

¹ The effect of recycled individuals in the
² Jolly-Seber model with tag loss Complete tag
³ loss in capture-recapture studies affect
⁴ abundance estimates: an elephant seal case
⁵ study.

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11 ABSTRACT:

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

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

29 **Introduction**

30 Mark-recapture studies utilize statistical techniques to estimate population parameters. Over
31 k sample times, individuals are captured, tagged with unique tags, released and potentially
32 recaptured at subsequent sampling times. The Jolly-Seber model (Jolly, 1965; Seber, 1965) is
33 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 ~~it's~~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

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

70 In order to determine whether the simulation framework provided a reasonable approximation
71 to the real world, we analyzed the effects of recycled individuals in long-term census data of
72 elephant seals (*Mirounga leonina*) ~~. For this particular population, seals could be identified~~
73 ~~even if they lost both tags given that they had a permanent brand (McMahon & White, 2009)~~
74 ~~. shown in Figure 1.~~



75

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

77 **Materials and Methods**

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

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

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

85 Assumptions of the JSTL model with constant survival. Data are typically in the form of
86 tag histories for each individual in the study. Let ω_{ijd} denote the entries of the tag history
87 for individual i at time j , tag d ; $i = 1, \dots, n_{obs}$, $j = 1, \dots, k$, capture, and tag retention
88 probabilities and time-varying entry probabilities are as follows: $d = 1, 2$; with ω_{ijd} equally
89 1 or 0 if the individual was seen with tag d or not. Capture histories ω^* used in most
90 capture-recapture studies can be easily obtained from the tag histories ω and are a series
91 of 1s and 0s depicting whether or not an individual was captured at each sample time. We
92 focus on the case with constant parameters as used in our simulation study. Let ϕ denote
93 the survival probability, p the capture probability, λ the tag retention probability, and b_t the
94 entry probability for time t . Ψ and χ are recursive functions of parameters that deal with
95 an individual's history up to the first time seen (f_i) and after the last time seen (l_i) with n_t
96 tags respectively.

- 97 • The effect of reeeyed individuals is negligible
- 98 • All individuals (marked and unmarked) are equally catchable, and that capture
99 probabilities for all individuals are the same for all individuals at all sample times
- 100 • All individuals (marked and unmarked) have equal survival probabilities between all
101 sample times
- 102 • All individuals have equal entry (birth or immigration) probabilities, but entry
103 probabilities can vary between sample times
- 104 • All marked individuals have equal tag retention probabilities between all sample times
- 105
- 106 • For double-tagged individuals, tag loss is independent between tags
- 107 • There is independence across all individuals

- 108 • The sampling period is relatively short compared to the interval between sampling
 109 times

110 **Likelihood and Estimation**

111 The JSTL model is developed under the idea of a superpopulation (the number of individuals
 112 that will enter population at some point during the study) (Schwarz & Arnason, 1996) and
 113 this allows the likelihood to be formulated into ~~three~~two parts: 1) a model for the observed
 114 number of unique tag histories (n_{obs}) given the superpopulation size (L_1^A), N and 2) a
 115 model for the recaptures (in the form of capture history frequencies n_{ω_i}) given the observed
 116 number of unique tag histories (L_1^B), and 3) a model for n_{obs}). The full likelihood is given
 117 by the product of these components as follows:

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

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

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

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

121 where T_d is the probability of being double tagged, l_{id} is the last sample time where tag d
 122 was present, and n_{t_j} is the number of individuals lost on capture (L_3). The third component
 123 L_3 , is typically used for harvest or fisheries data when known deaths occur. In this study
 124 and in the elephant seal application, we assume there is no possibility of loss on capture,
 125 thus the third component of the likelihood simplifies to 1. The full likelihood is given by

126 the product of the components of the likelihood ($L = L_1^A \times L_1^B$) and can be found in the
127 Online Supplement tags on individual i at time j . A table of notation is provided in the
128 supplementary material with further details on the Ψ and χ functions.

