

¹ Complete tag loss in capture-recapture studies
² affect abundance estimates: an elephant seal
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, similarly in Figure 1.



70
71 FIGURE 1: *Photograph of elephant seal (*Mirounga leonina*) at Macquarie Island,*
72 *Australia*

73 Materials and Methods

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

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

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

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

$$93 L = \binom{N}{n_{obs}} \left\{ \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{(N-n_{obs})} \left\{ 1 - \sum_{j=0}^{k-1} b_j (1-p) \chi_{(0,j+1,0)} \right\}^{n_{obs}} \times \\ \left(\begin{matrix} n_{obs} \\ n_{\omega_1}, n_{\omega_2}, \dots, n_{\omega_m} \end{matrix} \right) \prod_{i=1}^m \left[\psi_{f_i} T_d \left\{ \prod_{j=f_i}^{l_i} p^{w*_{ij}} (1-p)^{(1-w*_{ij})} \right\} \left\{ \prod_{j=f_i}^{l_i-1} \phi \right\} \right] \times$$

94

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

95

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

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

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

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

112 Likelihood and Estimation

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

¹¹⁶ article (and its supplementary information files).

¹¹⁷ **Experimental Design**

¹¹⁸ To study the effect of recycled individuals on parameter estimates of this model, we conducted
¹¹⁹ a simulation study. Data sets varied both in super-population size, parameter values, and
¹²⁰ percent double tagged. We generated data for the JSTL model with constant survival,
¹²¹ capture, and tag retention probabilities for a double-tagging experiment. Super-population
¹²² sizes of 1000 and 100 000 were considered in order to study the effect of population size. For
¹²³ the super-population size of 100 000, experiments with ten sample times were considered.
¹²⁴ For the super-population size of 1000 we considered experiments with five, seven and ten
¹²⁵ sample times in order to determine the effect of the study length. For each population size,
¹²⁶ we tested different proportions of double-tagged versus single-tagged individuals (0.5 and 1).
¹²⁷ Survival, capture, and tag retention probability parameters were varied in a 3^3 experimental
¹²⁸ design with low (0.2), medium (0.5) and high (0.9) values for all parameters. The entry rates
¹²⁹ were fixed to be $1/k$ at each of the sampling times.

¹³⁰ We considered the set of parameter values to be reasonable values that might be encountered
¹³¹ in practice and also produce informative capture-recapture scenarios. Tag retention rates
¹³² can vary by species, age of the tag, tag type, tag location, behaviour, season, and individual
¹³³ quality (size of an animal for example in seals). For example, tag retention rates have ranged
¹³⁴ from 13% (Fogarty *et al.*, 1980) to 95% (Gonzalez-Vicente *et al.*, 2012) in lobsters. Other
¹³⁵ studies report tag retention rates of 65% in male elephant seals (Pistorius *et al.*, 2000) and
¹³⁶ 88% in Adelie penguins (Ainley & DeMaster, 1980). Mean retention of visible implant tags
¹³⁷ has been recorded as 32% in small rockpool fish (Griffiths, 2002). Turtles in particular
¹³⁸ experience high tag loss rates. For example Bellini *et al.* (2001) reports the probability of tag
¹³⁹ loss in hawksbill turtles as 0.57 and Bjorndal *et al.* (1996) observed the probability of tag
¹⁴⁰ loss in green nesting turtles to be as high as 0.38. Thus, we chose a wide range of tag loss

¹⁴¹ parameter values to try to capture the diversity among published tag loss rates.

¹⁴² **Simulation of Data**

¹⁴³ For all of the parameter combinations of super-population size ($N = 1000, 100\,000$), fraction
¹⁴⁴ double-tagged (0.5, 1), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$
¹⁴⁵ 0.2, 0.5, 0.9) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where
¹⁴⁶ the simulated data met all the assumptions of the model.

¹⁴⁷ For each individual, we simulated a capture history using the following algorithm:

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

¹⁴⁹ 2. For each sample time after entry (until death or first capture) determine if the individual
¹⁵⁰ survives to that sample time (with probability ϕ). If they are still alive, determine if
¹⁵¹ they are first captured (with probability p). If they are captured, determine whether
¹⁵² they are single or double-tagged.

¹⁵³ 3. For each sample time after first capture (until death, loss of all tags or the end of the
¹⁵⁴ study) determine if the individual survives to that sample time (with probability ϕ).
¹⁵⁵ Then if they are still alive, determine if they lose any of their tags (with probability
¹⁵⁶ $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with
¹⁵⁷ probability p). If they have lost all of their tags, consider them as a new individual
¹⁵⁸ entering the population at this sample time.

