

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

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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~~ 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 ~~capture 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,

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



71

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

73 *Australia*

74 **Materials and Methods**

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

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

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

$$L = \binom{N}{n_{obs}} \left\{ \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{(N-n_{obs})} \left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{n_{obs}} \times$$

94

$$\binom{n_{\text{obs}}}{n_{\omega_1}, n_{\omega_2}, \dots, n_{\omega_m}} \prod_{i=1}^m \left[\psi_{f_i} T_d \left\{ \prod_{j=f_i}^{l_i} p^{w_{ij}} (1-p)^{(1-w_{ij})} \right\} \left\{ \prod_{j=f_i}^{l_i-1} \phi \right\} \times \right.$$

95

$$\prod_{d=1}^2 \left\{ \left(\prod_{j=f_i}^{l_{id}-1} \lambda \right) \left(1 - \prod_{j=l_{id}}^{q_{id}-1} \lambda \right)^{I(l_{id} \neq l_i)} \right\} \times \chi_{f_i, l_i, n_{t_{l_i}}} \times$$

96

$$\left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{-n_{\text{obs}}}$$

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

100 Assumptions of the JSTL model (under constant ϕ , p , and λ parameters) are similar to the
 101 Jolly-Seber model (Schwarz & Arnason, 1996) including all individuals have equal entry (birth
 102 or immigration) probabilities, but entry probabilities can vary between sample times, capture
 103 probabilities are the same for all individuals at all sample times, all individuals (marked and
 104 unmarked) have equal survival probabilities between all sample times, the sampling period is
 105 relatively short compared to the interval between sampling times, and there is independence
 106 across all individuals. The incorporation of tag loss into the model comes with the additional
 107 assumption that all marked individuals have equal tag retention probabilities between all
 108 sample times and for double-tagged individuals, tag loss is independent between tags. Finally,
 109 the JSTL model assumes that the effect of recycled individuals is negligible and it is this
 110 assumption that we explore.

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

¹¹³ **Likelihood and Estimation**

¹¹⁴ Maximum likelihood parameter estimates are found using a Newton-Raphson type method.
¹¹⁵ Estimated standard errors are computed using the delta theorem. Models were implemented
¹¹⁶ using R software (R Core Team, 2014). Code from this study are included in this published
¹¹⁷ article (and its supplementary information files).

¹¹⁸ **Experimental Design**

¹¹⁹ To study the effect of recycled individuals on parameter estimates of this model, we conducted
¹²⁰ a simulation study. Data sets varied both in super-population size, parameter values, and
¹²¹ percent double tagged. We generated data for the JSTL model with constant survival,
¹²² capture, and tag retention probabilities for a double-tagging experiment. Super-population
¹²³ sizes of 1000 and 100 000 were considered in order to study the effect of population size. For
¹²⁴ the super-population size of 100 000, experiments with ten sample times were considered.
¹²⁵ For the super-population size of 1000 we considered experiments with five, seven and ten
¹²⁶ sample times in order to determine the effect of the ~~length of the study~~ study length. For
¹²⁷ each population size, we tested different proportions of double-tagged versus single-tagged
¹²⁸ individuals (0.5 and 1). Survival, capture, and tag retention probability parameters were
¹²⁹ varied in a 3^3 experimental design with low (0.2), medium (0.5) and high (0.9) values for
¹³⁰ all parameters. The entry rates were fixed to be $1/k$ at each of the sampling times. ~~No~~
¹³¹ ~~individuals were lost on capture.~~

¹³² We considered the set of parameter values to be reasonable values that might be encountered
¹³³ in practice and also produce informative capture-recapture scenarios. Tag retention rates
¹³⁴ can vary by species, age of the tag, tag type, tag location, behaviour, season, and individual
¹³⁵ quality (size of an animal for example in seals). For example, tag retention rates have ranged
¹³⁶ from 13% (Fogarty *et al.*, 1980) to 95% (Gonzalez-Vicente *et al.*, 2012) in lobsters. Other
¹³⁷ studies report tag retention rates of 65% in male elephant seals (Pistorius *et al.*, 2000) and

138 88% in Adelie penguins (Ainley & DeMaster, 1980). Mean retention of visible implant tags
139 has been recorded as 32% in small rockpool fish (Griffiths, 2002). Turtles in particular
140 experience high tag loss rates. For example Bellini *et al.* (2001) reports the probability of tag
141 loss in hawksbill turtles as 0.57 and Bjorndal *et al.* (1996) observed the probability of tag
142 loss in green nesting turtles to be as high as 0.38. Thus, we chose a wide range of tag loss
143 parameter values to try to capture the diversity among published tag loss rates.

