

¹ Complete tag loss in capture-recapture studies
² affect 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 and Statistics, Middlebury College, Middlebury, VT, USA

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

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

⁶

⁷ *Corresponding author: Mathematics and Statistics, University of Victoria, PO Box 1700

⁸ STN CSC, Victoria, BC, Canada, V3W 2Y2; lcowen@uvic.ca

9 ABSTRACT:

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

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

27 **Introduction**

28 Mark-recapture studies utilize statistical techniques to estimate population parameters. Over
29 k sample times, individuals are captured, tagged with unique tags, released and potentially
30 recaptured at subsequent sampling times. The Jolly-Seber model (Jolly, 1965; Seber, 1965) is
31 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 following tag history over three sampling occasions {11 01 00} 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 capture 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

59 to be negligible. However, in situations where tag retention is low and survival and recapture
60 probabilities are high it is suspected that recycled individuals will bias population size
61 estimates upwards. The motivation for this study was to investigate the effect of recycled
62 individuals on parameter estimates in the JSTL model through a simulation study and
63 determine under which conditions researchers need to be concerned. This study is important
64 as the assumption that the effect is negligible has not been fully tested and quantified, and
65 most studies that rely on marking individuals typically experience tag loss. Thus, there is a
66 need to account for recycled individuals given the desire for accurate and robust estimates
67 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 elephant seals (*Mirounga leonina*) shown in Figure 1.



71

72 FIGURE 1: Photograph of elephant seal (*Mirounga leonina*) at Macquarie Island

⁷³ **Materials and Methods**

⁷⁴ **The Jolly-Seber Model with Tag Loss (JSTL)**

⁷⁵ Full development of the JSTL model is given by (Cowen & Schwarz, 2006) and summarized
⁷⁶ in the Online Supplement including a table of notation.

⁷⁷ Many different models can be specified for the JSTL model where parameters are homogeneous
⁷⁸ or heterogeneous with respect to time or group. We consider the case of the JSTL model
⁷⁹ where capture, survival, and tag retention probabilities are constant over time (Cowen &
⁸⁰ Schwarz, 2006).

⁸¹ Assumptions of the JSTL model with constant survival, capture, and tag retention probabilities
⁸² and time-varying entry probabilities are as follows:

- ⁸³ • The effect of recycled individuals is negligible
- ⁸⁴ • All individuals (marked and unmarked) are equally catchable, and that capture proba-
⁸⁵ bilities for all individuals are the same for all individuals at all sample times
- ⁸⁶ • All individuals (marked and unmarked) have equal survival probabilities between all
⁸⁷ sample times
- ⁸⁸ • All individuals have equal entry (birth or immigration) probabilities, but entry proba-
⁸⁹ bilities can vary between sample times
- ⁹⁰ • All marked individuals have equal tag retention probabilities between all sample times
- ⁹¹ • For double-tagged individuals, tag loss is independent between tags
- ⁹² • There is independence across all individuals
- ⁹³ • The sampling period is relatively short compared to the interval between sampling
times

95 Likelihood and Estimation

96 The JSTL model is developed under the idea of a superpopulation (the number of individuals
97 that will enter population at some point during the study) (Schwarz & Arnason, 1996) and
98 this allows the likelihood to be formulated into three parts: 1) a model for the observed
99 number of unique tag histories given the superpopulation size (L_1^A), 2) a model for the
100 recaptures given the observed number of unique tag histories (L_1^B), and 3) a model for the
101 number of individuals lost on capture (L_3). The third component L_3 , is typically used for
102 harvest or fisheries data when known deaths occur. In this study and in the elephant seal
103 application, we assume there is no possibility of loss on capture, thus the third component of
104 the likelihood simplifies to 1. The full likelihood is given by the product of the components
105 of the likelihood ($L = L_1^A \times L_1^B$) and can be found in the Online Supplement.