129 Assumptions of the JSTL model (under constant ϕ , p , and λ parameters) are similar to
130 the Jolly-Seber model (Schwarz & Arnason, 1996) including all individuals have equal entry
131 (birth or immigration) probabilities, but entry probabilities can vary between sample times;
132 capture probabilities are the same for all individuals at all sample times, all individuals
133 (marked and unmarked) have equal survival probabilities between all sample times, the
134 sampling period is relatively short compared to the interval between sampling times,
135 and there is independence across all individuals. The incorporation of tag loss into the
136 model comes with the additional assumption that all marked individuals have equal tag
137 retention probabilities between all sample times and for double-tagged individuals, tag loss
138 is independent between tags. Finally, the JSTL model assumes that the effect of recycled
139 individuals is negligible and it is this assumption that we explore.

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

143 **Likelihood and Estimation**

144 Maximum likelihood parameter estimates are found using a Newton-Raphson type method.
145 Estimated standard errors are computed using the delta theorem. Models were imple-
146 mented using R software (R Core Team, 2014),~~and code can be obtained from the second~~
147 ~~author~~. ~~Code from this study are included in this published article (and its supplementary~~
148 ~~information files)~~.

¹⁴⁹ **Experimental Design**

¹⁵⁰ To study the effect of recycled individuals on parameter estimates of this model, we conducted
¹⁵¹ a simulation study. Data ~~were simulated and analyzed using R 3.1.1 (R Core Team, 2014).~~
¹⁵² ~~Data~~-sets varied both in super-population size, parameter values, and percent double tagged.
¹⁵³ We generated data for the JSTL model with constant survival, capture, and tag retention
¹⁵⁴ probabilities for a double-tagging experiment. Super-population sizes of 1000 and 100 000
¹⁵⁵ were considered in order to study the effect of population size. For the super-population size
¹⁵⁶ of 100 000, experiments with ten sample times were considered. For the super-population
¹⁵⁷ size of 1000 we considered experiments with five, seven and ten sample times in order to
¹⁵⁸ determine the effect of the length of the study. For each population size, we tested different
¹⁵⁹ proportions of double-tagged versus single-tagged individuals (0.5 and 1). Survival, capture,
¹⁶⁰ and tag retention probability parameters were varied in a 3^3 experimental design with low
¹⁶¹ (0.2), medium (0.5) and high (0.9) values for all parameters. The entry rates were fixed to be
¹⁶² $1/k$ at each of the sampling times. No individuals were lost on capture.

¹⁶³ We considered the set of parameter values to be reasonable values that might be encountered
¹⁶⁴ in practice and also produce informative capture-recapture scenarios. Tag retention rates
¹⁶⁵ can vary by species, age of the tag, tag type, tag location, behaviour, season, and individual
¹⁶⁶ quality (size of an animal for example in seals). For example, tag retention rates have ranged
¹⁶⁷ from 13% (Fogarty *et al.*, 1980) to 95% (Gonzalez-Vicente *et al.*, 2012) in lobsters. Other
¹⁶⁸ studies report tag retention rates of 65% in male elephant seals (Pistorius *et al.*, 2000) and
¹⁶⁹ 88% in Adelie penguins (Ainley & DeMaster, 1980). Mean retention of visible implant tags
¹⁷⁰ has been recorded as 32% in small rockpool fish (Griffiths, 2002). Turtles in particular
¹⁷¹ experience high tag loss rates. For example Bellini *et al.* (2001) reports the probability of tag
¹⁷² loss in hawksbill turtles as 0.57 and Bjorndal *et al.* (1996) observed the probability of tag
¹⁷³ loss in green nesting turtles to be as high as 0.38. Thus, we chose a wide range of tag loss
¹⁷⁴ parameter values to try to capture the diversity among published tag loss rates.

175 **Simulation of Data**

176 For all of the parameter combinations of super-population size ($N = 1000, 100\ 000$), fraction
177 double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
178 0.2, 0.5, 0.9) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
179 the simulated data met all the assumptions of the model.

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

181 1. Determine when the individual enters the population utilizing the entry probabilities.

