

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

⁴

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

¹ Mathematics~~and Statistics~~, 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 ~~following tag history over three sampling occasions~~ tag history {11 01 00} over three sampling occasions was double tagged at sample time 1, lost a tag between times 1 and 2, and may have lost its last tag between sample times 2 and 3 and then have been recaptured at sample time 3 resulting in a new individual with ~~capture tag~~ history {00 00 11}. If the rate of tag loss is small, bias in the population estimate will also be small for the Peterson estimators (?). 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

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

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



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

72 Materials and Methods

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

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

85 The JSTL model is developed under the idea of a **superpopulation** (the
 86 number of individuals that will enter **the** population at some point during the study) (?)
 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 **superpopulation** size (N)
 89 and 2) a model for the recaptures (in the form of capture history frequencies n_{ω_i}) given the
 90 observed number of unique tag histories (n_{obs}). The full likelihood is given by the product of
 91 these components 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 the supplementary material 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
 99 the Jolly-Seber model (?) including all individuals have equal entry (birth or immigration)
 100 probabilities, but entry probabilities can vary between sample times; capture probabilities
 101 are the same for all individuals at all sample times, all individuals (marked and unmarked)
 102 have equal survival probabilities between all sample times, the sampling period is relatively
 103 short compared to the interval between sampling times, and there is independence across
 104 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 (?) or group (?).

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 (?). Code from this study are included in this published article (and its

¹¹⁵ 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 both in super-population size, parameter values, and
¹¹⁹ percent double tagged. We generated data for the JSTL model with constant survival,
¹²⁰ capture, and tag retention probabilities for a double-tagging experiment. Super-population
¹²¹ sizes of 1000 and 100 000 were considered in order to study the effect of population size. For
¹²² the super-population size of 100 000, experiments with ten sample times were considered.

¹²³ For the super-population size of 1000 we considered experiments with five, seven and ten
¹²⁴ sample times in order to determine the effect of the ~~length of the study~~ study length. For
¹²⁵ each population size, we tested different proportions of double-tagged versus single-tagged
¹²⁶ individuals (0.5 and 1). Survival, capture, and tag retention probability parameters were
¹²⁷ varied in a 3^3 experimental design with low (0.2), medium (0.5) and high (0.9) values for
¹²⁸ all parameters. The entry rates were fixed to be $1/k$ at each of the sampling times. ~~No~~
¹²⁹ ~~individuals were lost on capture.~~

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% (?) to 95% (?) in lobsters. Other studies report tag retention rates of 65% in male
¹³⁵ elephant seals (?) and 88% in Adelie penguins (?). Mean retention of visible implant tags
¹³⁶ has been recorded as 32% in small rockpool fish (?). Turtles in particular experience high tag
¹³⁷ loss rates. For example ? reports the probability of tag loss in hawksbill turtles as 0.57 and
¹³⁸ ? observed the probability of tag loss in green nesting turtles to be as high as 0.38. Thus,
¹³⁹ we chose a wide range of tag loss parameter values to try to capture the diversity among

