

¹ Complete tag loss in capture-recapture studies
² affects abundance estimates: an elephant seal
³ case study.

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⁵ Emily Malcolm-White¹, Clive R. McMahon², Laura L.E. Cowen^{3*},

¹ Mathematics, Middlebury College, Middlebury, VT, USA

² Sydney Institute for Marine Science, Mosman, NSW, Australia

³ Mathematics and Statistics, University of Victoria, Victoria, BC, Canada

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⁷ Running Head: Complete Tag Loss in Capture-Recapture Studies

⁸ *Corresponding author: Mathematics and Statistics, University of Victoria, PO Box 1700

⁹ STN CSC, Victoria, BC, Canada, V3W 2Y2; lcowen@uvic.ca

10 ABSTRACT:

- 11 1. In capture-recapture studies, recycled individuals occur when individuals
12 lose all of their tags and are recaptured as though they were new individuals.
13 Typically, the effect of these recycled individuals is assumed negligible.
- 14 2. Through a simulation-based study of double tagging experiments, we ex-
15 amined the effect of recycled individuals on parameter estimates in the
16 Jolly-Seber model with tag loss (Cowen & Schwarz, 2006). We validated the
17 simulation framework using long-term census data of elephant seals.
- 18 3. Including recycled individuals did not affect estimates of capture, survival,
19 and tag-retention probabilities. However, with low tag-retention rates, high
20 capture rates, and high survival rates, recycled individuals produced over-
21 estimates of population size. For the elephant seal case study, we found
22 population size estimates to be between 8 and 53% larger when recycled
23 individuals were ignored.
- 24 4. Ignoring the effects of recycled individuals can cause large biases in population
25 size estimates. These results are particularly noticeable in longer studies.

26 KEY WORDS: Abundance; Capture-mark-recapture; Complete tag loss;
27 Demography; Double-tagging; Elephant seal; Jolly-Seber; Recycled individual.

28 **Introduction**

29 Mark-recapture studies utilize statistical techniques to estimate population parameters. Over
30 k sample times, individuals are captured, tagged with unique tags, released and potentially
31 recaptured at subsequent sampling times. The Jolly-Seber model (Jolly, 1965; Seber, 1965) is
32 used to model open populations since it can estimate parameters of interest such as population

size and survival rates (Pollock *et al.*, 1990). An important assumption of this model is that individuals never lose their tags. However, when this assumption is violated, serious bias can occur in the parameter and variance estimates (Arnason & Mills, 1981). Double-tagging, the placement of two tags on an individual, can be used to estimate tag retention rates. Double tagging studies have been used for a wide variety of species (for example cod: Björnsson *et al.* 2011, lobsters: Xu *et al.* 2014:, sea turtles: Bjorndal *et al.* 1996, elephant seals: Pistorius *et al.* 2000, black bears: Diefenbach & Alt 1998) to investigate probabilities of tag loss or tag shedding rates. Often a mixture of single- and double-tagged individuals is used for practical purposes. Cowen & Schwarz (2006) incorporated tag-loss by developing the Jolly-Seber tag-loss (JSTL) model for experiments where some fraction of individuals are double tagged. This model was further extended to account for heterogeneity in capture between groups (Xu *et al.*, 2014). In the simplest form of the JSTL model, it is assumed that every individual present in the population at sample time k has capture, survival, and tag retention probabilities that are homogeneous for all individuals in the population across all sampling occasions. However, these assumptions are rarely met and can induce significant bias in the parameter estimates (Schwarz *et al.*, 2012).

Occasionally in mark-recapture experiments, previously captured individuals lose all of their tags (complete tag loss). These individuals are either recognized upon recapture (for example, through scarring or fin clipping), and not re-tagged, or if unrecognized, these individuals would be tagged again and treated as “new” individuals. Individuals who lose both tags and are recaptured and re-tagged are known as recycled individuals. For example, an individual with the tag history $\{11\ 01\ 00\}$ over three sampling occasions was double tagged at sample time 1, lost a tag between times 1 and 2, and may have lost its last tag between sample times 2 and 3 and then have been recaptured at sample time 3 resulting in a new individual with tag history $\{00\ 00\ 11\}$. If the rate of tag loss is small, bias in the population estimate will also be small for the Peterson estimators (Seber & Felton, 1965). Typically in the Jolly-Seber and JSTL models, the effect of recycled individuals is assumed to be negligible. However, in situations

60 where tag retention is low and survival and recapture probabilities are high it is suspected
61 that recycled individuals will bias population size estimates upwards. The motivation for
62 this study was to investigate the effect of recycled individuals on parameter estimates in the
63 JSTL model through a simulation study and determine under which conditions researchers
64 need to be concerned. This study is important as the assumption that the effect is negligible
65 has not been fully tested and quantified, and most studies that rely on marking individuals
66 typically experience tag loss. Thus, there is a need to account for recycled individuals given
67 the desire for accurate and robust estimates for management and conservation purposes.
68 In order to determine whether the simulation framework provided a reasonable approximation
69 to the real world, we analyzed the effects of recycled individuals in long-term census data of
70 southern elephant seals (Figure 1).

