

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

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

¹ Mathematics, Middlebury College, Middlebury, VT, USA

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

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

⁶

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

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

9 ABSTRACT:

- 10 1. In capture-recapture studies, recycled individuals occur when individuals
11 lose all of their tags and are recaptured as though they were new individuals.
12 Typically, the effect of these recycled individuals is assumed negligible.
- 13 2. Through a simulation-based study of double tagging experiments, we ex-
14 amined the effect of recycled individuals on parameter estimates in the
15 Jolly-Seber model with tag loss (?). We validated the simulation framework
16 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 (??) is used to model
31 open populations since it can estimate parameters of interest such as population size and

survival rates (?). 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 (?). 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: ?, lobsters: ?:, sea turtles: ?, elephant seals: ?, black bears: ?) to investigate probabilities of tag loss or tag shedding rates. Often a mixture of single- and double-tagged individuals is used for practical purposes. ? 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 (?). 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 (?).

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 (?). Typically in the Jolly-Seber and JSTL models, the effect of recycled individuals is assumed to be negligible. However, in situations where tag retention is low and survival and recapture probabilities are high it is suspected that recycled individuals will bias population size estimates upwards. The motivation for

59 this study was to investigate the effect of recycled individuals on parameter estimates in the
60 JSTL model through a simulation study and determine under which conditions researchers
61 need to be concerned. This study is important as the assumption that the effect is negligible
62 has not been fully tested and quantified, and most studies that rely on marking individuals
63 typically experience tag loss. Thus, there is a need to account for recycled individuals given
64 the desire for accurate and robust estimates for management and conservation purposes.

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



68
69 FIGURE 1: Elephant seal (*Mirounga leonina*) at Macquarie Island, Australia.

70 Materials and Methods

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

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

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

$$88 L = \binom{N}{n_{obs}} \left\{ \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{(N-n_{obs})} \left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{n_{obs}} \times \\ \binom{n_{obs}}{n_{\omega_1}, n_{\omega_2}, \dots, n_{\omega_m}} \prod_{i=1}^m \left[\psi_{f_i} T_d \left\{ \prod_{j=f_i}^{l_i} p^{w^*_{ij}} (1-p)^{(1-w^*_{ij})} \right\} \left\{ \prod_{j=f_i}^{l_i-1} \phi \right\} \times \right. \\ \left. \prod_{d=1}^2 \left\{ \left(\prod_{j=f_i}^{l_{id}-1} \lambda \right) \left(1 - \prod_{j=l_{id}}^{q_{id}-1} \lambda \right)^{I(l_{id} \neq l_i)} \right\} \times \chi_{f_i, l_i, n_{t_{l_i}}} \right]^{n_{\omega_i}}$$

90

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

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

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

106 Many different models can be specified for the JSTL model where parameters are homogeneous
107 or heterogeneous with respect to time (?) or group (?).

108 **Likelihood and Estimation**

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

¹¹³ **Experimental Design**

¹¹⁴ To study the effect of recycled individuals on parameter estimates of this model, we conducted
¹¹⁵ a simulation study. Data sets varied **both** in super-population size, parameter values, and
¹¹⁶ percent double tagged. We generated data for the JSTL model with constant survival,
¹¹⁷ capture, and tag retention probabilities for a double-tagging experiment. Super-population
¹¹⁸ sizes of 1000 and 100 000 were considered in order to study the effect of population size. For
¹¹⁹ the super-population size of 100 000, experiments with ten sample times were considered.
¹²⁰ For the super-population size of 1000 we considered experiments with five, seven and ten
¹²¹ sample times in order to determine the effect of the study length. For each population size,
¹²² we tested different proportions of double-tagged versus single-tagged individuals (0.5 and 1).
¹²³ Survival, capture, and tag retention probability parameters were varied in a 3^3 experimental
¹²⁴ design with low (0.2), medium (0.5) and high (0.9) values for all parameters. The entry rates
¹²⁵ were fixed to be $1/k$ at each of the sampling times.