144 **Simulation of Data**

145 For all of the parameter combinations of super-population size ($N = 1000, 100\,000$), fraction
146 double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
147 0.2, 0.5, 0.9) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
148 the simulated data met all the assumptions of the model.

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

- 150 1. Determine when the individual enters the population utilizing the entry probabilities.
- 151 2. For each sample time after entry (until death or first capture) determine if the individual
152 survives to that sample time (with probability ϕ). If they are still alive, determine if
153 they are first captured (with probability p). If they are captured, determine whether
154 they are single or double-tagged.
- 155 3. For each sample time after first capture (until death, loss of all tags or the end of the
156 study) determine if the individual survives to that sample time (with probability ϕ).
157 Then if they are still alive, determine if they lose any of their tags (with probability
158 $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with
159 probability p). If they have lost all of their tags, consider them as a new individual
160 entering the population at this sample time.

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

170 Evaluation Criteria

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

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

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

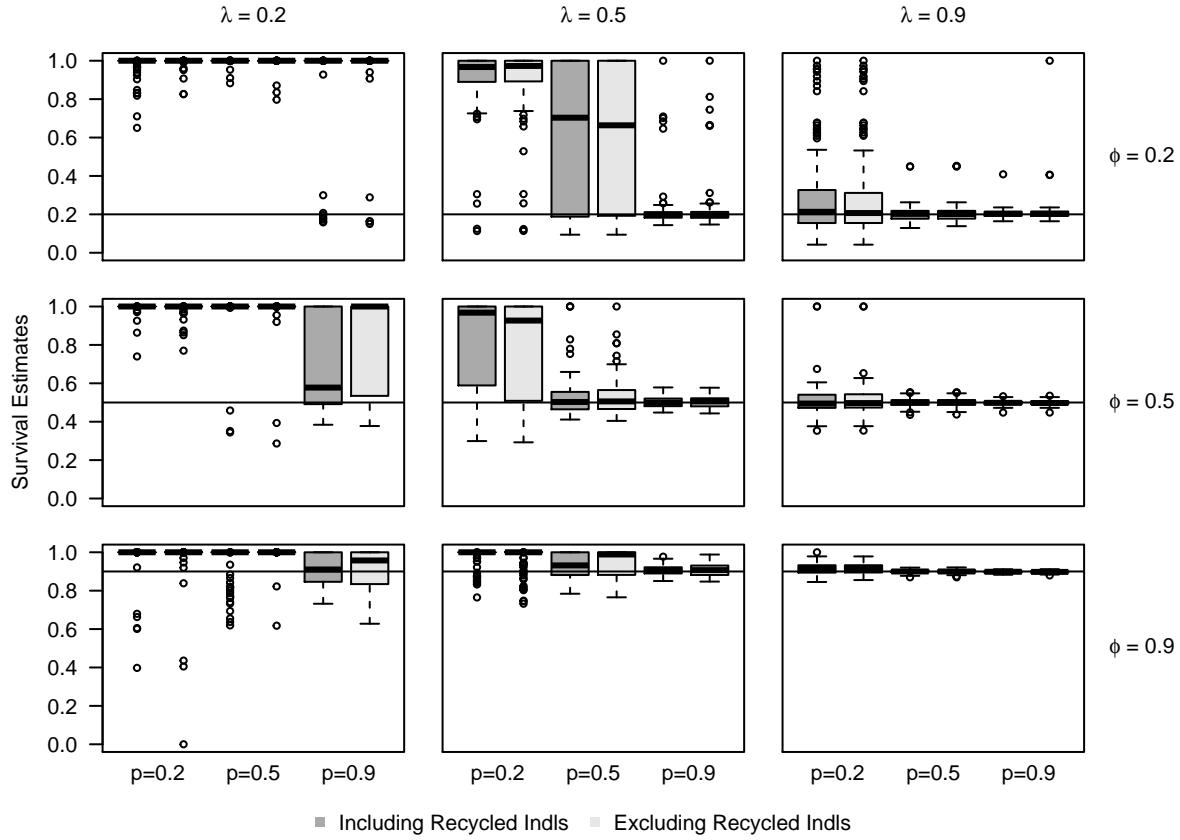
181 We compared the average parameter estimates to the true parameter values using relative
 182 bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
 183 relative bias from the analysis with the recycled individuals to the relative bias from the
 184 analysis without the recycled individuals. We calculated the difference in the two relative