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

110 Experimental Design

111 To study the effect of recycled individuals on parameter estimates of this model, we conducted
112 a simulation study. Data sets varied both in super-population size, parameter values, and
113 percent double tagged. We generated data for the JSTL model with constant survival,
114 capture, and tag retention probabilities for a double-tagging experiment. Super-population
115 sizes of 1000 and 100 000 were considered in order to study the effect of population size. For
116 the super-population size of 100 000, experiments with ten sample times were considered. For
117 the super-population size of 1000 we considered experiments with five, seven and ten sample
118 times in order to determine the effect of the length of the study. For each population size,
119 we tested different proportions of double-tagged versus single-tagged individuals (0.5 and 1).

120 Survival, capture, and tag retention probability parameters were varied in a 3^3 experimental
121 design with low (0.2), medium (0.5) and high (0.9) values for all parameters. The entry rates
122 were fixed to be $1/k$ at each of the sampling times. No individuals were lost on capture.

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

135 **Simulation of Data**

136 For all of the parameter combinations of super-population size ($N = 1000, 100\,000$), fraction
137 double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
138 $0.2, 0.5, 0.9$) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
139 the simulated data met all the assumptions of the model.

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

- 141 1. Determine when the individual enters the population utilizing the entry probabilities.
- 142 2. For each sample time after entry (until death or first capture) determine if the individual
143 survives to that sample time (with probability ϕ). If they are still alive, determine if

144 they are first captured (with probability p). If they are captured, determine whether
145 they are single or double-tagged.

146 3. For each sample time after first capture (until death, loss of all tags or the end of the
147 study) determine if the individual survives to that sample time (with probability ϕ).
148 Then if they are still alive, determine if they lose any of their tags (with probability
149 $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with
150 probability p). If they have lost all of their tags, consider them as a new individual
151 entering the population at this sample time.

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

161 **Evaluation Criteria**

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

166 Given that the $\hat{\theta}_i$'s are the parameter estimates from each of the 100 simulations and θ the
167 value of the parameter, we calculated:

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

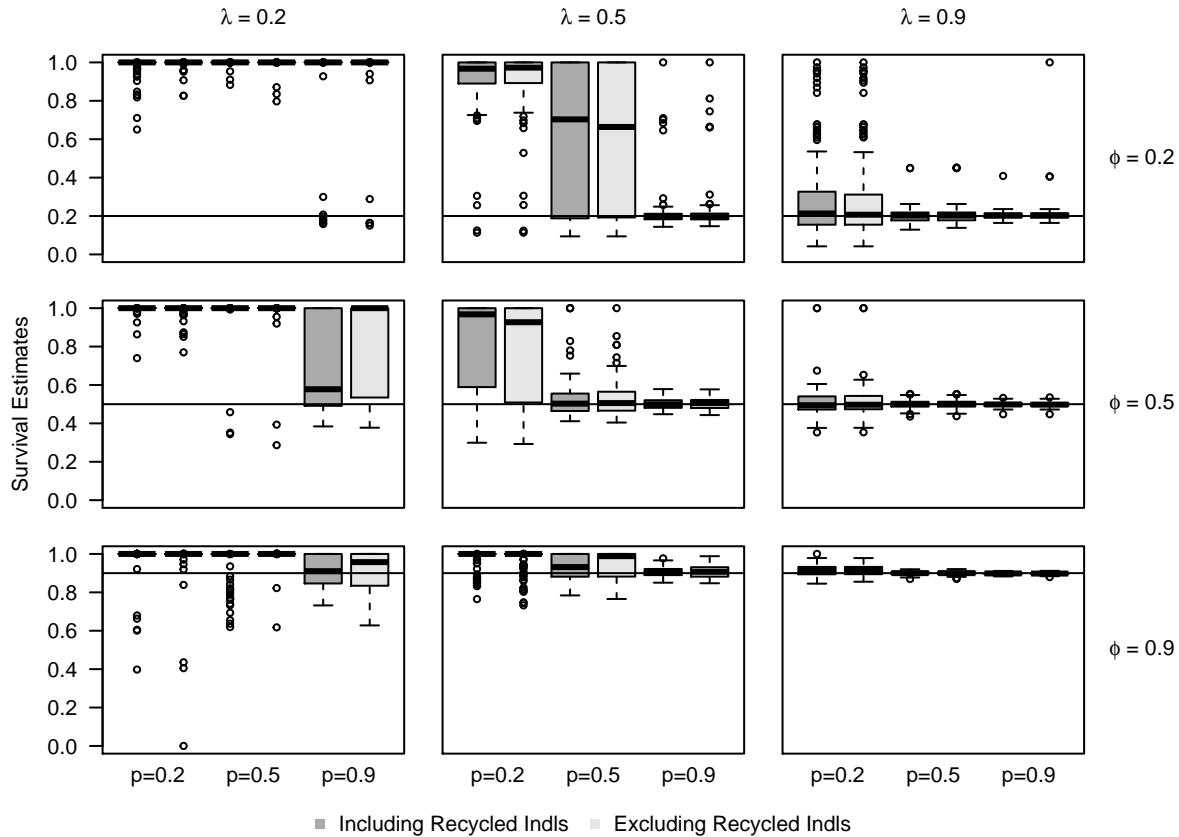
172 We compared the average parameter estimates to the true parameter values using relative
173 bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
174 relative bias from the analysis with the recycled individuals to the relative bias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