¹²⁶ We considered the set of parameter values to be reasonable values that might be encountered
¹²⁷ in practice and also produce informative capture-recapture scenarios. Tag retention rates
¹²⁸ can vary by species, age of the tag, tag type, tag location, behaviour, season, and individual
¹²⁹ quality (size of an animal for example in seals). For example, tag retention rates have ranged
¹³⁰ from 13% (?) to 95% (?) in lobsters. Other studies report tag retention rates of 65% in male
¹³¹ elephant seals (?) and 88% in Adelie penguins (?). Mean retention of visible implant tags
¹³² has been recorded as 32% in small rockpool fish (?). Turtles in particular experience high tag
¹³³ loss rates. For example ? reports the probability of tag loss in hawksbill turtles as 0.57 and
¹³⁴ ? observed the probability of tag loss in green nesting turtles to be as high as 0.38. Thus,
¹³⁵ we chose a wide range of tag loss parameter values to try to capture the diversity among
¹³⁶ published tag loss rates.

¹³⁷ **Simulation of Data**

¹³⁸ For all of the parameter combinations of super-population size ($N = 1000, 100\ 000$), fraction
¹³⁹ double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
¹⁴⁰ 0.2, 0.5, 0.9) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
¹⁴¹ the simulated data met all the assumptions of the model.

¹⁴² For each individual, we simulated a capture history using the following algorithm:

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

¹⁴⁴ 2. For each sample time after entry (until death or first capture) determine if the individual
¹⁴⁵ survives to that sample time (with probability ϕ). If they are still alive, determine if
¹⁴⁶ they are first captured (with probability p). If they are captured, determine whether
¹⁴⁷ they are single or double-tagged.

¹⁴⁸ 3. For each sample time after first capture (until death, loss of all tags or the end of the
¹⁴⁹ study) determine if the individual survives to that sample time (with probability ϕ).
¹⁵⁰ Then if they are still alive, determine if they lose any of their tags (with probability
¹⁵¹ $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with
¹⁵² probability p). If they have lost all of their tags, consider them as a new individual
¹⁵³ entering the population at this sample time.

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

¹⁶¹ generated during this study are included in this published article (and its supplementary
¹⁶² information files).

¹⁶³ **Evaluation Criteria**

¹⁶⁴ To evaluate the resulting parameter estimates from each of the simulations, we looked at
¹⁶⁵ several criteria including: average parameter estimate, relative bias of the estimates, the
¹⁶⁶ average standard error of the parameter estimates, the standard deviation of the parameter
¹⁶⁷ estimates, and root mean squared error (RMSE) of the parameter estimates.

¹⁶⁸ Let $\hat{\theta}_i$'s be the parameter estimates from each of the 100 simulations and θ the true parameter
¹⁶⁹ value, we calculated:

- ¹⁷⁰ • the mean parameter estimate as $\bar{\hat{\theta}} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$
- ¹⁷¹ • average standard error of the parameter estimate as $SE(\hat{\theta}) = \frac{1}{100} \sum_{i=1}^{100} SE(\hat{\theta}_i)$.
- ¹⁷² • the standard deviation of the parameter estimates as $SD(\hat{\theta}) = \sqrt{\frac{1}{99} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.
- ¹⁷³ • the RMSE of the parameter estimates as $RMSE = \sqrt{\frac{1}{100} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.