¹⁴⁰ 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

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

Evaluation Criteria

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

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

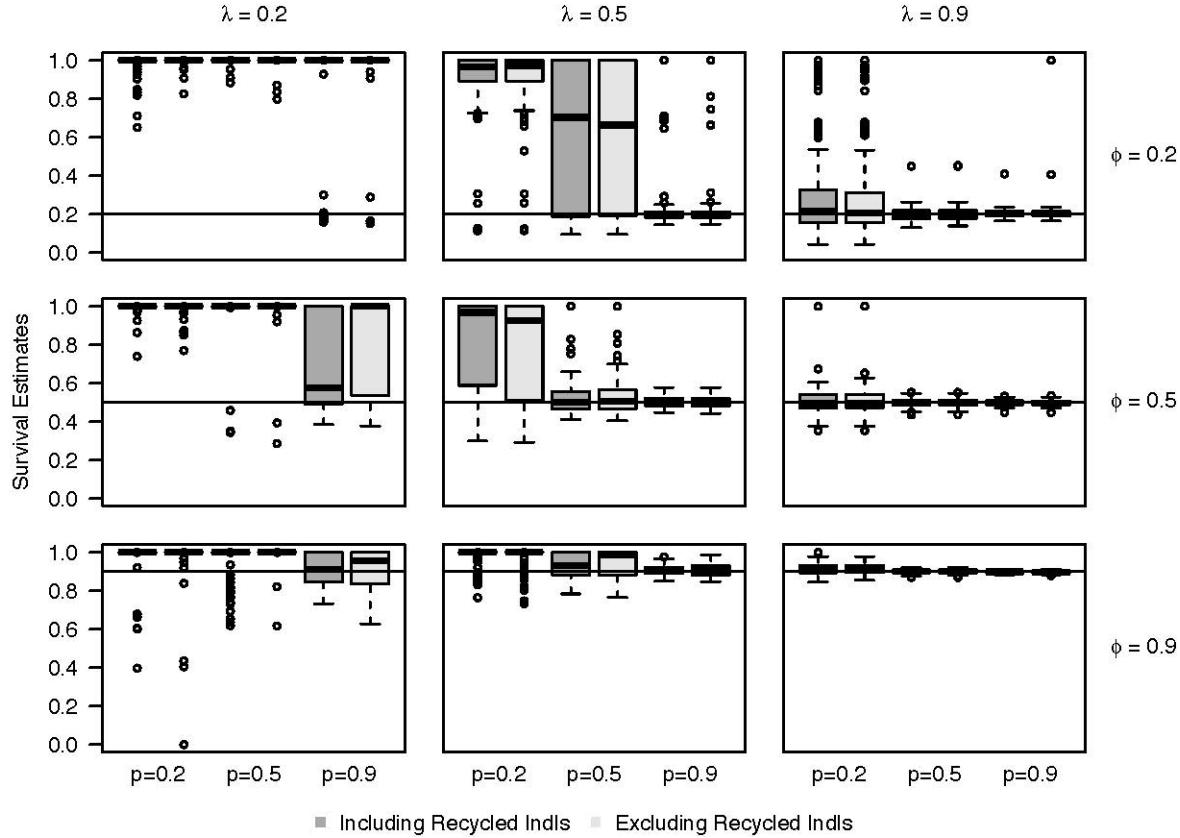
- the mean parameter estimate as $\bar{\hat{\theta}} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$
- average standard error of the parameter estimate as $SE(\hat{\theta}) = \frac{1}{100} \sum_{i=1}^{100} SE(\hat{\theta}_i)$.
- the standard deviation of the parameter estimates as $SD(\hat{\theta})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

We compared the average parameter estimates to the true parameter values using relative bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the relative bias from the analysis with the recycled individuals to the relative bias from the analysis without the recycled individuals. We calculated the difference in the two relative biases and consider this to be the relative bias that was contributed entirely by the recycled 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 Online Supplement (Figs A1-A4). Although there is bias in the survival estimates for
¹⁹⁰ several of the parameter combinations, the bias is similar between the analysis including and
¹⁹¹ ~~the analysis~~-excluding the recycled individuals for both super-population sizes ($N = 1000$ and
¹⁹² 100 000) and for both double-tagging rates ($T_2 = 0.5, 1$). In fact, the differences in relative
¹⁹³ bias due to recycled individuals for the parameters ϕ , p and λ is small (<0.01) for all 108
¹⁹⁴ parameter combinations considered. In general, the SE, SD and RMSE of the estimates of
¹⁹⁵ ϕ , p and λ are similar for both the analysis including and excluding recycled individuals for
¹⁹⁶ the parameter combinations considered. It seems that the treatment of recycled individuals
¹⁹⁷ has little effect, if any, on the accuracy of the JSTL estimators for survival, capture, and
¹⁹⁸ tag-retention probabilities. Box plots of capture and tag retention estimates for all models
¹⁹⁹ can also be found in the Online Supplement (Figs A5-A12).

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 are
²⁰³ presented for the parameter combination where $\phi = 0.9$, $p = 0.9$ and $\lambda = 0.2$ for both the
²⁰⁴ analysis ~~with and without~~ including and excluding recycled individuals for varying population
²⁰⁵ size and 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 ~~with and without reecyed individuals included~~including and
 239 excluding recycled individuals, across all scenarios.