178 Simulation Results

179 The survival estimates are biased for some parameter combinations of survival, capture, and
180 tag retention probabilities. As an example, box plots of survival estimates for data with
181 super-population size $N=1000$ and 100% double tagging are provided (Fig. 2). Box plots of
182 survival estimates for other super-population sizes and double-tagging rates are provided in
183 the Online Supplement (Figs A1-A4). Although there is bias in the survival estimates for
184 several of the parameter combinations, the bias is similar between the analysis including and
185 the analysis excluding the recycled individuals for both super-population sizes ($N = 1000$ and
186 100 000) and for both double-tagging rates ($T_2 = 0.5, 1$). In fact, the differences in relative
187 bias due to recycled individuals for the parameters ϕ , p and λ is small (<0.01) for all 108
188 parameter combinations considered. In general, the SE, SD and RMSE of the estimates of
189 ϕ , p and λ are similar for both the analysis including and excluding recycled individuals for
190 the parameter combinations considered. It seems that the treatment of recycled individuals
191 has little effect, if any, on the accuracy of the JSTL estimators for survival, capture, and

192 tag-retention probabilities. Box plots of capture and tag retention estimates for all models
 193 can also be found in the Online Supplement (Figs A6-A13).

194 There is slightly more bias due to recycled individuals for parameter combinations where the
 195 probability of double tagging (T_2) was only 0.5, compared to the parameter combinations
 196 where all individuals were double tagged. As an example, relative bias of the parameters are
 197 presented for the parameter combination where $\phi = 0.9, p = 0.9$ and $\lambda = 0.2$ for both the
 198 analysis with and without recycled individuals for varying population size and double-tagging
 199 probabilities (Table 1).



200 ■ Including Recycled Indls ■ Excluding Recycled Indls

201 FIGURE 2: Survival probability estimates for simulated data with super-
 202 population size $N = 1000$ with 100% double-tagging for different tag retention
 203 probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.2, 0.5, 0.9$), and
 204 different capture probabilities ($p = 0.2, 0.5, 0.9$) using the JSTL model from a
 205 ten-sample-time study. Box plots of the estimates of ϕ for the model analyzed

206 including and excluding the recycled individuals are provided. The black line
 207 indicates the true value of ϕ used to simulate the data for each model.

