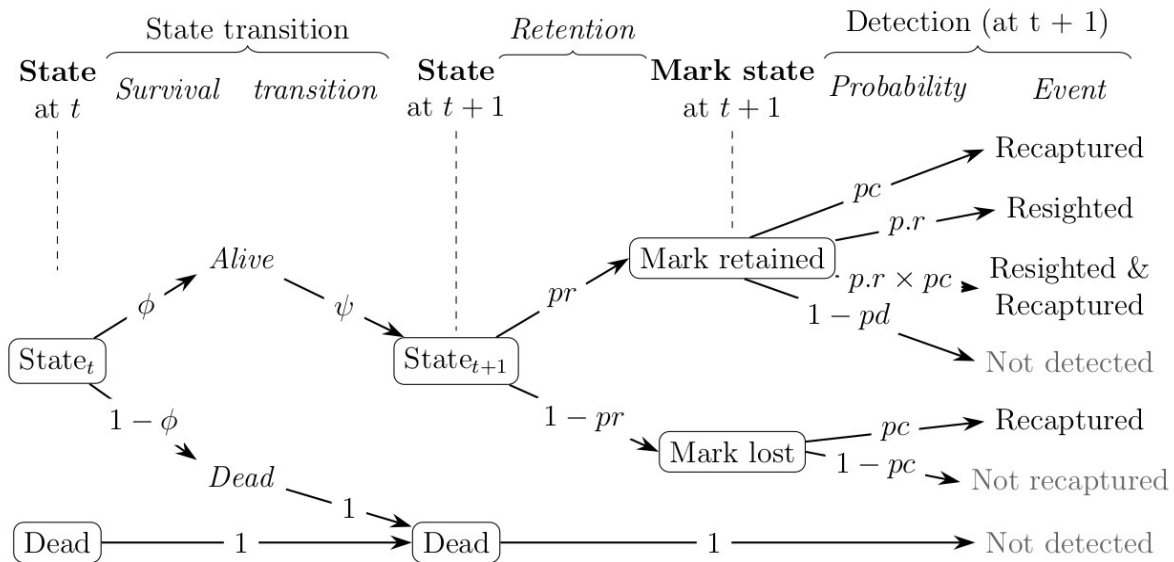


Scenario	Survival	Detection
Scenario 1	Long-lived (high survival)	High detection rate (capture & resighting)
Scenario 2	Long-lived (high survival)	Low detection rate (capture & resighting)
Scenario 3	Short-lived (low survival)	Low detection rate (capture & resighting)
Scenario 4	Short-lived (low survival)	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
$p_{cA}$	Capture probability in state "A"	U(0.6,0.7) [0.65]	U(0.6,0.7)-0.5 [0.15]
$p_{cB}$	Capture probability in state "B"	U(0.7,0.8) [0.75]	U(0.7,0.8)-0.5 [0.25]
$p_{cC}$	Capture probability in state "C"	U(0.65,0.75) [0.7]	U(0.65,0.75)-0.5 [0.2]
$p_{cD}$	Capture probability in state "D"	0	0
$p_{rA}$	Resighting probability in state "A"	0.85	0.35
$p_{rB}$	Resighting probability in state "B"	0.95	0.45
$p_{rC}$	Resighting probability in state "C"	0.9	0.4
$p_{rD}$	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 resighting 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.



535  
536  
537  
538  
539  
540  
541  
542  
543  
544  
545  
546  
547  
548  
549  
550  
551  
552  
553  
554  
555  
556  
557  
558  
559  
560

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  $\phi$  (depending on time and state at  $t$ ) and can then change state with probability  $\psi$  (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  $pc \cdot p.r$ , or finally not be detected at all with probability  $1 - pd = (1 - pc) \cdot (1 - p.r)$ .