185 biases and consider this to be the relative bias that was contributed entirely by the recycled
186 individuals being tagged as “new” individuals.

187 Simulation Results

188 The survival estimates are biased for some parameter combinations of survival, capture, and
189 tag retention probabilities. As an example, box plots of survival estimates for data with
190 super-population size $N=1000$ and 100% double tagging are provided (Fig. 2). Box plots of
191 survival estimates for other super-population sizes and double-tagging rates are provided in
192 the Online Supplement (Figs A1-A4). Although there is bias in the survival estimates for
193 several of the parameter combinations, the bias is similar between the analysis including and
194 ~~the analysis~~-excluding the recycled individuals for both super-population sizes ($N = 1000$ and
195 100 000) and for both double-tagging rates ($T_2 = 0.5, 1$). In fact, the differences in relative
196 bias due to recycled individuals for the parameters ϕ , p and λ is small (<0.01) for all 108
197 parameter combinations considered. In general, the SE, SD and RMSE of the estimates of
198 ϕ , p and λ are similar for both the analysis including and excluding recycled individuals for
199 the parameter combinations considered. It seems that the treatment of recycled individuals
200 has little effect, if any, on the accuracy of the JSTL estimators for survival, capture, and
201 tag-retention probabilities. Box plots of capture and tag retention estimates for all models
202 can also be found in the Online Supplement (Figs A5-A12).

203 There is slightly more bias due to recycled individuals for parameter combinations where the
204 probability of double tagging (T_2) was only 0.5, compared to the parameter combinations
205 where all individuals were double tagged. As an example, relative bias of the parameters are
206 presented for the parameter combination where $\phi = 0.9, p = 0.9$ and $\lambda = 0.2$ for both the
207 analysis ~~with and without~~including and excluding recycled individuals for varying population
208 size and double-tagging probabilities (Table 1).



209

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

217

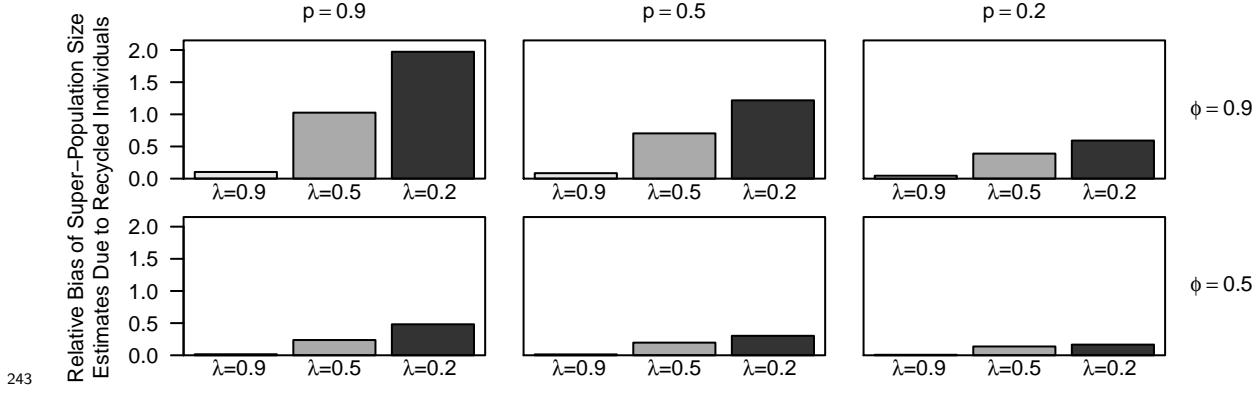
TABLE 1: The mean relative bias of the parameters from the model analyzed including (R) and excluding (R') the recycled individuals for data with high survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag retention ($\lambda = 0.2$) for different super-populations sizes ($N = 1000, 100\,000$) and

222 different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from a
 223 ten-sample-time study.