71 Materials and Methods

72 The Jolly-Seber Model with Tag Loss (JSTL)

73 Full development of the JSTL model is given by (Cowen & Schwarz, 2006). Data are typically
74 in the form of tag histories for each individual in the study. Let ω_{ijd} denote the entries of
75 the tag history for individual i at time j , tag d ; $i = 1, \dots, n_{obs}$, $j = 1, \dots, k$, $d = 1, 2$; with
76 ω_{ijd} equaling 1 or 0 if the individual was seen with tag d or not. Capture histories ω^* used
77 in most capture-recapture studies can be easily obtained from the tag histories ω and are a
78 series of 1's and 0's depicting whether or not an individual was captured at each sample time.
79 We focus on the case with constant parameters as used in our simulation study. Let ϕ denote
80 the survival probability, p the capture probability, λ the tag retention probability, and b_t the
81 entry probability for time t . Ψ and χ are recursive functions of parameters that deal with an
82 individual's history up to the first time seen (f_i) and after the last time seen (l_i) with n_t tags
83 respectively.

84 The JSTL model is developed under the idea of a super-population (the number of individuals
 85 that will enter the population at some point during the study) (Schwarz & Arnason, 1996)
 86 and this allows the likelihood to be formulated into two parts: 1) a model for the observed
 87 number of unique tag histories (n_{obs}) given the super-population size (N) and 2) a model for
 88 the recaptures (in the form of capture history frequencies n_{ω_i}) given the observed number of
 89 unique tag histories (n_{obs}). The full likelihood is given by the product of these components
 90 as follows:

$$\begin{aligned}
 L = & \binom{N}{n_{obs}} \left\{ \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{(N-n_{obs})} \left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{n_{obs}} \times \\
 & \binom{n_{obs}}{n_{\omega_1}, n_{\omega_2}, \dots, n_{\omega_m}} \prod_{i=1}^m \left[\psi_{f_i} T_d \left\{ \prod_{j=f_i}^{l_i} p^{w_{ij}} (1-p)^{(1-w_{ij})} \right\} \left\{ \prod_{j=f_i}^{l_i-1} \phi \right\} \times \right. \\
 & \left. \prod_{d=1}^2 \left\{ \left(\prod_{j=f_i}^{l_{id}-1} \lambda \right) \left(1 - \prod_{j=l_{id}}^{q_{id}-1} \lambda \right)^{I(l_{id} \neq l_i)} \right\} \times \chi_{f_i, l_i, n_{t_{l_i}}} \right]^{n_{\omega_i}} \times \\
 & \left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{-n_{obs}}
 \end{aligned}$$

91 where T_d is the probability of being double tagged, l_{id} is the last sample time where tag d
 92 was present, and n_{t_j} is the number of tags on individual i at time j . A table of notation is
 93 provided in Appendix A with further details on the Ψ and χ functions.

94 Assumptions of the JSTL model (under constant ϕ , p , and λ parameters) are similar to the
 95 Jolly-Seber model (Schwarz & Arnason, 1996) including all individuals have equal entry (birth
 96 or immigration) probabilities but entry probabilities can vary between sample times, capture
 97 probabilities are the same for all individuals at all sample times, all individuals (marked and
 98 unmarked) have equal survival probabilities between all sample times, the sampling period is
 99 relatively short compared to the interval between sampling times, and there is independence
 100 across all individuals. The incorporation of tag loss into the model comes with the additional
 101 assumption that all marked individuals have equal tag retention probabilities between all
 102

105 sample times and for double-tagged individuals, tag loss is independent between tags. Finally,
106 the JSTL model assumes that the effect of recycled individuals is negligible and it is this
107 assumption that we explore.

108 Many different models can be specified for the JSTL model where parameters are homogeneous
109 or heterogeneous with respect to time (Cowen & Schwarz, 2006) or group (Xu *et al.*, 2014).

110 **Likelihood and Estimation**

111 Maximum likelihood parameter estimates are found using a Newton-Raphson type method.
112 Estimated standard errors are computed using the delta theorem. Models were implemented
113 using R software (R Core Team, 2014). Code from this study are included in this published
114 article (and its supplementary information files).