561  
562  
563  
564  
565  
566  
567  
568  
569  
570  
571  
572  
573  
574  
575  
576  
577  
578  
579  
580  
581  
582  
583  
584  
585  
586  
587  
588  
589  
590  
591  
592  
593  
594  
595  
596  
597  
598  
599  
600  
601  
602  
603  
604  
605  
606  
607  
608  
609  
610

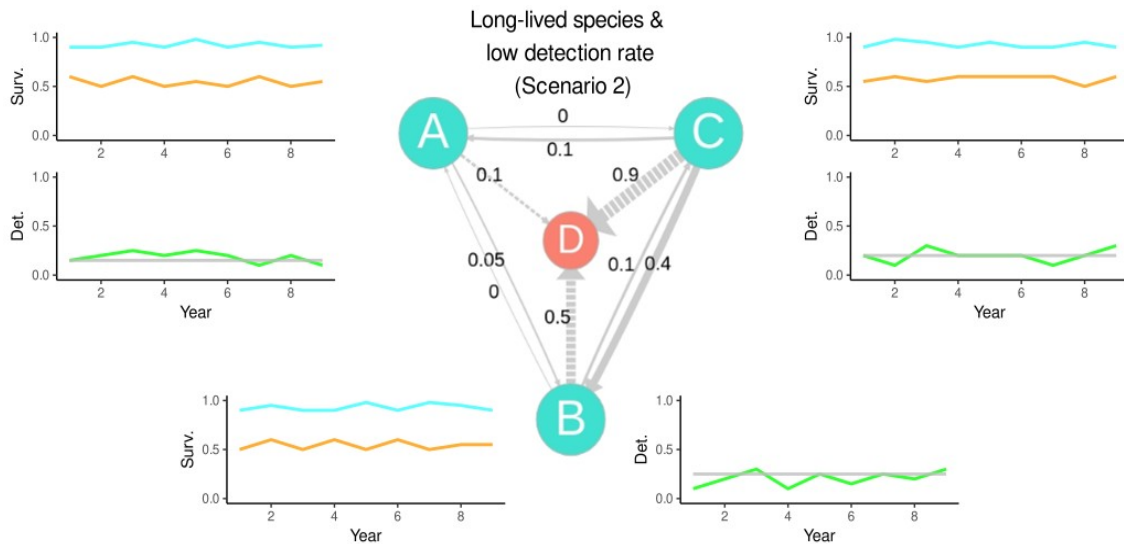


Figure 3: Schematic description of parameter values used to simulate data under scenario 2 (long-lived species with low detection). Central graph: solid arrows correspond to possible transitions of females and dashed arrows to those of males. The size of the arrows is proportional to the probability 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.

611  
612  
613  
614  
615  
616  
617  
618  
619  
620  
621  
622  
623  
624  
625  
626