208

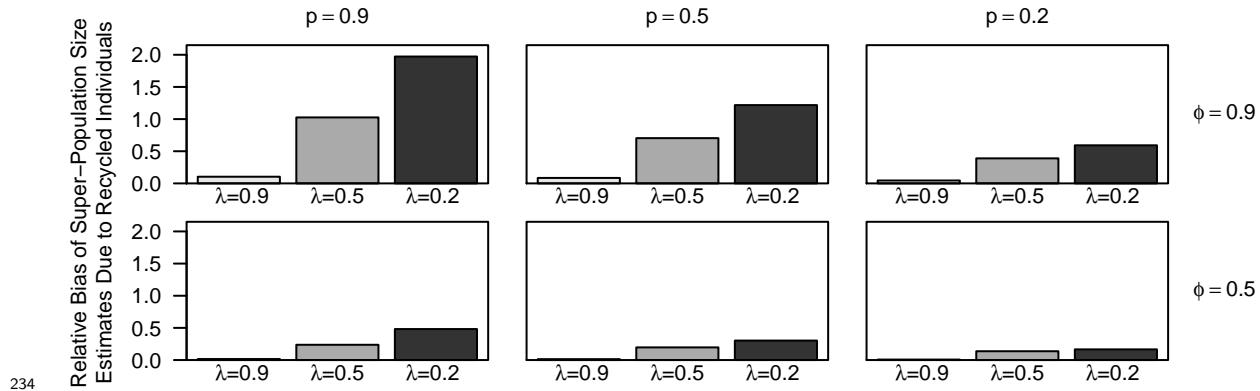
209 TABLE 1: The mean relative bias of the parameters from the model analyzed
 210 including (R) and excluding (R') the recycled individuals for data with high
 211 survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag
 212 retention ($\lambda = 0.2$) for different super-populations sizes ($N = 1000, 100\,000$) and
 213 different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from a
 214 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

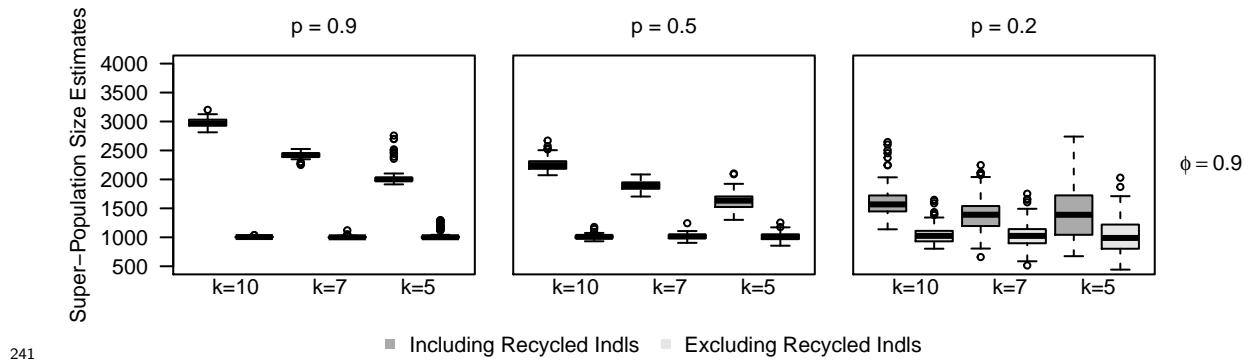
215

216 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
 217 estimated probability of never being seen. In the scenarios where many recycled individuals
 218 were recaptured and considered as “new” individuals (included), the number of observed
 219 individuals, n_{obs} , is larger than it should be and thus, \hat{N} is biased upwards. By recognizing
 220 recycled individuals upon recapture, this bias can be corrected. The relative bias in the
 221 super-population size (\hat{N}) due to recycled individuals is highest in the scenario with high
 222 survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as
 223 predicted (Fig. 3, Table 1). The relative bias is small for all scenarios where tag retention was
 224 high, but relative bias increases as tag retention decreases. The relative bias in \hat{N} decreases
 225 as capture probability decreases, but recycled individuals appear to still have some effect on

