

¹ Complete tag loss in capture-recapture studies
² affects 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 tag history $\{11\ 01\ 00\}$ over three sampling occasions was double tagged at sample time 1, lost a tag between times 1 and 2, and may have lost its last tag between sample times 2 and 3 and then have been recaptured at sample time 3 resulting in a new individual with tag history $\{00\ 00\ 11\}$. If the rate of tag loss is small, bias in the population estimate will also be small for the Peterson estimators (Seber & Felton, 1965). Typically in the Jolly-Seber and JSTL models, the effect of recycled individuals is assumed to be negligible. However, in situations

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

67 In order to determine whether the simulation framework provided a reasonable approximation
68 to the real world, we analyzed the effects of recycled individuals in long-term census data of
69 southern elephant seals (Figure 1).



70

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

72 Materials and Methods

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

74 Full development of the JSTL model is given by (Cowen & Schwarz, 2006). Data are typically
 75 in the form of tag histories for each individual in the study. Let ω_{ijd} denote the entries of
 76 the tag history for individual i at time j , tag d ; $i = 1, \dots, n_{obs}$, $j = 1, \dots, k$, $d = 1, 2$; with
 77 ω_{ijd} equaling 1 or 0 if the individual was seen with tag d or not. Capture histories ω^* used
 78 in most capture-recapture studies can be easily obtained from the tag histories ω and are a
 79 series of 1's and 0's depicting whether or not an individual was captured at each sample time.

80 We focus on the case with constant parameters as used in our simulation study. Let ϕ denote
 81 the survival probability, p the capture probability, λ the tag retention probability, and b_t the
 82 entry probability for time t . Ψ and χ are recursive functions of parameters that deal with an
 83 individual's history up to the first time seen (f_i) and after the last time seen (l_i) with n_t tags
 84 respectively.

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

$$92 L = \binom{N}{n_{obs}} \left\{ \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{(N-n_{obs})} \left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{n_{obs}} \times \\ \left(\begin{matrix} n_{obs} \\ n_{\omega_1}, n_{\omega_2}, \dots, n_{\omega_m} \end{matrix} \right) \prod_{i=1}^m \left[\psi_{f_i} T_d \left\{ \prod_{j=f_i}^{l_i} p^{w*_{ij}} (1-p)^{(1-w*_{ij})} \right\} \left\{ \prod_{j=f_i}^{l_i-1} \phi \right\} \right] \times$$

93

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

94

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

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

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

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

111 Likelihood and Estimation

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

115 article (and its supplementary information files).

116 Experimental Design

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

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

¹⁴⁰ parameter values to try to capture the diversity among published tag loss rates.

¹⁴¹ **Simulation of Data**

¹⁴² For all of the parameter combinations of super-population size ($N = 1000, 100\,000$), fraction
¹⁴³ double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
¹⁴⁴ 0.2, 0.5, 0.9) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
¹⁴⁵ the simulated data met all the assumptions of the model.

¹⁴⁶ For each individual, we simulated a capture history using the following algorithm:

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

¹⁴⁸ 2. For each sample time after entry (until death or first capture) determine if the individual
¹⁴⁹ survives to that sample time (with probability ϕ). If they are still alive, determine if
¹⁵⁰ they are first captured (with probability p). If they are captured, determine whether
¹⁵¹ they are single or double-tagged.

¹⁵² 3. For each sample time after first capture (until death, loss of all tags or the end of the
¹⁵³ study) determine if the individual survives to that sample time (with probability ϕ).
¹⁵⁴ Then if they are still alive, determine if they lose any of their tags (with probability
¹⁵⁵ $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with
¹⁵⁶ probability p). If they have lost all of their tags, consider them as a new individual
¹⁵⁷ entering the population at this sample time.

¹⁵⁸ By keeping track of all the recycled individuals, this algorithm provides us with two data
¹⁵⁹ sets: one that includes the recycled individuals (assumes individuals, who have complete tag
¹⁶⁰ loss, are tagged again upon recapture and treated as new individuals) and one that excludes
¹⁶¹ recycled individuals (assumes that individuals, who have complete tag loss, can be recognized
¹⁶² upon recapture and are not re-tagged). The JSTL model was fit to the 100 simulated data

¹⁶³ sets twice (once including and once excluding recycled individuals). We assumed that any
¹⁶⁴ difference between the two analyses was due entirely to the recycled individuals. All data
¹⁶⁵ generated during this study are included in this published article (and its supplementary
¹⁶⁶ information files).

¹⁶⁷ **Evaluation Criteria**

¹⁶⁸ To evaluate the resulting parameter estimates from each of the simulations, we looked at
¹⁶⁹ several criteria including: average parameter estimate, relative bias of the estimates, the
¹⁷⁰ average standard error of the parameter estimates, the standard deviation of the parameter
¹⁷¹ estimates, and root mean squared error (RMSE) of the parameter estimates.