182 2. For each sample time after entry (until death or first capture) determine if the individual
183 survives to that sample time (with probability ϕ). If they are still alive, determine if
184 they are first captured (with probability p). If they are captured, determine whether
185 they are single or double-tagged.

186 3. For each sample time after first capture (until death, loss of all tags or the end of the
187 study) determine if the individual survives to that sample time (with probability ϕ).
188 Then if they are still alive, determine if they lose any of their tags (with probability
189 $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with
190 probability p). If they have lost all of their tags, consider them as a new individual
191 entering the population at this sample time.

192 By keeping track of all the recycled individuals, this algorithm provides us with two data
193 sets: one that includes the recycled individuals (assumes individuals, who have complete tag
194 loss, are tagged again upon recapture and treated as new individuals) and one that ~~doesn't~~
195 ~~include~~ excludes recycled individuals (assumes that individuals, who have complete tag loss,
196 can be recognized upon recapture and are not re-tagged). The JSTL model was fit to the 100
197 simulated data sets twice (once ~~with and once without~~ including and once excluding recycled
198 individuals). We assumed that any difference between the two analyses was due entirely to

199 the recycled individuals. All data generated during this study are included in this published
200 article (and its supplementary information files).

201 **Evaluation Criteria**

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

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

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

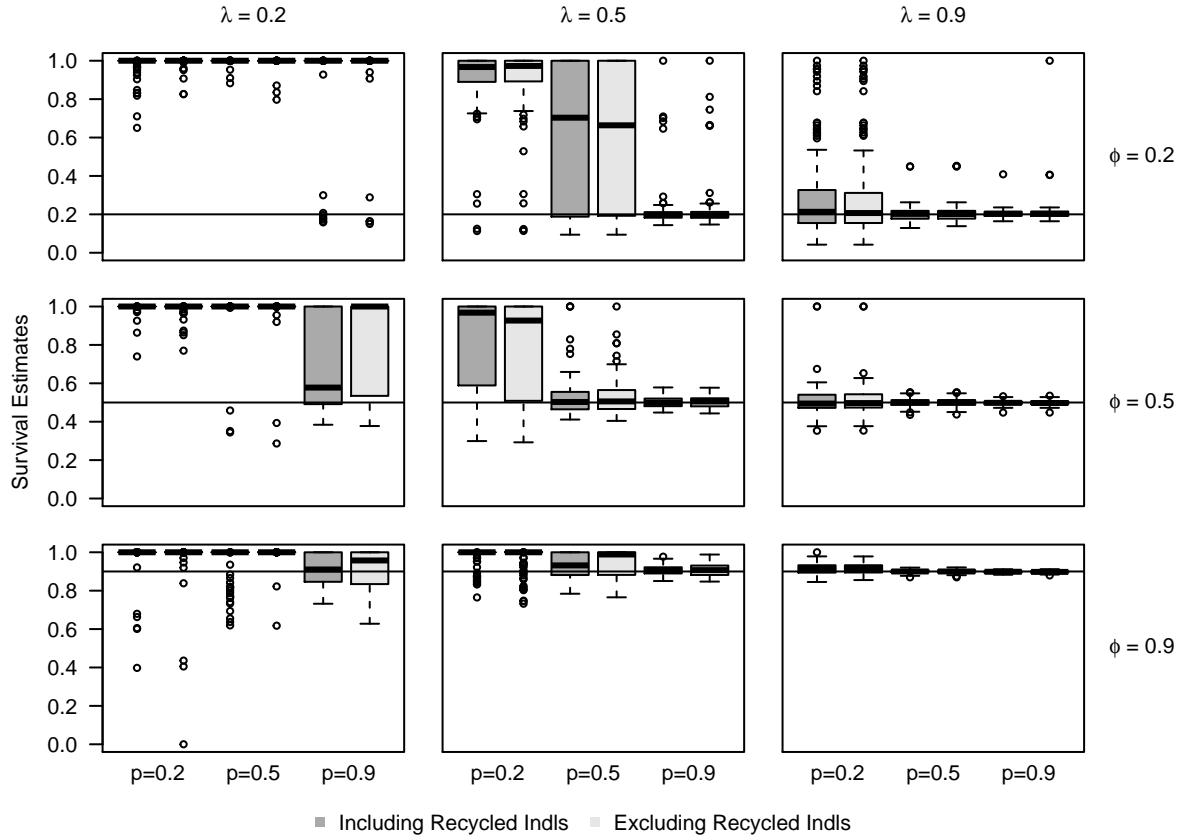
212 We compared the average parameter estimates to the true parameter values using relative
213 bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
214 relative bias from the analysis with the recycled individuals to the relative bias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