115 **Experimental Design**

116 To study the effect of recycled individuals on parameter estimates of this model, we conducted
117 a simulation study. Data sets varied in super-population size, parameter values, and percent
118 double tagged. We generated data for the JSTL model with constant survival, capture,
119 and tag retention probabilities for a double-tagging experiment. Super-population sizes of
120 1000 and 100 000 were considered in order to study the effect of population size. For the
121 super-population size of 100 000, experiments with ten sample times were considered. For
122 the super-population size of 1000 we considered experiments with five, seven and ten sample
123 times in order to determine the effect of the study length. For each population size, we tested
124 different proportions of double-tagged versus single-tagged individuals (0.5 and 1). Survival,
125 capture, and tag retention probability parameters were varied in a 3^3 experimental design
126 with low (0.2), medium (0.5) and high (0.9) values for all parameters. The entry rates were
127 fixed to be $1/k$ at each of the sampling times.

128 We considered the set of parameter values to be reasonable values that might be encountered
129 in practice and also produce informative capture-recapture scenarios. Tag retention rates
130 can vary by species, age of the tag, tag type, tag location, behaviour, season, and individual
131 quality (size of an animal for example in seals). For example, tag retention rates have ranged
132 from 13% (Fogarty *et al.*, 1980) to 95% (Gonzalez-Vicente *et al.*, 2012) in lobsters. Other
133 studies report tag retention rates of 65% in male elephant seals (Pistorius *et al.*, 2000) and
134 88% in Adelie penguins (Ainley & DeMaster, 1980). Mean retention of visible implant tags
135 has been recorded as 32% in small rockpool fish (Griffiths, 2002). Turtles in particular
136 experience high tag loss rates. For example Bellini *et al.* (2001) reports the probability of tag
137 loss in hawksbill turtles as 0.57 and Bjorndal *et al.* (1996) observed the probability of tag
138 loss in green nesting turtles to be as high as 0.38. Thus, we chose a wide range of tag loss
139 parameter values to try to capture the diversity among published tag loss rates.

140 **Simulation of Data**

141 For all of the parameter combinations of super-population size ($N = 1000, 100\ 000$), fraction
142 double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
143 $0.2, 0.5, 0.9$) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
144 the simulated data met all the assumptions of the model.

145 For each individual, we simulated a capture history using the following algorithm:

- 146 1. Determine when the individual enters the population utilizing the entry probabilities.
- 147 2. For each sample time after entry (until death or first capture) determine if the individual
148 survives to that sample time (with probability ϕ). If they are still alive, determine if
149 they are first captured (with probability p). If they are captured, determine whether
150 they are single or double-tagged.
- 151 3. For each sample time after first capture (until death, loss of all tags or the end of the

study) determine if the individual survives to that sample time (with probability ϕ). Then if they are still alive, determine if they lose any of their tags (with probability $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with probability p). If they have lost all of their tags, consider them as a new individual entering the population at this sample time.

By keeping track of all the recycled individuals, this algorithm provides us with two data sets: one that includes the recycled individuals (assumes individuals, who have complete tag loss, are tagged again upon recapture and treated as new individuals) and one that excludes recycled individuals (assumes that individuals, who have complete tag loss, can be recognized upon recapture and are not re-tagged). The JSTL model was fit to the 100 simulated data sets twice (once including and once excluding recycled individuals). We assumed that any difference between the two analyses was due entirely to the recycled individuals. All data generated during this study are included in this published article (and its supplementary information files).

166 Evaluation Criteria

To evaluate the resulting parameter estimates from each of the simulations, we looked at several criteria including: average parameter estimate, relative bias of the estimates, the average standard error of the parameter estimates, the standard deviation of the parameter estimates, and root mean squared error (RMSE) of the parameter estimates.

Let $\hat{\theta}_i$'s be the parameter estimates from each of the 100 simulations and θ the true parameter value, we calculated:

- 173 • the mean parameter estimate as $\bar{\theta} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$
- 174 • average standard error of the parameter estimate as $SE(\hat{\theta}) = \sqrt{\frac{1}{100} \sum_{i=1}^{100} SE(\hat{\theta}_i)^2}$.
- 175 • the standard deviation of the parameter estimates as $SD(\hat{\theta}) = \sqrt{\frac{1}{99} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\theta})^2}$.

- 176 • the RMSE of the parameter estimates as $\text{RMSE} = \sqrt{\frac{1}{100} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.

177 We compared the average parameter estimates to the true parameter values using relative
178 bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
179 relative bias from the analysis with the recycled individuals to the relative bias from the
180 analysis without the recycled individuals. We calculated the difference in the two relative
181 biases and consider this to be the relative bias that was contributed entirely by the recycled
182 individuals being tagged as “new” individuals.