¹⁷² Let $\hat{\theta}_i$'s be the parameter estimates from each of the 100 simulations and θ the true parameter
¹⁷³ value, we calculated:

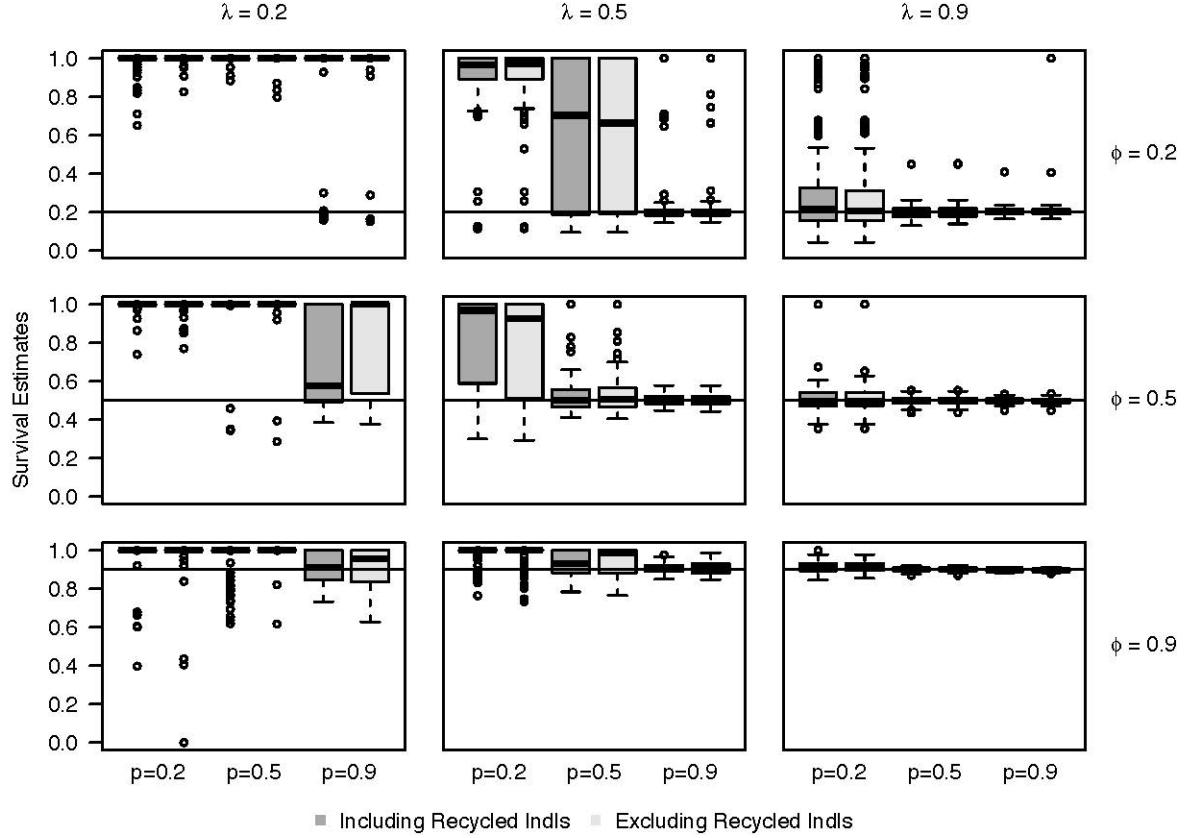
- ¹⁷⁴ • the mean parameter estimate as $\bar{\hat{\theta}} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$
- ¹⁷⁵ • average standard error of the parameter estimate as $SE(\hat{\theta}) = \frac{1}{100} \sum_{i=1}^{100} SE(\hat{\theta}_i)$.
- ¹⁷⁶ • the standard deviation of the parameter estimates as $SD(\hat{\theta}) = \sqrt{\frac{1}{99} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.
- ¹⁷⁷ • the RMSE of the parameter estimates as $RMSE = \sqrt{\frac{1}{100} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.

¹⁷⁸ We compared the average parameter estimates to the true parameter values using relative
¹⁷⁹ bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
¹⁸⁰ relative bias from the analysis with the recycled individuals to the relative bias from the
¹⁸¹ analysis without the recycled individuals. We calculated the difference in the two relative
¹⁸² biases and consider this to be the relative bias that was contributed entirely by the recycled
¹⁸³ individuals being tagged as “new” individuals.