218 **Simulation Results**

219 The ~~relative bias of the~~ survival estimates are biased for some parameter combinations of
220 survival, capture, and tag retention probabilities. As an example, box plots of survival

estimates for data with super-population size $N=1000$ and 100% double tagging are provided (Fig. 12). Box plots of survival estimates for other super-population sizes and double-tagging rates are provided in the Online Supplement (Figs A1-A4). Although there is bias in the survival estimates for several of the parameter combinations, the bias is similar between the analysis with including and the analysis without excluding the recycled individuals included for both super-population sizes ($N = 1000$ and 100 000) and for both double-tagging rates ($T_2 = 0.5, 1$). In fact, the differences in relative bias due to recycled individuals for the parameters ϕ , p and λ is small (<0.01) for all 108 parameter combinations considered. In general, the SE, SD and RMSE of the estimates of ϕ , p and λ are similar for both the analysis with and without including and excluding recycled individuals for the parameter combinations considered. It seems that the treatment of recycled individuals has little effect, if any, on the accuracy of the JSTL estimators for survival, capture, and tag-retention probabilities. Box plots of capture and tag retention estimates for all models can also be found in the Online Supplement (Figs A5-A12).

~~Results are similar for both the super-population sizes of 1000 and 100 000 for all parameter combinations of survival, capture, and tag retention probabilities (Table 1).~~ There is slightly more bias due to recycled individuals for parameter combinations where the probability of double tagging (T_2) was only 0.5, compared to the parameter combinations where all individuals were double tagged. As an example, relative bias of the parameters are presented for the parameter combination where $\phi = 0.9, p = 0.9$ and $\lambda = 0.2$ for both the analysis with and without recycled individuals for varying population size and double-tagging probabilities (Table 1).



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FIGURE 42: 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 with including and without excluding the recycled individuals are provided. The black line indicates the true value of ϕ used to simulate the data for each model.

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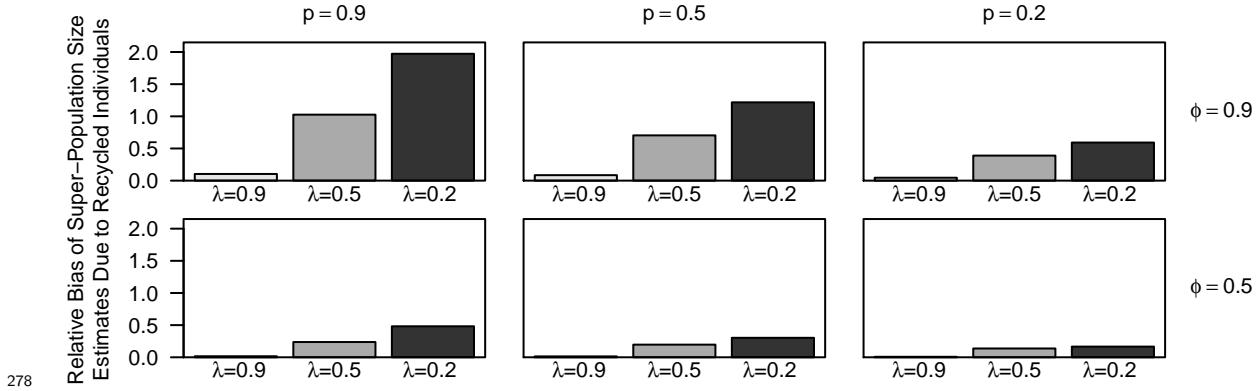
TABLE 1: The mean relative bias of the parameters from the model analyzed with including (R) and without excluding (R') the recycled individuals for data with high survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag retention ($\lambda = 0.2$) for different super-populations sizes ($N = 1000, 100\,000$)