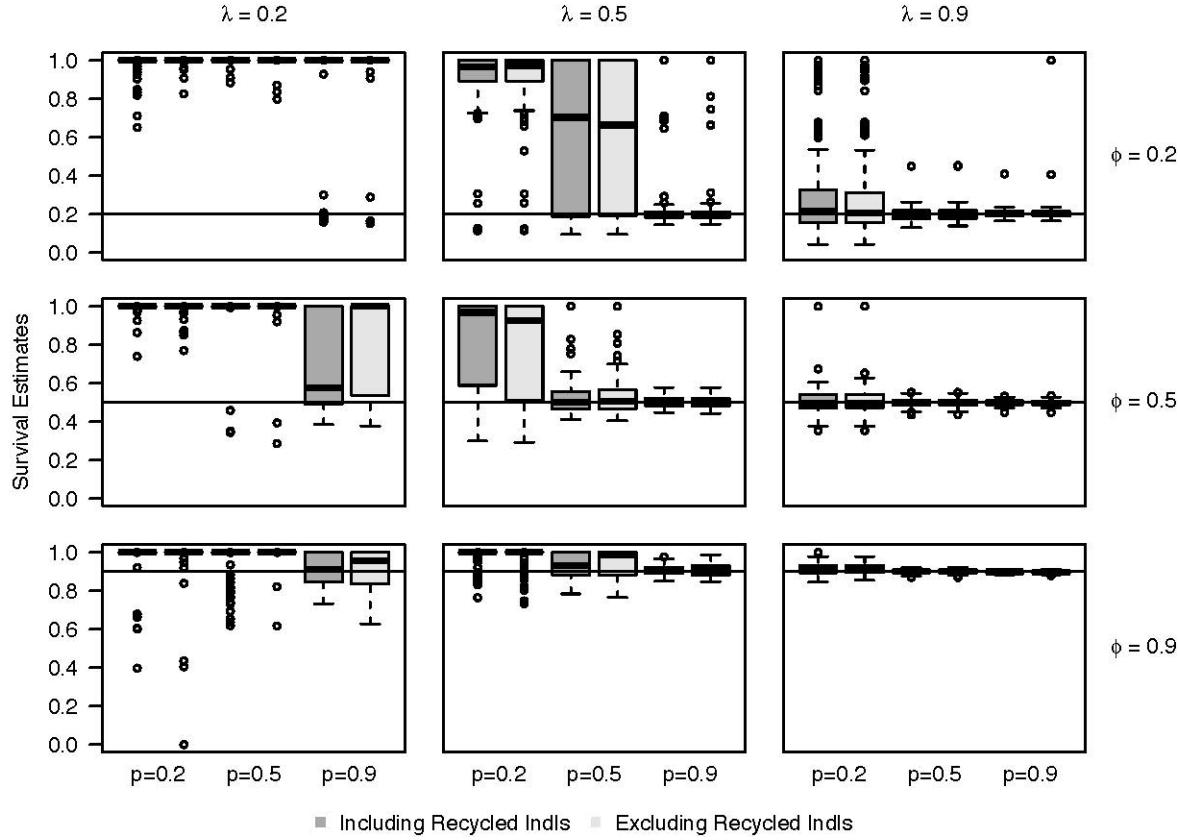
¹⁷⁴ We compared the average parameter estimates to the true parameter values using relative
¹⁷⁵ bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
¹⁷⁶ relative bias from the analysis with the recycled individuals to the relative bias from the
¹⁷⁷ analysis without the recycled individuals. We calculated the difference in the two relative
¹⁷⁸ biases and consider this to be the relative bias that was contributed entirely by the recycled
¹⁷⁹ individuals being tagged as “new” individuals.

¹⁸⁰ **Simulation Results**

¹⁸¹ The survival estimates are biased for some parameter combinations of survival, capture, and
¹⁸² 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. 2). Box plots of survival estimates for other super-population sizes and double-tagging rates are provided in the [Online Supplement Appendix](#) (Figs A1-A6). Although there is bias in the survival estimates for several of the parameter combinations, the bias is similar between the analysis including and excluding the recycled individuals 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 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 Appendix](#) (Figs A7-A17).

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 including and excluding recycled individuals for varying population size and double-tagging probabilities (Table 1).



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

210

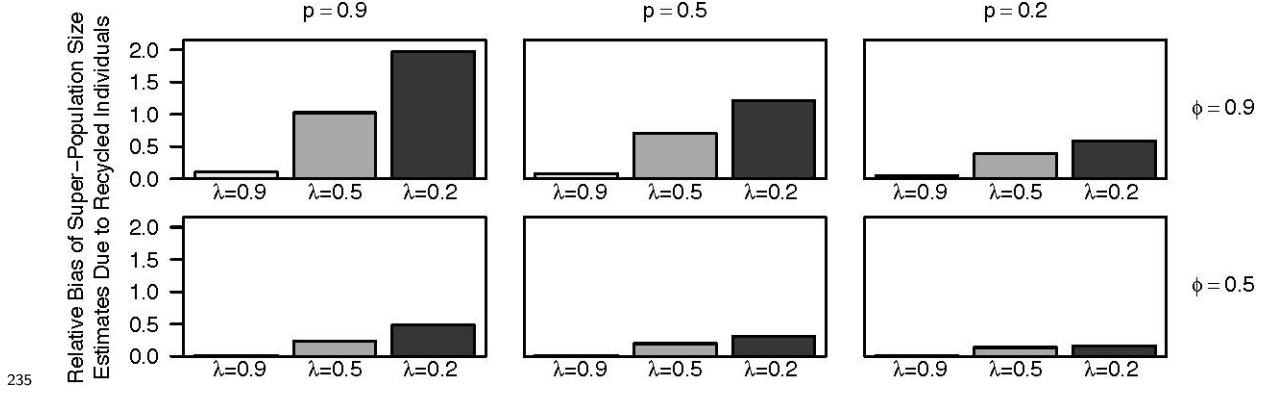
211 TABLE 1: The mean relative bias of the parameters from the model analyzed
 212 including (R) and excluding (R') the recycled individuals for data with high
 213 survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag
 214 retention ($\lambda = 0.2$) for different super-populations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