¹⁵⁹ By keeping track of all the recycled individuals, this algorithm provides us with two data
¹⁶⁰ sets: one that includes the recycled individuals (assumes individuals, who have complete tag
¹⁶¹ loss, are tagged again upon recapture and treated as new individuals) and one that excludes
¹⁶² recycled individuals (assumes that individuals, who have complete tag loss, can be recognized
¹⁶³ upon recapture and are not re-tagged). The JSTL model was fit to the 100 simulated data

¹⁶⁴ sets twice (once including and once excluding recycled individuals). We assumed that any
¹⁶⁵ difference between the two analyses was due entirely to the recycled individuals. All data
¹⁶⁶ generated during this study are included in this published article (and its supplementary
¹⁶⁷ information files).

¹⁶⁸ **Evaluation Criteria**

¹⁶⁹ To evaluate the resulting parameter estimates from each of the simulations, we looked at
¹⁷⁰ several criteria including: average parameter estimate, relative bias of the estimates, the
¹⁷¹ average standard error of the parameter estimates, the standard deviation of the parameter
¹⁷² estimates, and root mean squared error (RMSE) of the parameter estimates.

¹⁷³ Let $\hat{\theta}_i$'s be the parameter estimates from each of the 100 simulations and θ the true parameter
¹⁷⁴ value, we calculated:

- ¹⁷⁵ • the mean parameter estimate as $\bar{\hat{\theta}} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$
- ¹⁷⁶ • average standard error of the parameter estimate as $SE(\hat{\theta}) = \frac{1}{100} \sum_{i=1}^{100} SE(\hat{\theta}_i)$.
- ¹⁷⁷ • the standard deviation of the parameter estimates as $SD(\hat{\theta}) = \sqrt{\frac{1}{99} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.
- ¹⁷⁸ • the RMSE of the parameter estimates as $RMSE = \sqrt{\frac{1}{100} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.

¹⁷⁹ We compared the average parameter estimates to the true parameter values using relative
¹⁸⁰ bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the
¹⁸¹ relative bias from the analysis with the recycled individuals to the relative bias from the
¹⁸² analysis without the recycled individuals. We calculated the difference in the two relative
¹⁸³ biases and consider this to be the relative bias that was contributed entirely by the recycled
¹⁸⁴ individuals being tagged as “new” individuals.