226 the estimates even when capture probabilities are low ($p = 0.2$). The relative bias in \hat{N} is
 227 high for scenarios where survival probability is high, and decreases as survival probability
 228 decreases. In all scenarios where survival probability is low ($\phi = 0.2$) individuals are unlikely
 229 to survive long enough to be able to be tagged, lose tag(s) and be recaptured as “new”
 230 individuals. When survival probability is low, the relative bias due to the recycled individuals
 231 is small (less than 0.15) and hence not shown in Fig. 3. SE, SD, and RMSE of \hat{N} varies, but
 232 remains similar between the analyses with and without recycled individuals included, across
 233 all scenarios.



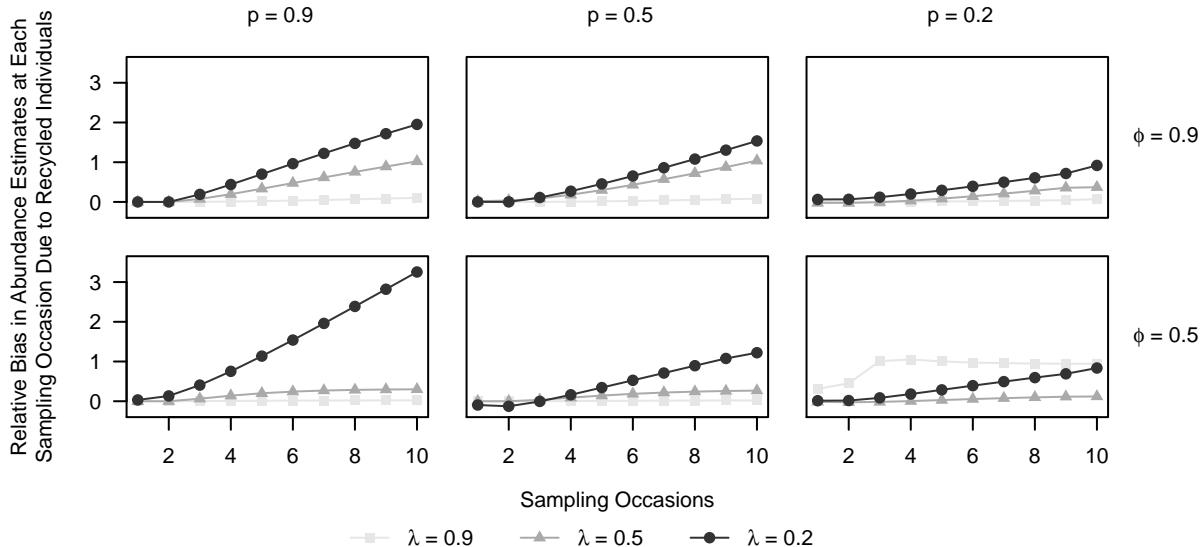
235 FIGURE 3: The difference in mean relative bias of the super-population estimate
 236 (\hat{N}) between the model analyzed including and excluding the recycled individuals
 237 for data with super-population size $N = 100\ 000$ with 100% double-tagging
 238 for different tag retention probabilities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



241 ■ Including Recycled Indl's □ Excluding Recycled Indl's

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

247 There is more bias in \hat{N} due to recycled individuals in longer experiments (Fig. 4). With a
 248 larger number of sampling occasions, there is more time for individuals to be captured and
 249 tagged, lose their tags, and survive to be recaptured (be recycled). In shorter studies, there
 250 are fewer numbers of recycled individuals and thus the bias in \hat{N} due to recycled individuals is
 251 lower although not unnoticeable in the worst case scenarios (low tag retention, high survival
 252 and high capture probabilities). Box plots of super-population size (N) for all scenarios are
 253 available in the Online Supplement (Figs A20-A25).