184 Simulation Results

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

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



206

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

214

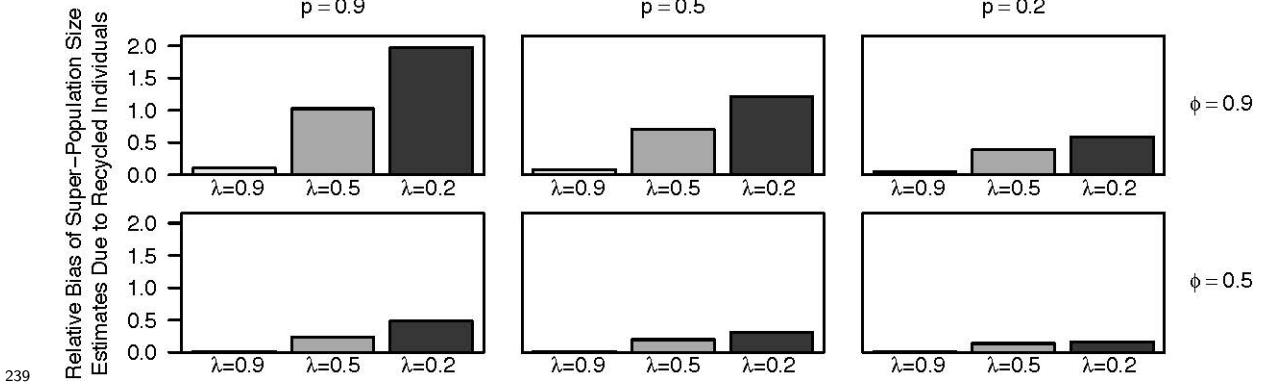
215 TABLE 1: The mean relative bias of the parameters from the model analyzed
 216 including (R) and excluding (R') the recycled individuals for data with high
 217 survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag
 218 retention ($\lambda = 0.2$) for different super-populations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

219 different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from a
220 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

221

222 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
223 estimated probability of never being seen. In the scenarios where many recycled individuals
224 were recaptured and considered as “new” individuals (included), the number of observed
225 individuals, n_{obs} , is larger than it should be and thus, \hat{N} is biased upwards. By recognizing
226 recycled individuals upon recapture, this bias can be corrected. The relative bias in the
227 super-population size (\hat{N}) due to recycled individuals is highest in the scenario with high
228 survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as
229 predicted (Fig. 3, Table 1). The relative bias is small for all scenarios where tag retention was
230 high, but relative bias increases as tag retention decreases. The relative bias in \hat{N} decreases as
231 capture probability decreases, but recycled individuals appear to still have some effect on the
232 estimates even when capture probabilities are low ($p = 0.2$). The relative bias in \hat{N} is high for
233 scenarios where survival probability is high, and decreases as survival probability decreases.
234 In all scenarios where survival probability is low ($\phi = 0.2$) individuals are unlikely to survive
235 long enough to be able to be tagged, lose tag(s) and be recaptured as “new” individuals.
236 When survival probability is low, the relative bias due to the recycled individuals is small
237 (less than 0.15) and hence not shown in Fig. 3. SE, SD, and RMSE of \hat{N} varies, but remains
238 similar between the analyses including and excluding recycled individuals, across all scenarios.



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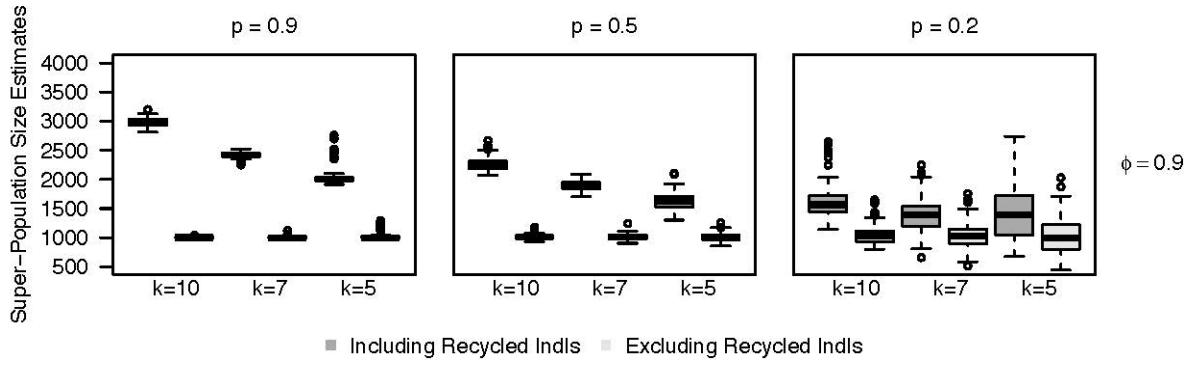
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FIGURE 3: The difference in mean relative bias of the super-population estimate (\hat{N}) between the model analyzed including and excluding the recycled individuals for data with super-population size $N = 100\ 000$ with 100% double-tagging for different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