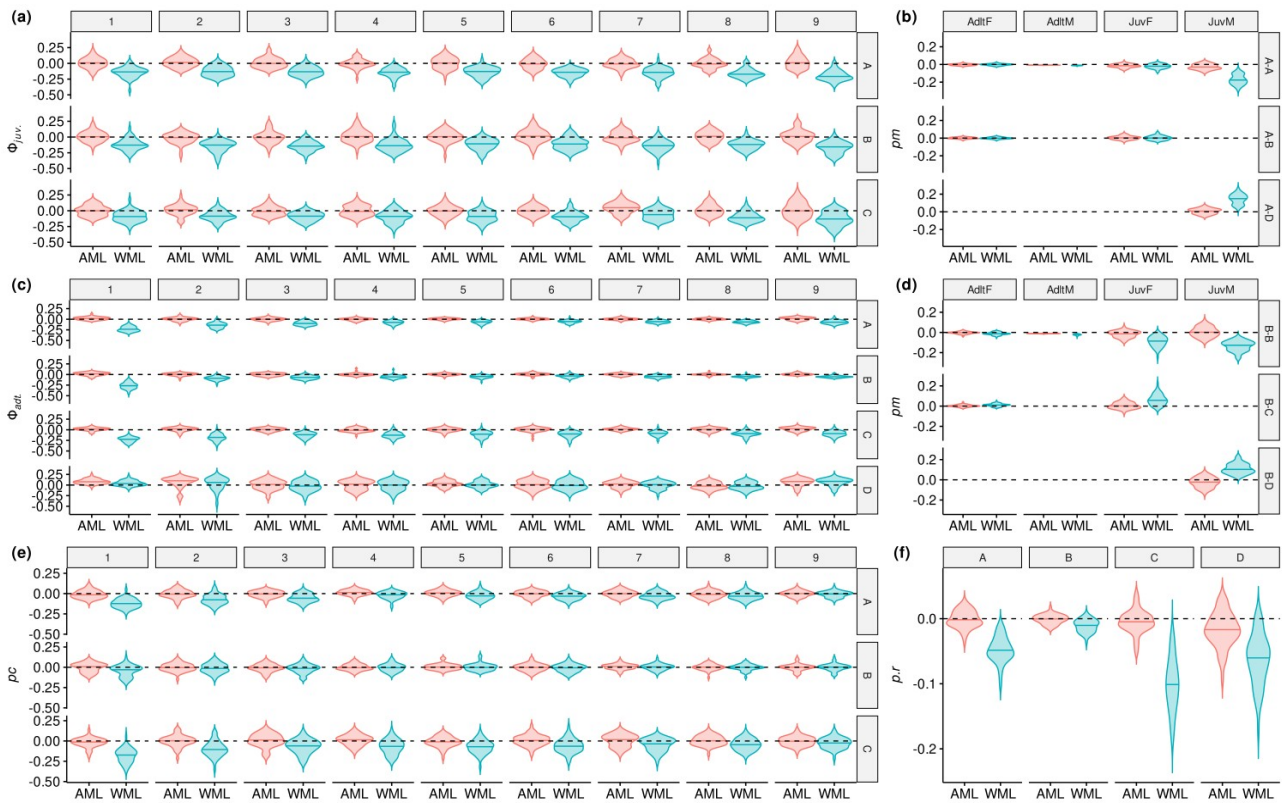


Figure 4: Comparison of bias for estimates of juvenile (a) and adult (c) survival, transition (b and d), capture (e) and resighting (f) probabilities between model accounting for mark loss (AML) or not (WML). All violin plots show the distribution of bias over 50 simulations from scenario 1 (long-lived 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.