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

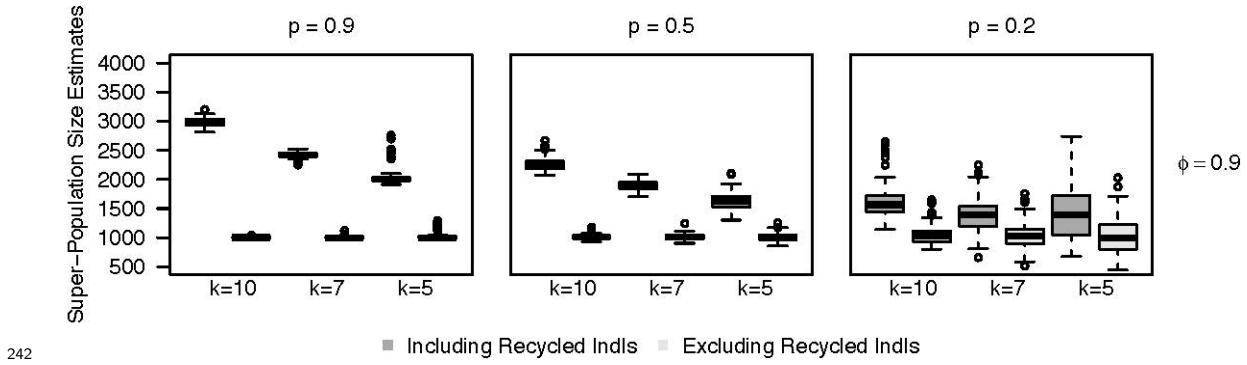
	N=1000				N=100 000			
	$T_2 = 1$		$T_2 = 0.5$		$T_2 = 1$		$T_2 = 0.5$	
	R	R'	R	R'	R	R'	R	R'
ϕ	0.00	0.00	0.06	0.05	0.00	0.00	0.11	0.10
p	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
λ	0.00	0.00	0.00	0.00	0.00	0.00	-0.09	-0.08
N	1.98	0.00	2.13	0.00	1.98	0.00	2.12	0.00

217

218 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
219 estimated probability of never being seen. In the scenarios where many recycled individuals
220 were recaptured and considered as “new” individuals (included), the number of observed
221 individuals, n_{obs} , is larger than it should be and thus, \hat{N} is biased upwards. By recognizing
222 recycled individuals upon recapture, this bias can be corrected. The relative bias in the
223 super-population size (\hat{N}) due to recycled individuals is highest in the scenario with high
224 survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as
225 predicted (Fig. 3, Table 1). The relative bias is small for all scenarios where tag retention was
226 high, but relative bias increases as tag retention decreases. The relative bias in \hat{N} decreases as
227 capture probability decreases, but recycled individuals appear to still have some effect on the
228 estimates even when capture probabilities are low ($p = 0.2$). The relative bias in \hat{N} is high for
229 scenarios where survival probability is high, and decreases as survival probability decreases.
230 In all scenarios where survival probability is low ($\phi = 0.2$) individuals are unlikely to survive
231 long enough to be able to be tagged, lose tag(s) and be recaptured as “new” individuals.
232 When survival probability is low, the relative bias due to the recycled individuals is small
233 (less than 0.15) and hence not shown in Fig. 3. SE, SD, and RMSE of \hat{N} varies, but remains
234 similar between the analyses including and excluding recycled individuals, across all scenarios.