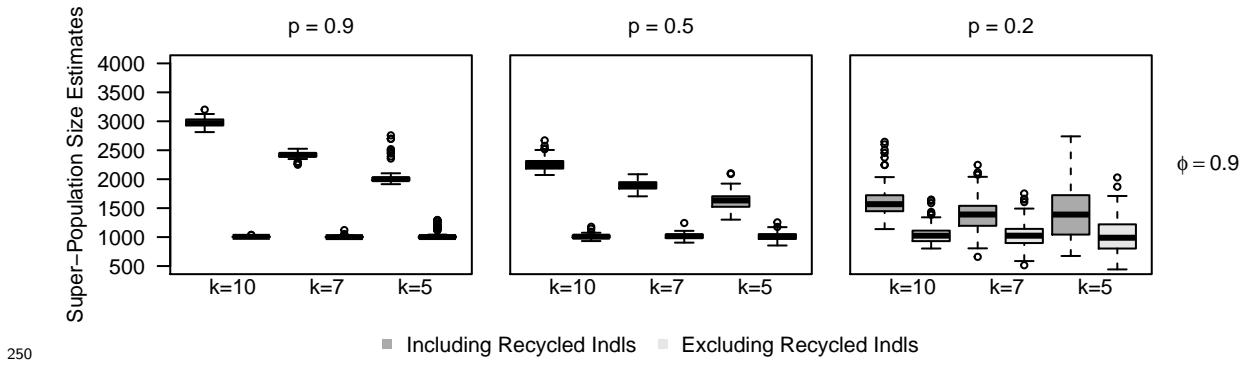
	N=1000				N=100 000			
	$T_2 = 1$		$T_2 = 0.5$		$T_2 = 1$		$T_2 = 0.5$	
	R	R'	R	R'	R	R'	R	R'
ϕ	0.00	0.00	0.06	0.05	0.00	0.00	0.11	0.10
p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
λ	0.00	0.00	0.00	0.00	0.00	0.00	-0.09	-0.08
N	1.98	0.00	2.13	0.00	1.98	0.00	2.12	0.00

224

225 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
 226 estimated probability of never being seen. In the scenarios where many recycled individuals
 227 were recaptured and considered as “new” individuals (included), the number of observed
 228 individuals, n_{obs} , is larger than it should be and thus, \hat{N} is biased upwards. By recognizing
 229 recycled individuals upon recapture, this bias can be corrected. The relative bias in the
 230 super-population size (\hat{N}) due to recycled individuals is highest in the scenario with high
 231 survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as
 232 predicted (Fig. 3, Table 1). The relative bias is small for all scenarios where tag retention was
 233 high, but relative bias increases as tag retention decreases. The relative bias in \hat{N} decreases as
 234 capture probability decreases, but recycled individuals appear to still have some effect on the
 235 estimates even when capture probabilities are low ($p = 0.2$). The relative bias in \hat{N} is high for
 236 scenarios where survival probability is high, and decreases as survival probability decreases.
 237 In all scenarios where survival probability is low ($\phi = 0.2$) individuals are unlikely to survive
 238 long enough to be able to be tagged, lose tag(s) and be recaptured as “new” individuals.
 239 When survival probability is low, the relative bias due to the recycled individuals is small
 240 (less than 0.15) and hence not shown in Fig. 3. SE, SD, and RMSE of \hat{N} varies, but remains
 241 similar between the analyses ~~with and without reecyed individuals included~~including and
 242 excluding recycled individuals, across all scenarios.