255 FIGURE 5: The difference in mean relative bias of the abundance estimates
 256 at each sample time (\hat{N}_j) between the model analyzed including and excluding
 257 the recycled individuals for data with super-population size $N=100\ 000$ with
 258 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$),
 259 survival probabilities ($\phi = 0.5$ and 0.9), and different capture probabilities ($p =$

260 0.2, 0.5, 0.9) using the JSTL model from a ten-sample-time study. Note that lines
261 are added between the points to emphasize the difference in values; no models
262 were fit to generate these lines.

263 In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to
264 the bias due to recycled individuals in \hat{N} , with relative bias in the \hat{N}_j 's increasing as tag
265 retention decreases, survival increases, and capture probability increases (Fig. 5). For all
266 scenarios, the relative bias in the estimates of abundance at each sample time j is smaller for
267 earlier sampling occasions and larger for later sampling occasions. Since the estimates of the
268 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
269 in the earlier abundance estimates is magnified in the later sampling occasions abundance
270 estimates. The scenario with $\phi = 0.5$, $p = 0.9$, and $\lambda = 0.2$ appears to have very high relative
271 bias in the abundance estimates in later sampling occasions (>3 for \hat{N}_{10}), which is caused by
272 a combination of more upward bias in the survival probability estimates for the analysis with
273 recycled individuals than without (Fig. A14) as well as upward bias in the super-population
274 size estimates. Plots of the mean abundance estimates for all scenarios are available in the
275 Online Supplement (Figs A18-A29).

276 **Case Study: Elephant Seals**

277 To validate the simulation framework, we analyzed data from a long-term mark-recapture
278 study of elephant seals on Macquarie Island. The data used for the case study consists
279 of 7 years between 1993 and 2000. Elephant seal pups were marked with two tags in the
280 inter-digital webbing of their hind flippers and were given a permanent hot-iron branding with
281 a unique identifier on their flank (McMahon *et al.*, 2009). This permanent branding allowed
282 for individual elephant seals to be identified even if they lost both tags. Thus, recycled
283 individuals could be easily identified.

284 We considered two analyses of the data:

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

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

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

294 As expected, the super-population size estimate for the analysis which included the recycled
295 individuals ($\hat{N} = 8985$) is 30% larger than the estimate in the analysis which excluded
296 recycled individuals ($\hat{N} = 6949$) who were recognized upon recapture. This relationship also
297 holds true for the abundance estimates at each sample time (Table 2). The difference in the
298 abundance estimates increases as time goes on, again validating the results of our simulation
299 study.

300 Similar to the simulations, there is not much difference in the estimates of survival, capture,
301 and tag-retention probabilities between the analysis including and excluding recycled indi-
302 viduals. For comparison to the previous simulations, we note that tag retention probability
303 for the elephant seals was estimated to be ≈ 0.8 (high). Standard error estimates are also
304 higher when recycled individuals are included in the analysis. The same pattern is seen in
305 the simulation studies (see Web Appendix A).

306 TABLE 2 *Estimates of survival probability (ϕ), capture probability (p), tag-*
307 *retention probability (λ), and annual population size (N_j) for the elephant seal*
308 *data analyzed with and without the recycled individuals. Estimated standard*
309 *errors (SE) are also presented.*

	Including Recycled		Excluding Recycled	
Parameter	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
310 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	

311 Discussion

312 Through both a simulation study and an elephant seal case study, we examined the effect of
 313 recycled individuals on parameter estimates from the Jolly-Seber tag loss model. In an attempt
 314 to emulate the many different real life scenarios researchers may face, we simulated over
 315 many different values of survival probability, capture probability, tag-retention probability,
 316 population size, study length, and proportion double tagged. While these scenarios do not
 317 cover all possible realistic mark-recapture experiments, our simulations are sufficient to show
 318 that the JSTL abundance estimates can be substantially biased by recycled individuals,
 319 especially when tag-retention is low combined with high survival, high capture rates, or both.
 320 This effect is especially noticeable in longer experiments. These results brings context to
 321 the assumption that the effect of recycled individuals is negligible in mark-recapture models.
 322 However, we show that in general, recycled individuals have little effect on the accuracy of

323 the survival, capture, and tag-retention probability estimates and that for short-term studies,
324 the effects are reduced.