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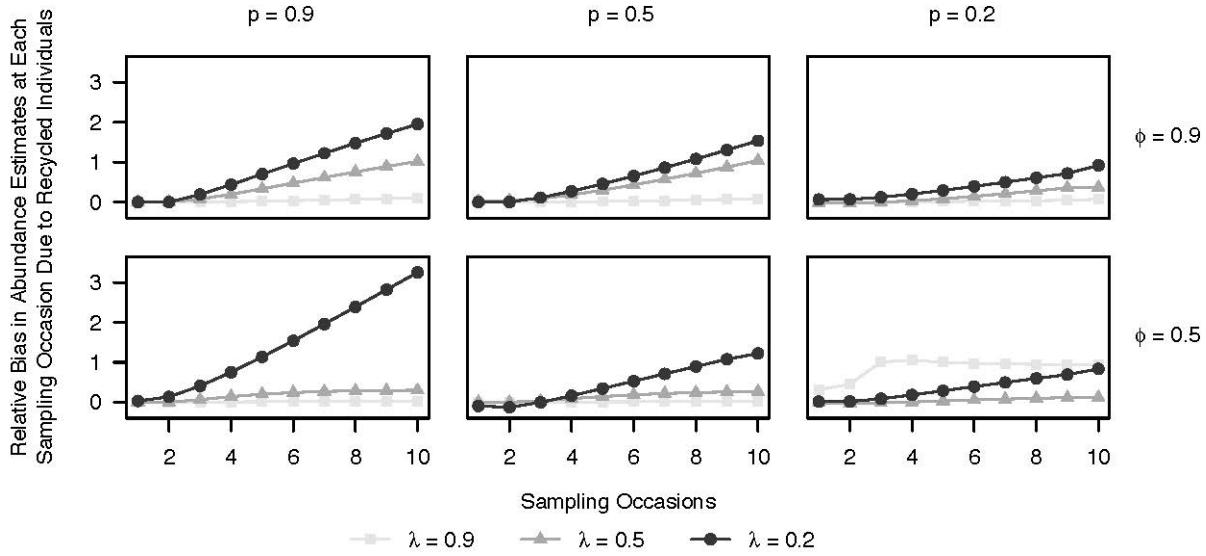
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FIGURE 4: Box plots of the estimates of N for the model analyzed including and excluding the recycled individuals for data with super-population size $N = 1000$ with 100% double-tagging for different capture probabilities ($p = 0.2, 0.5, 0.9$), and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

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

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



259

260 FIGURE 5: The difference in mean relative bias of the abundance estimates
 261 at each sample time (\hat{N}_j) between the model analyzed including and excluding
 262 the recycled individuals for data with super-population size $N=100\ 000$ with
 263 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$),
 264 survival probabilities ($\phi = 0.5$ and 0.9), and different capture probabilities ($p =$
 265 $0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study. Note that lines
 266 are added between the points to emphasize the difference in values; no models
 267 were fit to generate these lines.

268 In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to the
 269 bias due to recycled individuals in \hat{N} , with relative bias in the \hat{N}_j 's increasing as tag retention
 270 decreases, survival increases, and capture probability increases (Fig. 5). For all scenarios,
 271 the relative bias in the estimates of abundance at each sample time j is larger later in the

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

Case Study: Elephant Seals

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

We considered two analyses of the data:

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

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.*

For the elephant seal data, there were several differences in parameter estimates of the JSTL model when recycled individuals were included compared to when recycled individuals were

295 excluded. For this analysis, we used the same model as the simulation study where capture,
296 survival and tag retention rates were held constant.

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

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

308 TABLE 2 *Estimates of survival probability (ϕ), capture probability (p), tag-
309 retention probability (λ), and annual population size (N_j) for the elephant seal
310 data analyzed including and excluding recycled individuals. Estimated standard
311 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
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	

313 Discussion

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

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

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

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

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

348 Developing a model to incorporate recycled individuals is a similar problem to that of
349 incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model
350 to deal with tag-misreads in an open population capture-recapture setting. However most

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

Finally, the JSTL model we used did not include a component for loss on capture (when for example a fishery harvest occurs). It would be interesting for future work to include loss on capture to determine if recycled individuals are still problematic under this scenario. Increasing computation power and a larger community applying themselves to these problems has the potential to 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 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.

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

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386 Authors' Contributions

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

390 Data Accessibility

- 391 • Elephant seal data, generated data and scripts can be assessed through Dryad at:
392 <https://doi.org/10.5061/dryad.v6wwpzgr3>

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