183 **Simulation Results**

184 The survival estimates are biased for some parameter combinations of survival, capture, and
185 tag retention probabilities. As an example, box plots of survival estimates for data with
186 super-population size $N=1000$ and 100% double tagging are provided (Fig. 2). Box plots of
187 survival estimates for other super-population sizes and double-tagging rates are provided in
188 the Appendix (Figs A1-A6). Although there is bias in the survival estimates for several of
189 the parameter combinations, the bias is similar between the analysis including and excluding
190 the recycled individuals for both super-population sizes ($N = 1000$ and 100 000) and for both
191 double-tagging rates ($T_2 = 0.5, 1$). In fact, the differences in relative bias due to recycled
192 individuals for the parameters ϕ , p and λ is small (<0.01) for all 108 parameter combinations
193 considered. In general, the SE, SD and RMSE of the estimates of ϕ , p and λ are similar for
194 both the analysis including and excluding recycled individuals for the parameter combinations
195 considered. It seems that the treatment of recycled individuals has little effect, if any, on the
196 accuracy of the JSTL estimators for survival, capture, and tag-retention probabilities. Box
197 plots of capture and tag retention estimates for all models can also be found in the Appendix
198 (Figs A7-A17).

199 There is slightly more bias due to recycled individuals for parameter combinations where the

200 probability of double tagging (T_2) was only 0.5, compared to the parameter combinations
201 where all individuals were double tagged. As an example, relative bias of the parameters
202 are presented for the parameter combination where $\phi = 0.9$, $p = 0.9$ and $\lambda = 0.2$ for both
203 the analysis including and excluding recycled individuals for varying population size and
204 double-tagging probabilities (Table 1).

205 The estimate of super-population size (\hat{N}) is computed as $\hat{N} = n_{\text{obs}} / (1 - \hat{P}_0)$, where \hat{P}_0 is the
206 estimated probability of never being seen. In the scenarios where many recycled individuals
207 were recaptured and considered as “new” individuals (included), the number of observed
208 individuals, n_{obs} , is larger than it should be and thus, \hat{N} is biased upwards. By recognizing
209 recycled individuals upon recapture, this bias can be corrected. The relative bias in the
210 super-population size (\hat{N}) due to recycled individuals is highest in the scenario with high
211 survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as
212 predicted (Fig. 3, Table 1). The relative bias is small for all scenarios where tag retention was
213 high, but relative bias increases as tag retention decreases. The relative bias in \hat{N} decreases as
214 capture probability decreases, but recycled individuals appear to still have some effect on the
215 estimates even when capture probabilities are low ($p = 0.2$). The relative bias in \hat{N} is high for
216 scenarios where survival probability is high, and decreases as survival probability decreases.
217 In all scenarios where survival probability is low ($\phi = 0.2$) individuals are unlikely to survive
218 long enough to be able to be tagged, lose tag(s) and be recaptured as “new” individuals.
219 When survival probability is low, the relative bias due to the recycled individuals is small
220 (less than 0.15) and hence not shown in Fig. 3. SE, SD, and RMSE of \hat{N} varies, but remains
221 similar between the analyses including and excluding recycled individuals, across all scenarios.
222 There is more bias in \hat{N} due to recycled individuals in longer experiments (Fig. 4). With a
223 larger number of sampling occasions, there is more time for individuals to be captured and
224 tagged, lose their tags, and survive to be recaptured (be recycled). In shorter studies, there
225 are fewer numbers of recycled individuals and thus the bias in \hat{N} due to recycled individuals is
226 lower although not unnoticeable in the worst case scenarios (low tag retention, high survival

and high capture probabilities). Box plots of super-population size (N) for all scenarios are available in the Appendix (Figs A19-A24).

In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to the bias due to recycled individuals in \hat{N} , with relative bias in the \hat{N}_j 's increasing as tag retention decreases, survival increases, and capture probability increases (Fig. 5). For all scenarios, the relative bias in the estimates of abundance at each sample time j is larger later in the study. Since the estimates of the population sizes at each time j are computed iteratively as $\hat{N}_{j+1} = \hat{\phi}(\hat{N}_j) + \hat{b}_j(\hat{N})$, any bias in the earlier abundance estimates is magnified in the later sampling occasions abundance estimates. The scenario with $\phi = 0.5$, $p = 0.9$, and $\lambda = 0.2$ appears to have very high relative bias in the abundance estimates in later sampling occasions (>3 for \hat{N}_{10}), which is caused by a combination of more upward bias in the survival probability estimates for the analysis including recycled individuals (Fig. A1-A6) as well as upward bias in the super-population size estimates. Plots of the mean abundance estimates for all scenarios are available in the Appendix (Figs A25-A42).

Case Study: Elephant Seals

To validate the simulation framework, we analyzed seven years of data from a long-term mark-recapture study of elephant seals on Macquarie Island, Australia between 1993 and 2000. Elephant seal pups were marked with two tags in the inter-digital webbing of their hind flippers and were given a permanent hot-iron branding with a unique identifier on their flank (McMahon *et al.*, 2009). This permanent branding allowed for individual elephant seals to be identified even if they lost both tags. Thus, recycled individuals could be easily identified.