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

328 It is not surprising that survival estimates are not biased upwards when recycled individuals
329 are ignored. Survival estimates are essentially a relative measure of how many individuals
330 are around now versus the previous time step. Thus the bias in the numerator and the
331 denominator essentially cancels out (i.e. $\hat{\phi}_j \approx \hat{N}_j / \hat{N}_{j-1}$). Although the case study of elephant
332 seals validated some of the results from the simulation study (recycled individuals bias
333 abundance estimates upwards), some caution must be taken when comparing simulation
334 studies to the real world. There are many parameters that may differ or be uncertain, such
335 as entry probabilities, that may influence the results. Simplifications of the individuals in the
336 simulation studies may not take into account the complexities that arise in real life scenarios.

337 Although our study provides some evidence that recycled individuals have an effect on
338 estimators of the JSTL model in particular situations, there is room for improvement in our
339 approach and questions remain for future work. We only examined three levels of survival,
340 capture, and tag-retention probabilities (Low=0.2, Medium=0.5 and High=0.9) which was
341 intended to simulate across a variety of scenarios that may exist in real life. Future work could
342 examine levels of survival, capture, or tag retention for scenarios of interest for particular
343 populations or could simulate across more levels to try to get a better sense of the relationship
344 between the parameters and the effect of recycled individuals. Additionally, future work
345 could examine the effect of recycled individuals in situations where survival, capture or
346 tag-retention probabilities are thought to be time- or group-varying.

347 Developing a model to incorporate recycled individuals is a similar problem to that of
348 incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model

349 to deal with tag-misreads in an open population capture-recapture setting. However most
350 of the misidentification literature focusses on genetic or photographic identification errors.
351 Here multiple identities can be assigned to the same individual leading to overestimates in
352 population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result
353 that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of
354 using a latent multinomial to model the latent capture histories for a closed population model.
355 Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner
356 & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*,
357 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models
358 could be extended to include misidentification produced by complete tag loss.

359 Finally, the JSTL model we used did not include a component for loss on capture (when
360 for example a fishery harvest occurs). It would be interesting for future work to include
361 loss on capture to determine if recycled individuals are still problematic under this scenario.
362 There remains a great deal more to study including testing some of the many assumptions
363 that capture-mark-recapture analyses rely on. Increasing computation power and a larger
364 community applying themselves to these problems has the potential to inform researchers
365 and managers in a meaningful way, especially in terms of how we use imperfect observations
366 to estimate vital rates (survival and fecundity). Having more robust estimates of vital rates
367 is especially important if we are to effectively manage populations on an ever increasing list
368 of endangered species.

369 For researchers interested in conducting and analyzing mark-recapture studies to determine
370 abundance estimates, we stress the importance of using tags with high retention rates,
371 especially in situations where survival and capture rates are suspected to be high. As
372 long as tag-retention is high, the JSTL estimator of population size is only weakly affected
373 by recycled individuals. Longer studies should be particularly concerned about recycled
374 individuals biasing abundance estimates. In situations where it is possible, recognizing if an
375 individual has been captured previously (by scarring, marking, etc) can improve accuracy of

376 the abundance estimates. Permanent marking should be used where possible. If researchers
377 are only interested in the survival rates, they do not need to be concerned with the effect of
378 recycled individuals regardless of the study's tag-retention rates.

379 Acknowledgements

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

382 Authors' Contributions

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

386 Data Accessibility

387 Data Accessibility:

388 - Elephant seal data: Dryad doi: To be determined upon acceptance of paper. - Generated
389 data and scripts: Dryad doi: To be determined upon acceptance of paper.

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