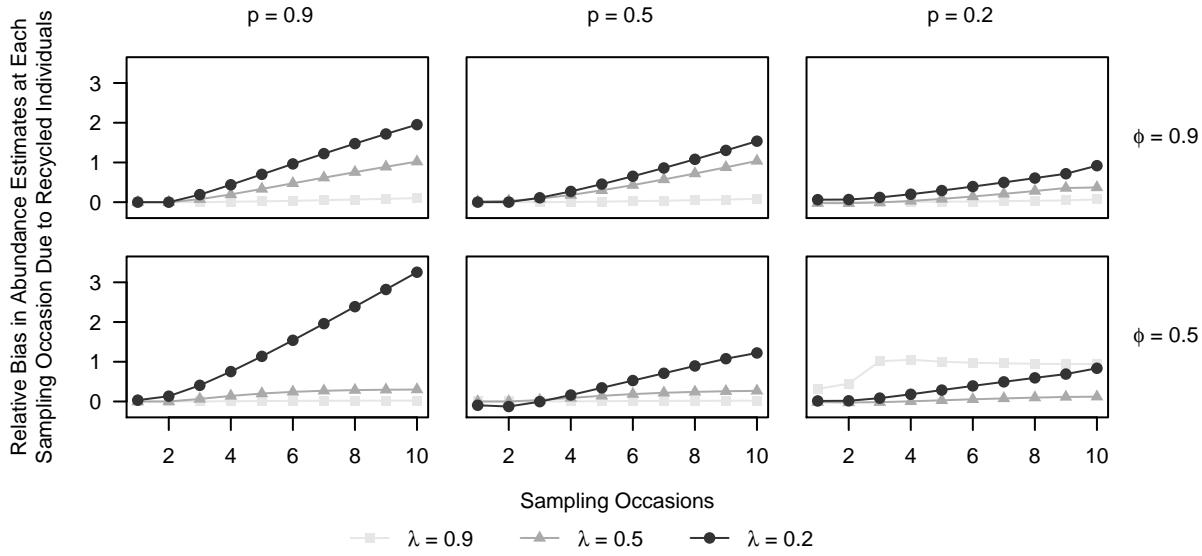
244 FIGURE 3: The difference in mean relative bias of the super-population estimate
 245 (\hat{N}) between the model analyzed including and excluding the recycled individuals
 246 for data with super-population size $N = 100\ 000$ with 100% double-tagging
 247 for different tag retention probabilities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



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

256 There is more bias in \hat{N} due to recycled individuals in longer experiments (Fig. 4). With a
 257 larger number of sampling occasions, there is more time for individuals to be captured and

258 tagged, lose their tags, and survive to be recaptured (be recycled). In shorter studies, there
 259 are fewer numbers of recycled individuals and thus the bias in \hat{N} due to recycled individuals is
 260 lower although not unnoticeable in the worst case scenarios (low tag retention, high survival
 261 and high capture probabilities). Box plots of super-population size (N) for all scenarios are
 262 available in the Online Supplement (Figs A19-A24).



263

264 FIGURE 5: The difference in mean relative bias of the abundance estimates
 265 at each sample time (\hat{N}_j) between the model analyzed including and excluding
 266 the recycled individuals for data with super-population size $N=100\ 000$ with
 267 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$),
 268 survival probabilities ($\phi = 0.5$ and 0.9), and different capture probabilities ($p =$
 269 $0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study. Note that lines
 270 are added between the points to emphasize the difference in values; no models
 271 were fit to generate these lines.

272 In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to the
 273 bias due to recycled individuals in \hat{N} , with relative bias in the \hat{N}_j 's increasing as tag retention
 274 decreases, survival increases, and capture probability increases (Fig. 5). For all scenarios, the
 275 relative bias in the estimates of abundance at each sample time j is **smaller for earlier sampling**

276 occasions and larger for later sampling occasions ~~larger later in the study~~. Since the estimates
277 of the population sizes at each time j are computed iteratively as $\hat{N}_{j+1} = \hat{\phi}(\hat{N}_j) + \hat{b}_j(\hat{N})$,
278 any bias in the earlier abundance estimates is magnified in the later sampling occasions
279 abundance estimates. The scenario with $\phi = 0.5$, $p = 0.9$, and $\lambda = 0.2$ appears to have
280 very high relative bias in the abundance estimates in later sampling occasions (>3 for \hat{N}_{10}),
281 which is caused by a combination of more upward bias in the survival probability estimates
282 for the analysis including recycled individuals (Fig. A1-A6) as well as upward bias in the
283 super-population size estimates. Plots of the mean abundance estimates for all scenarios are
284 available in the Online Supplement (Figs A19-A42).