256 and different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from
 257 a 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

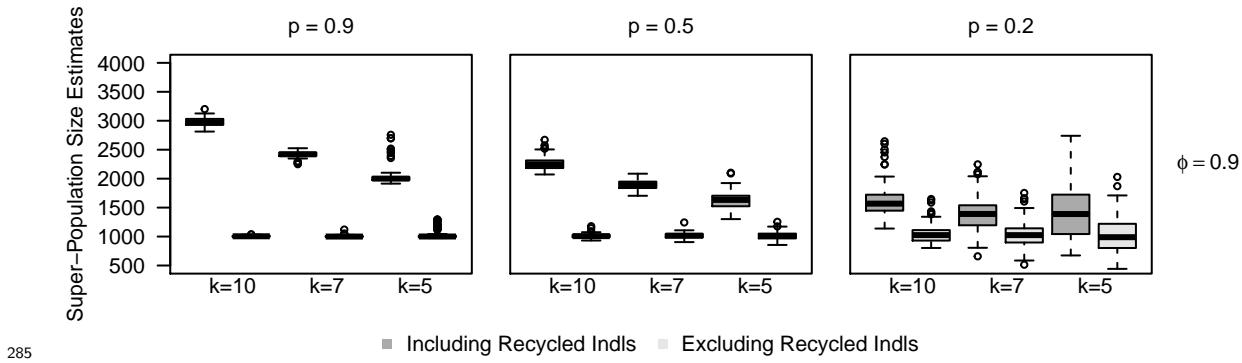
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259 The estimate of super-population size (\hat{N}) is computed as $\hat{N} = n_{\text{obs}}/(1 - \hat{P}_0)$, where \hat{P}_0
 260 is the estimated probability of never being seen. In the scenarios where many recycled
 261 individuals were recaptured and considered as “new” individuals (included), the number of
 262 observed individuals, n_{obs} , is larger than it should be and thus, \hat{N} is biased upwards. This
 263 ~~bias is corrected in the analysis without the recycled individuals considered~~ By recognizing
 264 recycled individuals upon recapture, this bias can be corrected. The relative bias in the
 265 super-population size (\hat{N}) due to recycled individuals is highest in the scenario with high
 266 survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as
 267 predicted (Fig. 23, Table 1). The relative bias is small for all scenarios where tag retention
 268 was high, but relative bias increases as tag retention decreases. The relative bias in \hat{N}
 269 decreases as capture probability decreases, but recycled individuals appear to still have some
 270 effect on the estimates even when capture probabilities are low ($p = 0.2$). The relative
 271 bias in \hat{N} is high for scenarios where survival probability is high, and decreases as survival
 272 probability decreases. In all scenarios where survival probability is low ($\phi = 0.2$) individuals
 273 are unlikely to survive long enough to be able to be tagged, lose tag(s) and be recaptured
 274 as “new” individuals. When survival probability is low, the relative bias due to the recycled
 275 individuals is small (less than 0.15) and hence not shown in Fig. 2–3. SE, SD, and RMSE of
 276 \hat{N} varies, but remains similar between the analyses with and without recycled individuals
 277 included, across all scenarios.