We considered two analyses of the data:

1. We assumed that recycled individuals could not be recognized upon recapture (ignoring branding) and were re-tagged as if they were new individuals. *Recycled individuals are included.* This scenario simulates analysis ignoring the effects of recycled individuals.

252 2. Recycled individuals were recognized upon recapture (by branding) and were re-tagged
253 with new tags identical to their lost tags. Thus, *recycled individuals are excluded*.

254 For the elephant seal data, there were several differences in parameter estimates of the JSTL
255 model when recycled individuals were included compared to when recycled individuals were
256 excluded. For this analysis, we used the same model as the simulation study where capture,
257 survival and tag retention rates were held constant.

258 As expected, the super-population size estimate for the analysis which included the recycled
259 individuals ($\hat{N} = 8985$) is 30% larger than the estimate in the analysis which excluded
260 recycled individuals ($\hat{N} = 6949$) who were recognized upon recapture. This relationship also
261 holds true for the abundance estimates at each sample time (Table 2). The difference in the
262 abundance estimates increases as time goes on, again validating the results of our simulation
263 study. Standard error estimates for \hat{N}_t are also higher when recycled individuals are included
264 in the analysis. The same pattern is seen in the simulation studies (see Appendix).

265 Similar to the simulations, there is not much difference in the estimates of survival, capture,
266 and tag-retention probabilities between the analysis including and excluding recycled indi-
267 viduals. For comparison to the previous simulations, the tag retention probability for the
268 elephant seals is estimated to be ≈ 0.8 (high).

269 Discussion

270 Through both a simulation study and an elephant seal case study, we examined the effect of
271 recycled individuals on parameter estimates from the Jolly-Seber tag loss model. In an attempt
272 to emulate the many different real life scenarios researchers may face, we simulated over
273 many different values of survival probability, capture probability, tag-retention probability,
274 population size, study length, and proportion double tagged. While these scenarios do not
275 cover all possible realistic mark-recapture experiments, our simulations are sufficient to show

276 that the JSTL abundance estimates can be substantially biased by recycled individuals,
277 especially when tag-retention is low combined with high survival, high capture rates, or both.

278 This effect is especially noticeable in longer experiments. These results bring context to the
279 assumption that the effect of recycled individuals is negligible in mark-recapture models.
280 However, we show that in general, recycled individuals have little effect on the accuracy of
281 the survival, capture, and tag-retention probability estimates and that for short-term studies,
282 the effects are reduced.

283 For longer term studies when survival and capture probabilities are low, the bias in abundance
284 estimates associated with recycled individuals is smaller. These are characteristics that might
285 be associated with small, endangered, or decreasing populations.

286 As expected, the survival estimates are typically unbiased when recycled individuals are
287 excluded. Survival estimates are essentially a relative measure of how many individuals
288 are around now versus the previous time step. Thus the bias in the numerator and the
289 denominator essentially cancels out (i.e. $\hat{\phi}_j \approx \hat{N}_j / \hat{N}_{j-1}$). Although the case study of elephant
290 seals validated some of the results from the simulation study (recycled individuals bias
291 abundance estimates upwards), some caution must be taken when comparing simulation
292 studies to the real world. There are many parameters that may differ or be uncertain, such
293 as entry probabilities, that may influence the results. Simplifications of the individuals in the
294 simulation studies may not take into account the complexities that arise in real life scenarios.

295 Although our study provides some evidence that recycled individuals have an effect on
296 estimators of the JSTL model in particular situations, there is room for improvement in
297 our approach and questions remain for future work. We only examined three levels of
298 survival, capture, and tag-retention probabilities (Low=0.2, Medium=0.5 and High=0.9)
299 which was intended to simulate across a variety of scenarios that may exist in real life. For
300 researchers with a particular population in mind, different levels of survival, capture, or tag
301 retention could be investigated. Additionally, future work could examine the effect of recycled

302 individuals in situations where survival, capture or tag-retention probabilities are thought to
303 be time- or group-varying.

304 Developing a model to incorporate recycled individuals is a similar problem to that of
305 incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model
306 to deal with tag-misreads in an open population capture-recapture setting. However most
307 of the misidentification literature focusses on genetic or photographic identification errors.
308 Here multiple identities can be assigned to the same individual leading to overestimates in
309 population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result
310 that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of
311 using a latent multinomial to model the latent capture histories for a closed population model.
312 Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner
313 & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*,
314 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models
315 could be extended to include misidentification produced by complete tag loss.