285 Case Study: Elephant Seals

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

293 We considered two analyses of the data:

- 294 1. We assumed that recycled individuals could not be recognized upon recapture (ignoring
295 branding) and were re-tagged as if they were new individuals. *Recycled individuals are*
296 *included*. This scenario simulates analysis ignoring the effects of recycled individuals.
- 297 2. Recycled individuals were recognized upon recapture (by branding) and were re-tagged
298 with new tags identical to their lost tags. Thus, *recycled individuals are excluded*.

299 For the elephant seal data, there were several differences in parameter estimates of the JSTL

300 model when recycled individuals were included compared to when recycled individuals were
301 excluded. For this analysis, we used the same model as the simulation study where capture,
302 survival and tag retention rates were held constant.

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

309 Similar to the simulations, there is not much difference in the estimates of survival, capture,
310 and tag-retention probabilities between the analysis including and excluding recycled individ-
311 uals. For comparison to the previous simulations, ~~we note that the~~ tag retention probability
312 for the elephant seals ~~was is~~ estimated to be ≈ 0.8 (high). Standard error estimates are also
313 higher when recycled individuals are included in the analysis. The same pattern is seen in
314 the simulation studies (see Web Appendix A).

315 TABLE 2 Estimates of survival probability (ϕ), capture probability (p), tag-
316 retention probability (λ), and annual population size (N_j) for the elephant seal
317 data analyzed with including and without the excluding recycled individuals.
318 Estimated standard 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
319 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	

320 **Discussion**

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

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

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

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

347 Although our study provides some evidence that recycled individuals have an effect on
348 estimators of the JSTL model in particular situations, there is room for improvement in our
349 approach and questions remain for future work. We only examined three levels of survival,
350 capture, and tag-retention probabilities (Low=0.2, Medium=0.5 and High=0.9) which was
351 intended to simulate across a variety of scenarios that may exist in real life. ~~Future work could~~
352 ~~examine~~ For researchers with a particular population in mind, different levels of survival,
353 capture, or tag retention ~~for scenarios of interest for particular populations or could simulate~~
354 ~~aeros~~ more levels to try to get a better sense of the relationship between the parameters
355 ~~and the effect of recycled individuals could be investigated~~. Additionally, future work could
356 examine the effect of recycled individuals in situations where survival, capture or tag-retention
357 probabilities are thought to be time- or group-varying.

358 Developing a model to incorporate recycled individuals is a similar problem to that of
359 incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model
360 to deal with tag-misreads in an open population capture-recapture setting. However most
361 of the misidentification literature focusses on genetic or photographic identification errors.
362 Here multiple identities can be assigned to the same individual leading to overestimates in
363 population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result
364 that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of
365 using a latent multinomial to model the latent capture histories for a closed population model.
366 Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner
367 & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*,
368 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models
369 could be extended to include misidentification produced by complete tag loss.

370 Finally, the JSTL model we used did not include a component for loss on capture (when
371 for example a fishery harvest occurs). It would be interesting for future work to include
372 loss on capture to determine if recycled individuals are still problematic under this scenario.

373 ~~There remains a great deal more to study including testing some of the many assumptions~~
374 ~~that capture-mark-recapture analyses rely on.~~ Increasing computation power and a larger
375 community applying themselves to these problems has the potential to inform researchers
376 and managers in a meaningful way, especially in terms of how we use imperfect observations
377 to estimate vital rates (survival and fecundity). Having more robust estimates of vital rates
378 is especially important if we are to effectively manage populations on an ever increasing list
379 of endangered species.

380 For researchers interested in conducting and analyzing mark-recapture studies to determine
381 abundance estimates, we stress the importance of using tags with high retention rates,
382 especially in situations where survival and capture rates are suspected to be high. As long as
383 tag-retention is high, the JSTL estimator of population size is only weakly affected by recycled
384 individuals. Longer studies should be particularly concerned about recycled individuals

385 biasing ~~abundance~~ abundance estimates. In situations where it is possible, recognizing if an
386 individual has been captured previously (by scarring, marking, etc) can improve accuracy of
387 the abundance estimates. Permanent marking should be used where possible. If researchers
388 are only interested in the survival rates, they do not need to be concerned with the effect of
389 recycled individuals regardless of the study's tag-retention rates.

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

395 Acknowledgements

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

398 Authors' Contributions

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

402 Data Accessibility

403 Data Accessibility:

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

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