628  
629  
630  
631

632  
633  
634  
635  
636  
637

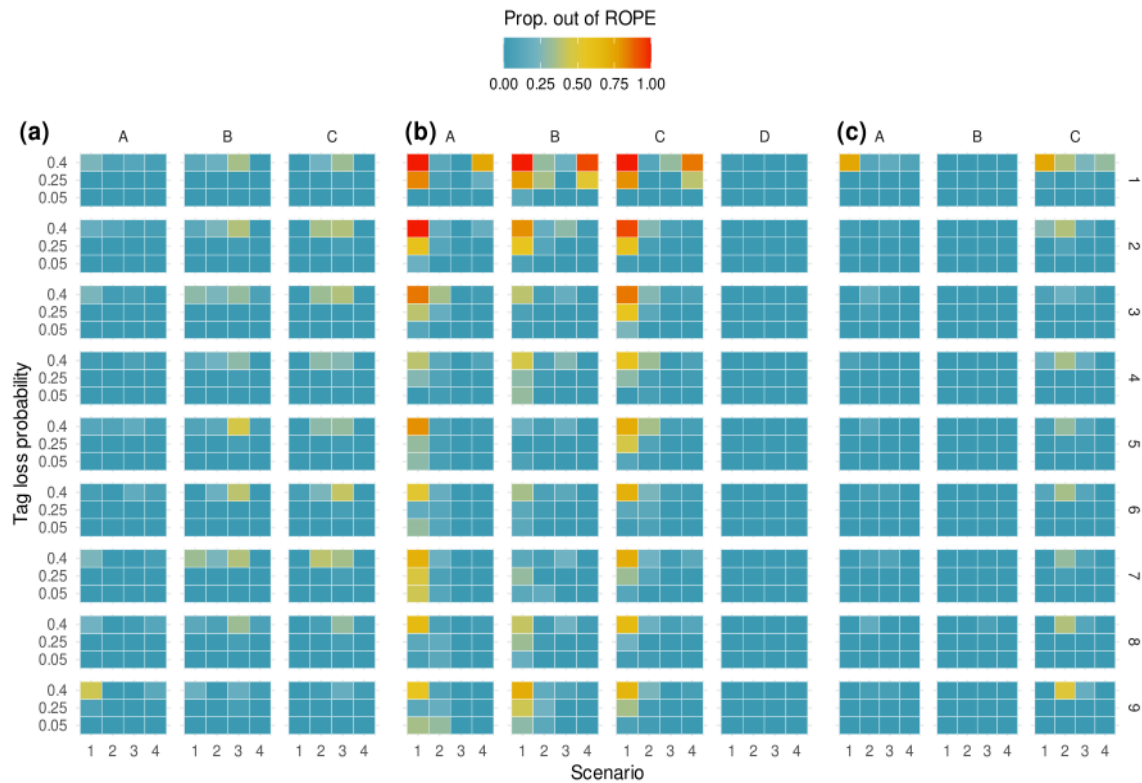


Figure 5: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between the model accounting for tag loss and recycling (ModelA) and the model ignoring them (ModelW). The ROPE corresponds to the interval 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.