316 Finally, the JSTL model we used did not include a component for loss on capture (when
317 for example a fishery harvest occurs). It would be interesting for future work to include
318 loss on capture to determine if recycled individuals are still problematic under this scenario.
319 Increasing computation power and a larger community applying themselves to these problems
320 has the potential to inform researchers and managers in a meaningful way, especially in terms
321 of how we use imperfect observations to estimate vital rates (survival and fecundity). Having
322 more robust estimates of vital rates is especially important if we are to effectively manage
323 populations on an ever increasing list of endangered species.

324 For researchers interested in conducting and analyzing mark-recapture studies to determine
325 abundance estimates, we stress the importance of using tags with high retention rates,
326 especially in situations where survival and capture rates are suspected to be high. As
327 long as tag-retention is high, the JSTL estimator of population size is only weakly affected

328 by recycled individuals. Longer studies should be particularly concerned about recycled
329 individuals biasing abundance estimates. In situations where it is possible, recognizing if an
330 individual has been captured previously (by scarring, marking, etc) can improve accuracy of
331 the abundance estimates. Permanent marking should be used where possible. If researchers
332 are only interested in the survival rates, they do not need to be concerned with the effect of
333 recycled individuals regardless of the study's tag-retention rates.

334 Alternatively, researchers could replace lost tags on a recaptured individual thereby minimizing
335 the occurrence of complete tag loss. Depending on model assumptions, the JSTL model
336 may not be appropriate for a study design involving retagging. Future work would involve
337 extending the JSTL model to incorporate re-tagged individuals and assess the performance
338 of recycled individuals within this framework.

339 Acknowledgements

340 Simulation studies and analyses were run on WestGrid/Compute Canada with assistance
341 from Dr. Belaid Moa. LC was supported by NSERC Discovery Grant 327025-2013.

342 Authors' Contributions

343 EMW and LC conceived the ideas, designed methodology, and analysed the data; CM
344 collected the data. All authors led the writing of the manuscript. All authors contributed
345 critically to the drafts and gave final approval for publication.

³⁴⁶ Data Accessibility

- ³⁴⁷ Data and R scripts available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v6wwpzgr3>

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417

418 TABLE 1: *The mean relative bias of the parameters from the model analyzed*
419 *including (R) and excluding (R') the recycled individuals for data with high*
420 *survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag*
421 *retention ($\lambda = 0.2$) for different super-populations sizes ($N = 1000, 100\,000$) and*
422 *different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from a*
423 *ten-sample-time study.*

	N=1000				N=100 000			
	$T_2 = 1$		$T_2 = 0.5$		$T_2 = 1$		$T_2 = 0.5$	
	R	R'	R	R'	R	R'	R	R'
ϕ	0.00	0.00	0.06	0.05	0.00	0.00	0.11	0.10
p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
λ	0.00	0.00	0.00	0.00	0.00	0.00	-0.09	-0.08
N	1.98	0.00	2.13	0.00	1.98	0.00	2.12	0.00

424

425 TABLE 2 Estimates of survival probability (ϕ), capture probability (p), tag-
 426 retention probability (λ), and annual population size (N_j) for the elephant seal
 427 data analyzed including and excluding recycled individuals. Estimated standard
 428 errors (SE) are also presented.

Parameter	Including Recycled		Excluding Recycled	
	Estimate	SE	Estimate	SE
ϕ	0.759	0.006	0.744	0.006
p	0.682	0.006	0.741	0.006
λ	0.792	0.005	0.799	0.005
N_{1994}	1740	48	1601	36
N_{1995}	1859	41	1717	40
N_{1996}	2515	46	2264	42
N_{1997}	3179	50	2727	43
N_{1998}	3793	54	2965	48
N_{1999}	4300	59	3229	46
N_{2000}	4973	65	3238	50
N	8985		6949	