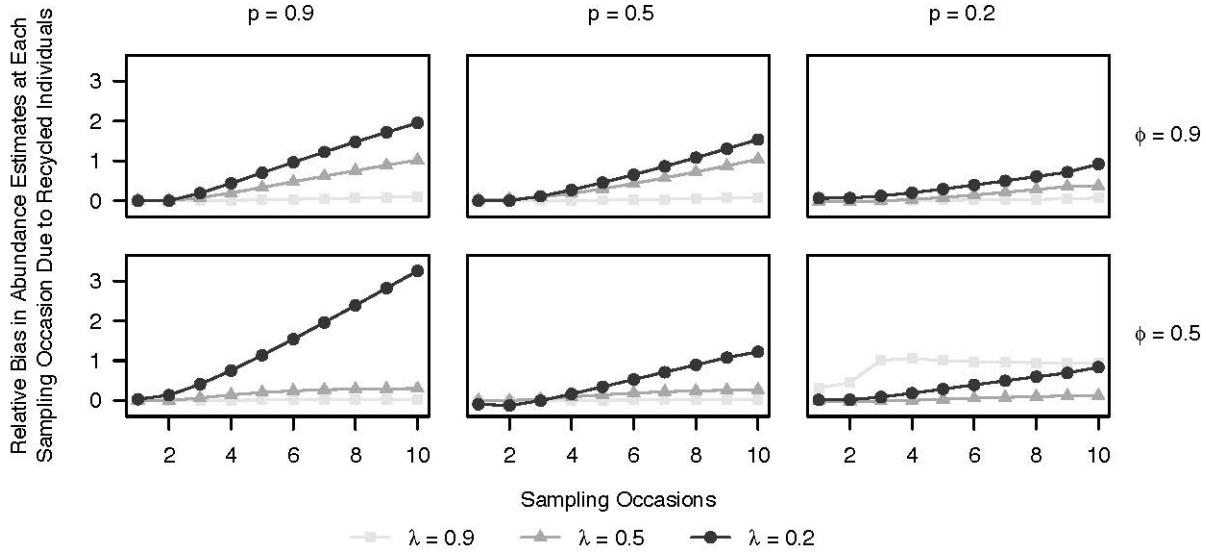
236 FIGURE 3: The difference in mean relative bias of the super-population estimate
 237 (\hat{N}) between the model analyzed including and excluding the recycled individuals
 238 for data with super-population size $N = 100\ 000$ with 100% double-tagging
 239 for different tag retention probabilities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



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

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

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



255

256 FIGURE 5: The difference in mean relative bias of the abundance estimates
 257 at each sample time (\hat{N}_j) between the model analyzed including and excluding
 258 the recycled individuals for data with super-population size $N=100\ 000$ with
 259 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$),
 260 survival probabilities ($\phi = 0.5$ and 0.9), and different capture probabilities ($p =$
 261 $0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study. Note that lines
 262 are added between the points to emphasize the difference in values; no models
 263 were fit to generate these lines.

264 In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to the
 265 bias due to recycled individuals in \hat{N} , with relative bias in the \hat{N}_j 's increasing as tag retention
 266 decreases, survival increases, and capture probability increases (Fig. 5). For all scenarios,
 267 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 [Online Supplement 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 (?). 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

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

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

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

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

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

311 Discussion

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

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

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

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

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

346 Developing a model to incorporate recycled individuals is a similar problem to that of incorpo-
347 rating misidentification of individuals. ? developed a model to deal with tag-misreads in an
348 open population capture-recapture setting. However most of the misidentification literature

349 focusses on genetic or photographic identification errors. Here multiple identities can be
350 assigned to the same individual leading to overestimates in population size if misidentification
351 is ignored (?). This is the same result that we see when recycled individuals are ignored. ?
352 introduced the notion of using a latent multinomial to model the latent capture histories
353 for a closed population model. Others have extended ?'s model to deal with multiple non-
354 invasive marks (??), heterogeneity in parameters (?) and open populations (?). These latent
355 multinomial models could be extended to include misidentification produced by complete tag
356 loss.

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

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

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

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383 Authors' Contributions

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

387 Data Accessibility

388 Data Accessibility:

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