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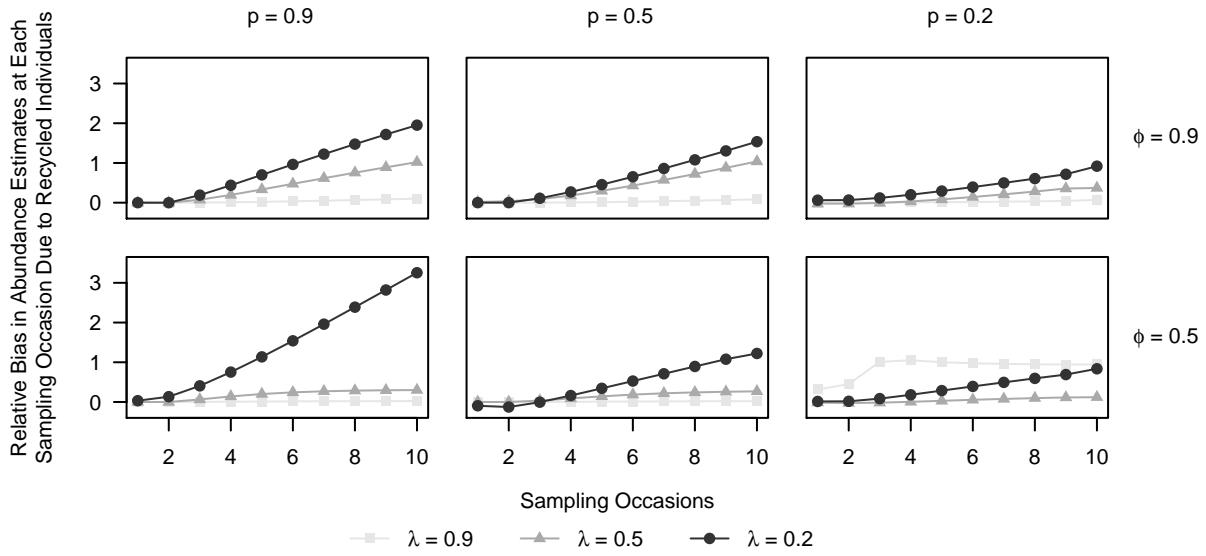
FIGURE 23: The difference in mean relative bias of the super-population estimate (\hat{N}) between the model analyzed with-including and without-excluding the recycled individuals for data with super-population size $N = 100\ 000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.2, 0.5, 0.9$), 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 34: Box plots of the estimates of N for the model analyzed with-including and without-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.

292 There is more bias in \hat{N} due to recycled individuals in longer experiments (Fig. 34). With a
 293 larger number of sampling occasions, there is more time for individuals to be captured and
 294 tagged, lose their tags, and survive to be recaptured (be recycled). In shorter studies, there
 295 are fewer numbers of recycled individuals and thus the bias in \hat{N} due to recycled individuals is
 296 lower although not unnoticeable in the worst case scenarios (low tag retention, high survival
 297 and high capture probabilities). Box plots of super-population size (N) for all scenarios are
 298 available in the Online Supplement (Figs A19-A24).



300 FIGURE 45: The difference in mean relative bias of the abundance estimates at
 301 each sample time (\hat{N}_j) between the model analyzed with including and without
 302 excluding the recycled individuals for data with super-population size $N=100$
 303 000 with 100% double-tagging for different tag retention probabilities ($\lambda =$
 304 0.2, 0.5, 0.9), survival probabilities ($\phi = 0.2, 0.5, 0.9$ $\phi = 0.5$ and 0.9), and different
 305 capture probabilities ($p = 0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-
 306 time study. Note that lines are added between the points to emphasize the
 307 difference in values; no models were fit to generate these lines.

308 In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to
 309 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. 45). For all scenarios, the relative bias in the estimates of abundance at each sample time j is smaller for earlier sampling occasions and larger for later sampling occasions. 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 ~~with recycled individuals than without including recycled individuals~~ (Fig. A14-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 Online Supplement (Figs A17-A28A19-A42).

321 Case Study: Elephant Seals

To validate the simulation framework, we analyzed data from a long-term mark-recapture study of elephant seals on Macquarie Island. The data used for the case study consists of 7 years 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 ~~analyzes~~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.
2. Recycled individuals were recognized upon recapture (by branding) and were re-tagged with new tags identical to their lost tags. Thus, recycled individuals are excluded.