185 Simulation Results

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

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

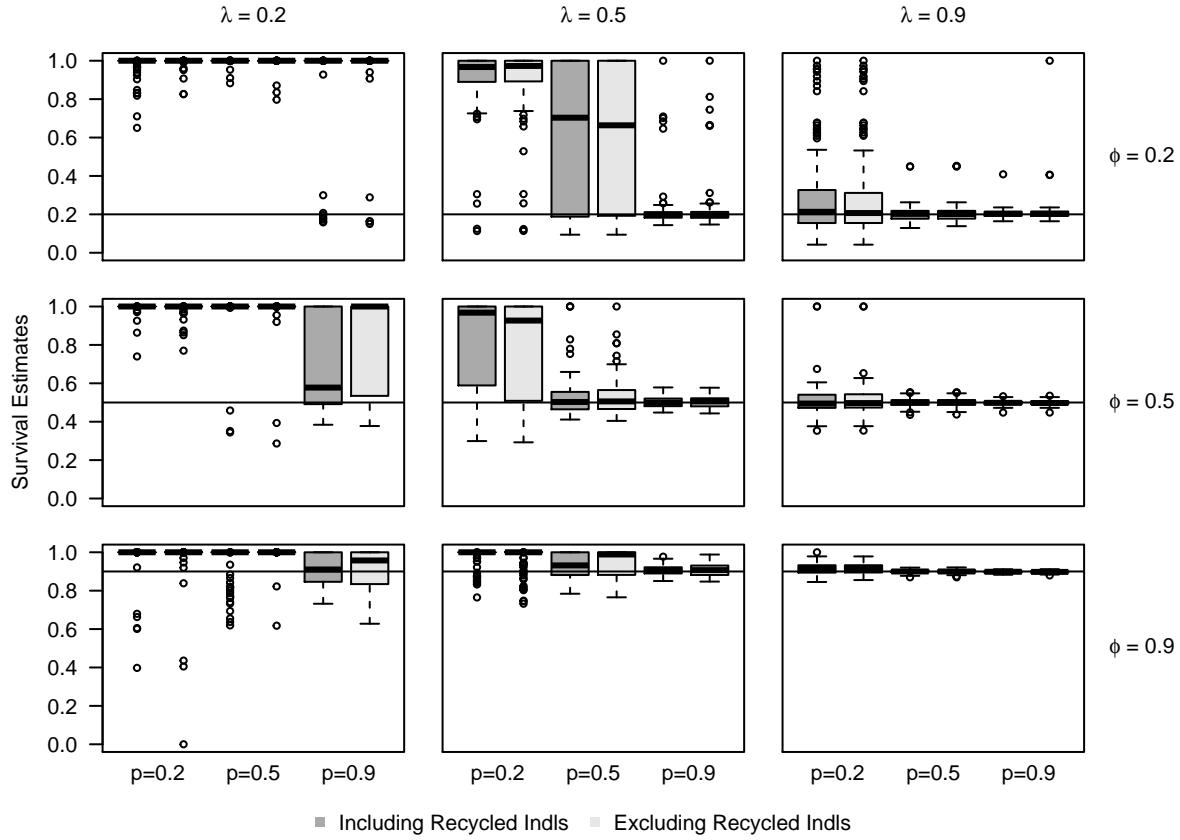


FIGURE 2: Survival probability estimates for simulated data with super-population size $N = 1000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.2, 0.5, 0.9$), and different capture probabilities ($p = 0.2, 0.5, 0.9$)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

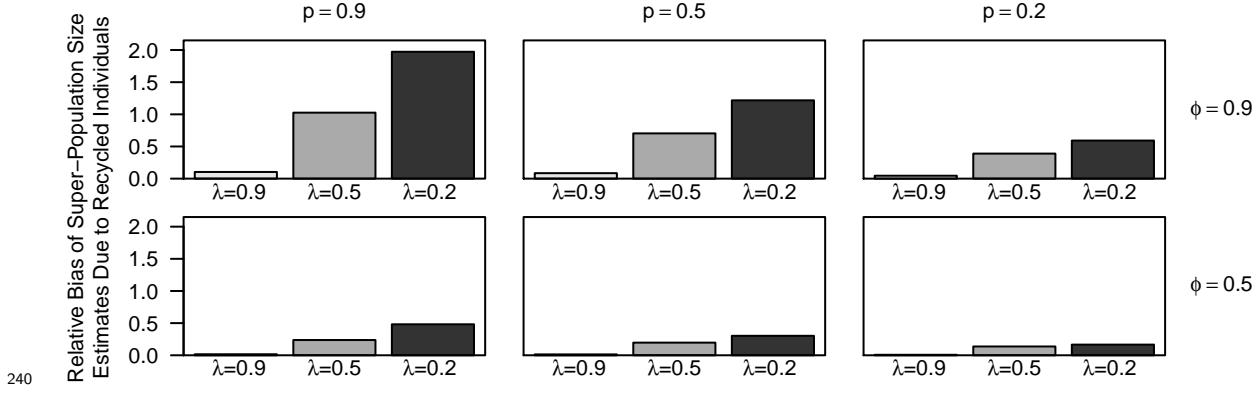
TABLE 1: The mean relative bias of the parameters from the model analyzed including (R) and excluding (R') the recycled individuals for data with high survival probability ($\phi = 0.9$), high capture probability ($p = 0.9$), and low tag retention ($\lambda = 0.2$) for different super-populations sizes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

220 different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from a
221 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

222

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



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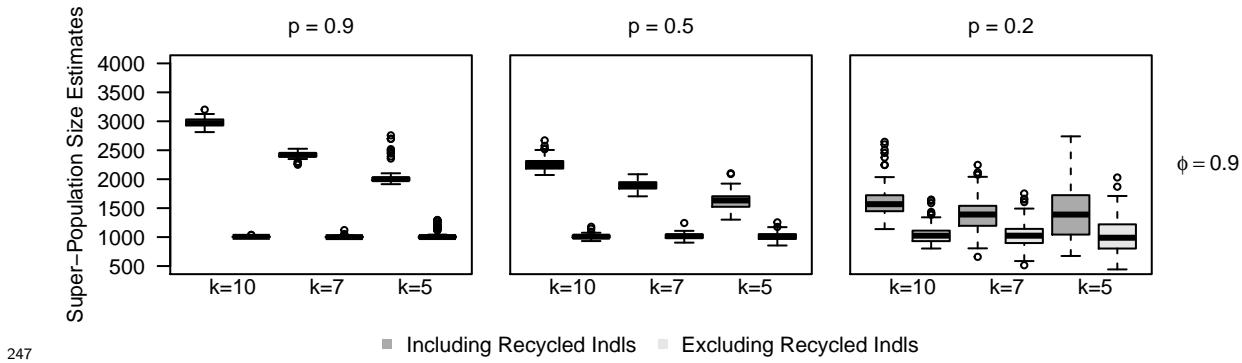
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FIGURE 3: The difference in mean relative bias of the super-population estimate (\hat{N}) between the model analyzed including and excluding the recycled individuals for data with super-population size $N = 100\ 000$ with 100% double-tagging for different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