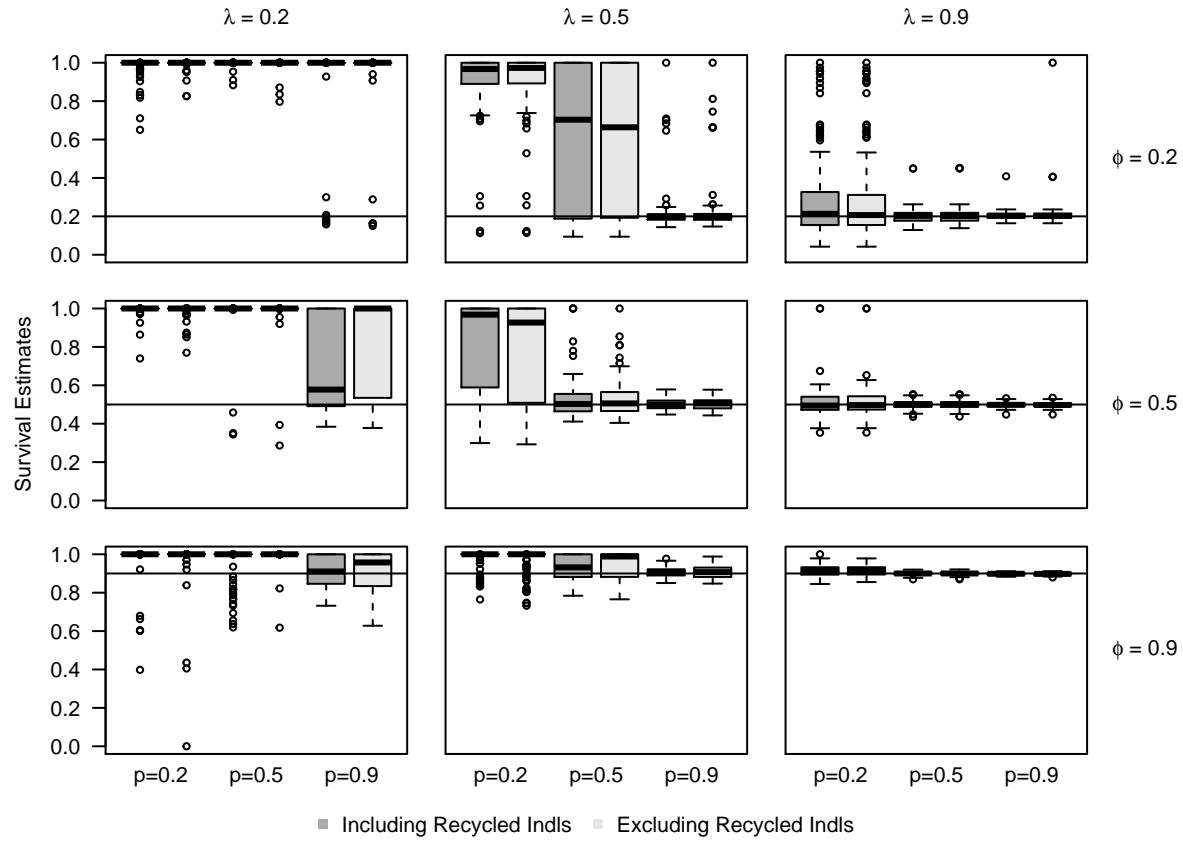
429



430

431 FIGURE 1: Elephant seal (*Mirounga leonina*) at Macquarie Island, Australia.

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433
434 FIGURE 2: Survival probability estimates for simulated data with super-
435 population size $N = 1000$ with 100% double-tagging for different tag retention
436 probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.2, 0.5, 0.9$), and
437 different capture probabilities ($p = 0.2, 0.5, 0.9$) using the JSTL model from a
438 ten-sample-time study. Box plots of the estimates of ϕ for the model analyzed
439 including and excluding the recycled individuals are provided. The black line
440 indicates the true value of ϕ used to simulate the data for each model.

441 Filename: Figure2_survival_GJSTL1-1.pdf

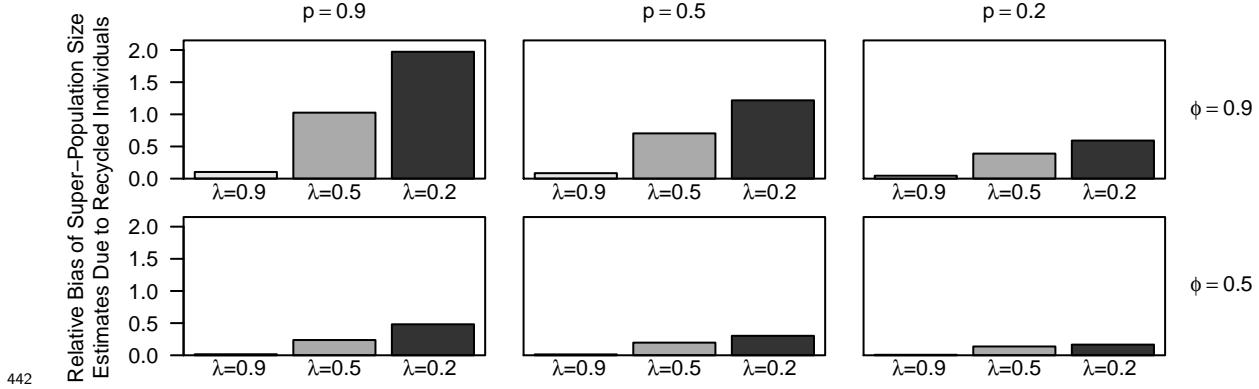


FIGURE 3: The difference in mean relative bias of the super-population estimate (\hat{N}) between the model analyzed including and excluding the recycled individuals for data with super-population size $N = 100\ 000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.5, 0.9$), and capture probabilities ($p = 0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study.