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

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

345 Similar to the simulations, there is not much difference in the estimates of survival, capture,
346 and tag-retention probabilities between the analysis ~~with and without~~ including and excluding
347 recycled individuals. For comparison to the previous simulations, we note that tag retention
348 probability for the elephant seals was estimated to be ≈ 0.8 (high). Standard error estimates
349 are also higher when recycled individuals are included in the analysis. The same pattern is
350 seen in the simulation studies (see Web Appendix A).

351 TABLE 2 *Estimates of survival probability (ϕ), capture probability (p), tag-*
352 *retention probability (λ), and annual population size (N_j) for the elephant seal*
353 *data analyzed with and without the recycled individuals. Estimated standard*
354 *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
355	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	

356 Discussion

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

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

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

373 It is not surprising that survival estimates are not biased upwards when recycled individuals
374 are ignored. Survival estimates are essentially a relative measure of how many individuals
375 are around now versus the previous time step. Thus the bias in the numerator and the
376 denominator essentially cancels out (i.e. $\hat{\phi}_j \approx \hat{N}_j / \hat{N}_{j-1}$).

377 Although the case study of elephant seals validated some of the results from the simulation
378 study (recycled individuals bias abundance estimates upwards), some caution must be
379 taken when comparing simulation studies to the real world. There are many parameters
380 that may differ or be uncertain, such as entry probabilities, that may influence the results.
381 Simplifications of the individuals in the simulation studies may not take into account the
382 complexities that arise in real life scenarios.

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

394 For researchers interested in conducting and analyzing mark-recapture studies, unsurprisingly
395 we stress the importance of using tags with high retention rates, especially in situations
396 where survival and capture rates are suspected to be high. As long as tag retention is
397 high, the JSTL estimator of population size is not affected by recycled individuals. In
398 situations where it is possible to recognize if an individual has been captured previously (by
399 scarring, marking, etc), excluding these recycled individuals from the analysis can improve
400 accuracy of the abundance estimates. Permanent marking should be used where possible. If
401 researchers are only interested in the survival rates, they do not need to be concerned with
402 the effect of recycled individuals regardless of the study's tag retention rates.

403 Developing a model to incorporate recycled individuals is a similar problem to that of
404 incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model
405 to deal with tag-misreads in an open population capture-recapture setting. However most
406 of the misidentification literature focusses on genetic or photographic identification errors.
407 Here multiple identities can be assigned to the same individual leading to overestimates in
408 population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result
409 that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of
410 using a latent multinomial to model the latent capture histories for a closed population model.
411 Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner
412 & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*,
413 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models
414 could be extended to include misidentification produced by complete tag loss.

415 Finally, the JSTL model we looked at used did not include a component for loss on capture
416 (when for example a fishery harvest occurs). It would be interesting for future work to include
417 loss on capture to determine if recycled individuals are still problematic under this scenario.
418 There remains a great deal more to study including testing some of the many assumptions
419 that capture-mark-recapture analyses rely on, many of which we know are violated in the real
420 world. Increasing computation power and a larger community applying themselves to these

problems has the potential to ~~answer and~~ inform researchers and managers in a meaningful way, especially in terms of how we use imperfect observations to estimate vital rates (survival and fecundity). Having more robust estimates of vital rates is especially important if we are to ~~manage efficiently~~ effectively manage populations on an ever increasing list of endangered species.

For researchers interested in conducting and analyzing mark-recapture studies to determine abundance estimates, we stress the importance of using tags with high retention rates, especially in situations where survival and capture rates are suspected to be high. As long as tag-retention is high, the JSTL estimator of population size is only weakly affected by recycled individuals. Longer studies should be particularly concerned about recycled individuals biasing abundance estimates. In situations where it is possible, recognizing if an individual has been captured previously (by scarring, marking, etc) can improve accuracy of the abundance estimates. Permanent marking should be used where possible. If researchers are only interested in the survival rates, they do not need to be concerned with the effect of recycled individuals regardless of the study's tag-retention rates.

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

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444 Authors' Contributions

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

448 Data Accessibility

449 Data Accessibility:

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

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