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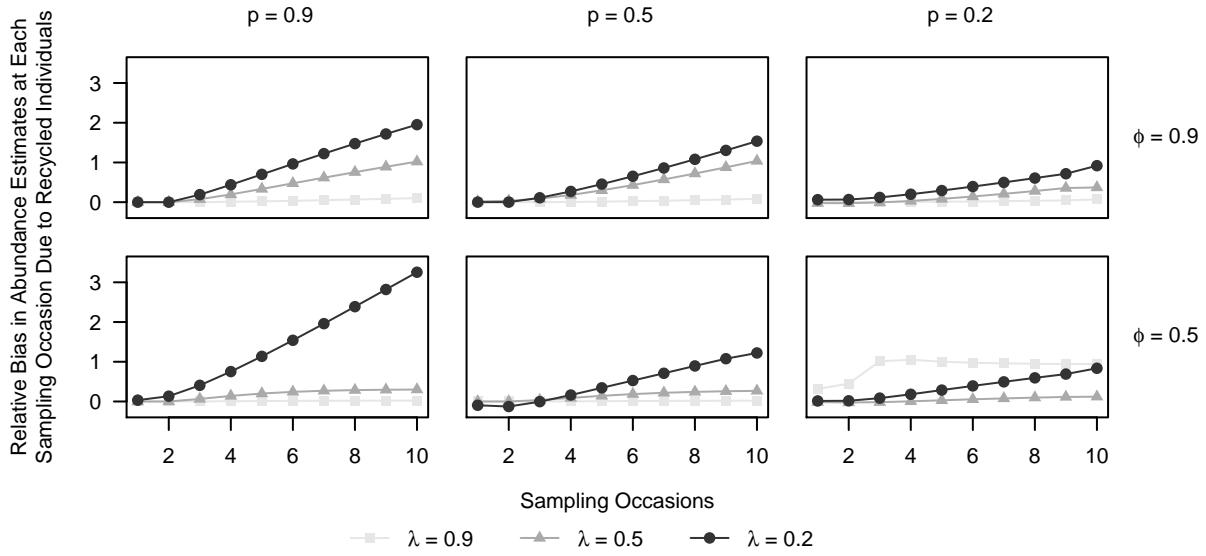
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FIGURE 4: Box plots of the estimates of N for the model analyzed including and excluding the recycled individuals for data with super-population size $N = 1000$ with 100% double-tagging for different capture probabilities ($p = 0.2, 0.5, 0.9$), and 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.

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

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



260

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

269 In general, the bias due to recycled individuals in the \hat{N}_j 's follows a similar pattern to the
 270 bias due to recycled individuals in \hat{N} , with relative bias in the \hat{N}_j 's increasing as tag retention
 271 decreases, survival increases, and capture probability increases (Fig. 5). For all scenarios,
 272 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 (Figs A19-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

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

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

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). Standard error estimates are also higher when
308 recycled individuals are included in the analysis. The same pattern is seen in the simulation
309 studies (see Web Appendix A).

310 TABLE 2 *Estimates of survival probability (ϕ), capture probability (p), tag-
311 retention probability (λ), and annual population size (N_j) for the elephant seal
312 data analyzed including and excluding recycled individuals. Estimated standard
313 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
314	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	

315 Discussion

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

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

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

332 As expected, the survival estimates are upbiased when recycled individuals are excluded.

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

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

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

353 of the misidentification literature focusses on genetic or photographic identification errors.
354 Here multiple identities can be assigned to the same individual leading to overestimates in
355 population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result
356 that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of
357 using a latent multinomial to model the latent capture histories for a closed population model.
358 Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner
359 & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*,
360 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models
361 could be extended to include misidentification produced by complete tag loss.

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

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

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

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388 Authors' Contributions

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

392 Data Accessibility

393 Data Accessibility:

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

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