639  
640  
641  
642  
643  
644  
645  
646  
647

648  
649  
650  
651  
652  
653  
654  
655

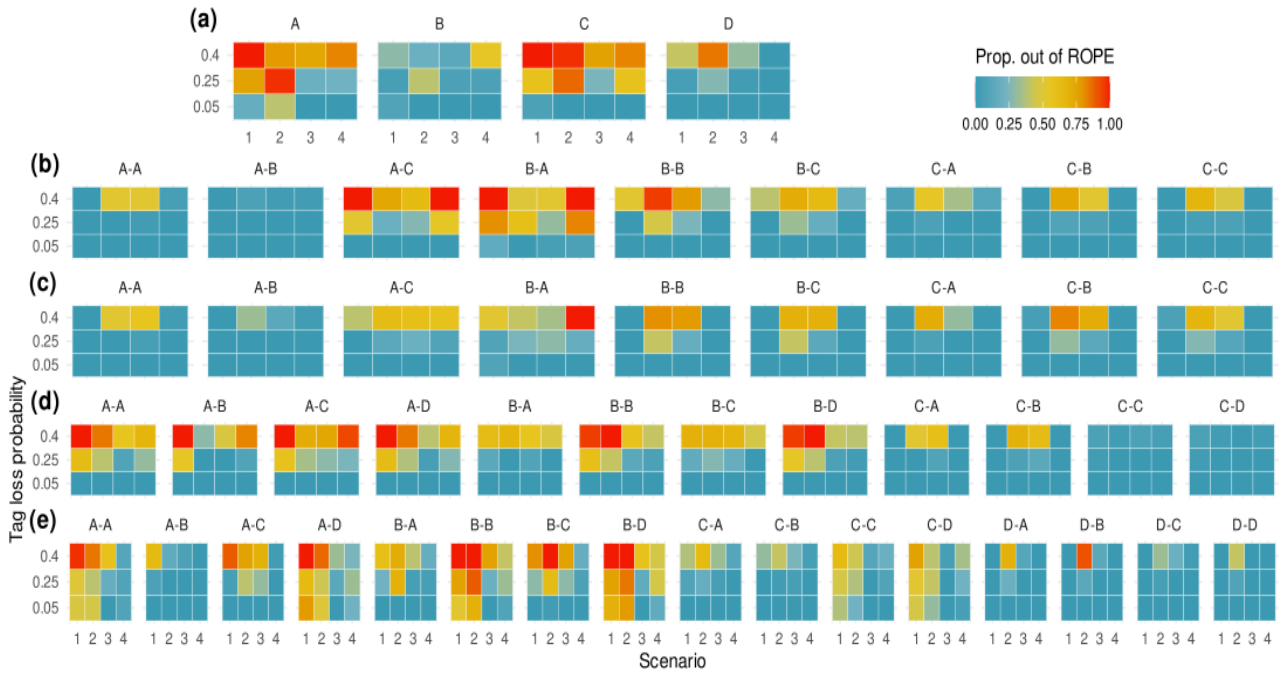


Figure 6: Tile-plots of the proportion of the distribution of the Earth Mover Distance (across 50 simulated datasets) out of the Region of Practical Equivalence (ROPE), between model accounting for tag loss and recycling (ModelA) and the model ignoring them (ModelW) for each simulated cases. The ROPE 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.