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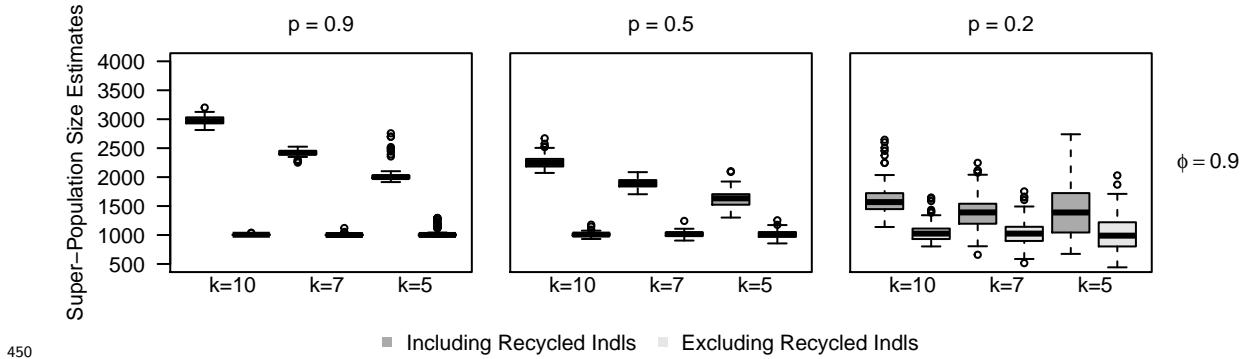
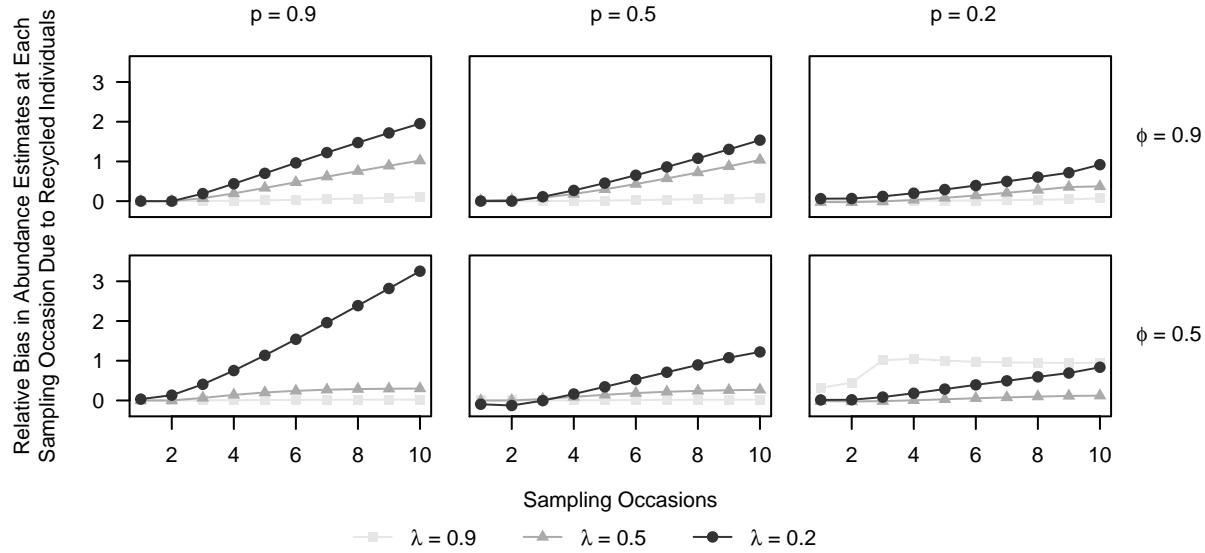


FIGURE 4: Box plots of the estimates of N for the model analyzed including and excluding the recycled individuals for data with super-population size $N = 1000$ with 100% double-tagging for different capture probabilities ($p = 0.2, 0.5, 0.9$), and constant survival ($\phi = 0.9$) and tag retention ($\lambda = 0.2$) probabilities using the JSTL model from experiments with $k = 10, 7$, and 5 sample-times.

456 Filename: Figure4_N_k-1.pdf



457

458 FIGURE 5: The difference in mean relative bias of the abundance estimates
 459 at each sample time (\hat{N}_j) between the model analyzed including and excluding
 460 the recycled individuals for data with super-population size $N=100\ 000$ with
 461 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$),
 462 survival probabilities ($\phi = 0.5$ and 0.9), and different capture probabilities ($p =$
 463 $0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study. Note that lines
 464 are added between the points to emphasize the difference in values; no models
 465 were fit to generate these lines.

466 Filename: Figure5_N_j-1.pdf