657  
658  
659  
660

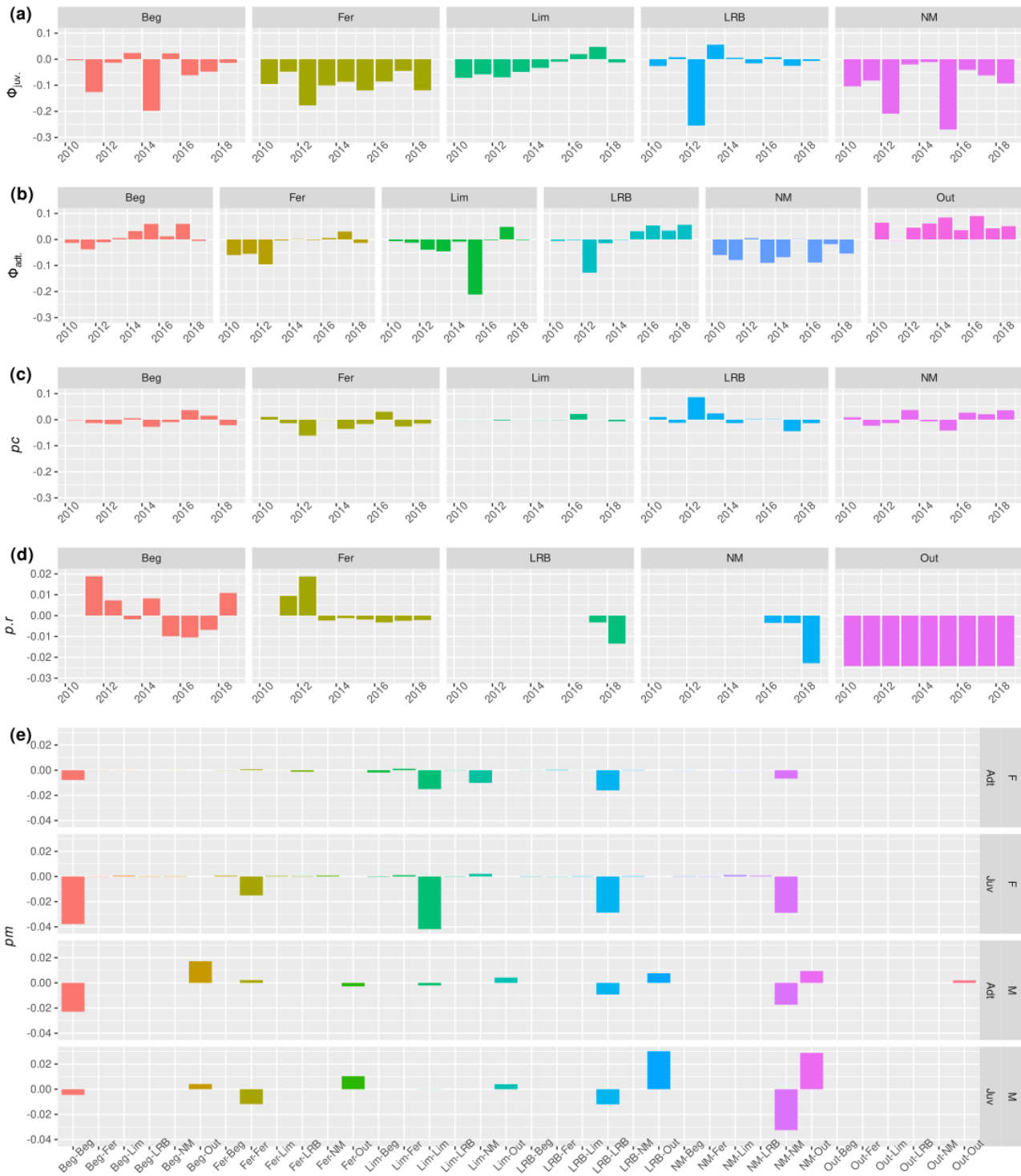


Figure 7: Differences in the medians of the posterior distributions of juvenile (a) and adult (b) survival, capture (c) resighting (d) and transition (e) probabilities between the model accounting for tag-loss and the model ignoring it, both estimated from the empirical data. Colonies are abbreviated: 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).

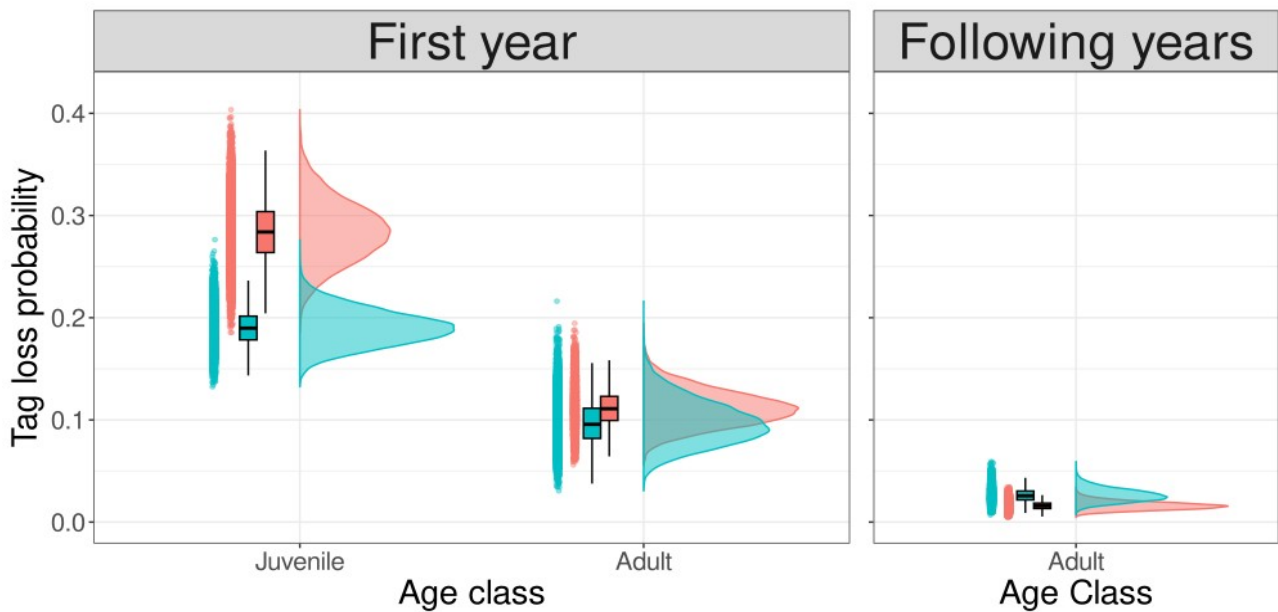


Figure 8: Posterior distribution of the tag loss probabilities according to age classes and time after marking in the *Myotis myotis* dataset. Left panel correspond to tag shedding rate during the year following the tag injection and the right panel for the following years (constant in time). In blue,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