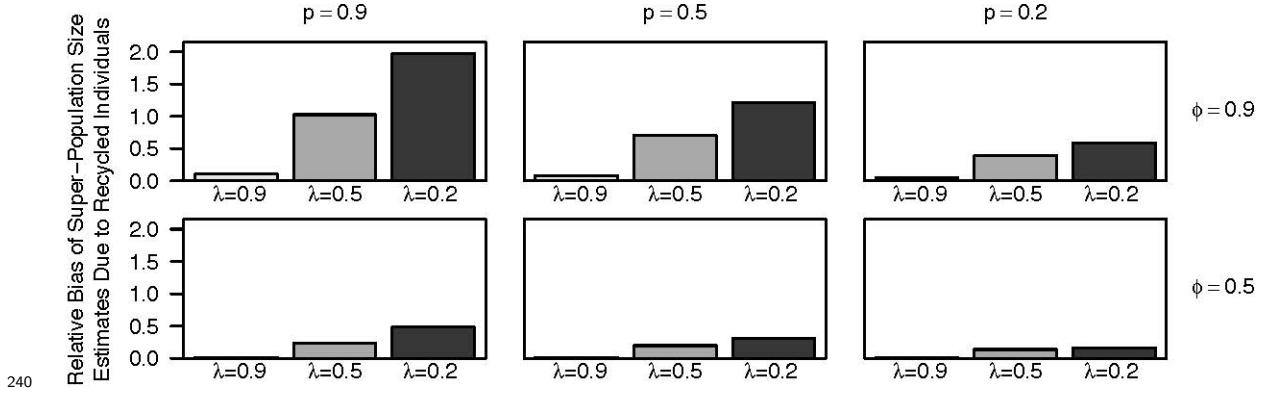


FIGURE 3: The difference in mean relative bias of the super-population estimate (\hat{N}) between the model analyzed including and excluding the recycled individuals for data with super-population size $N = 100\ 000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2,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

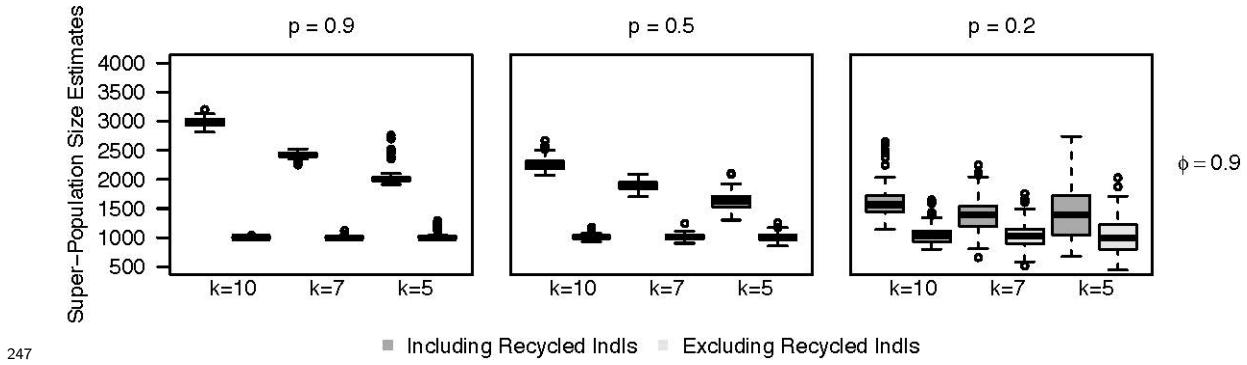
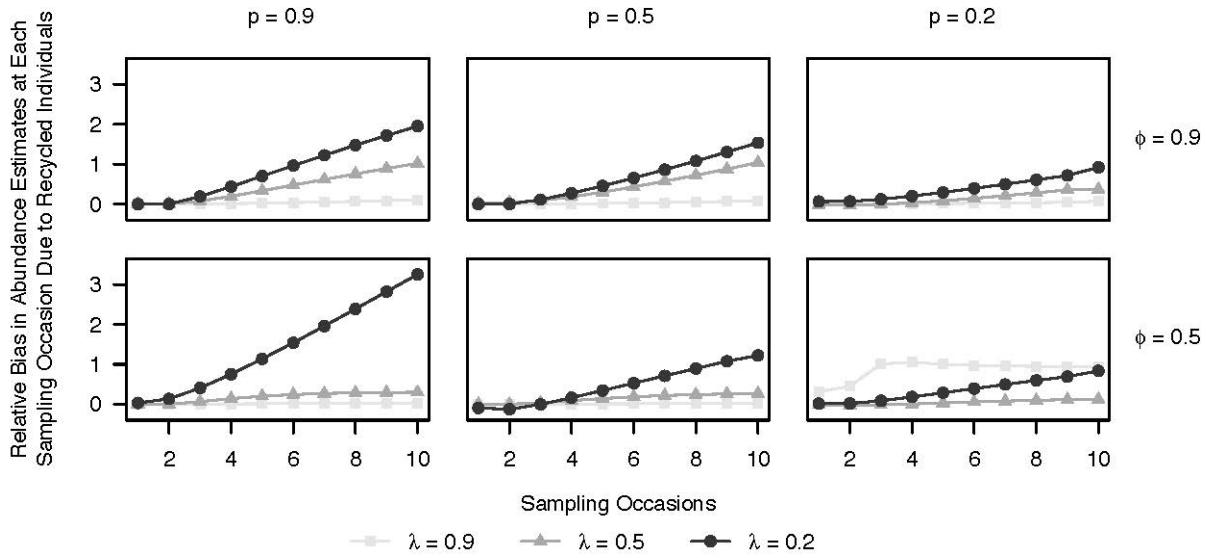


FIGURE 4: Box plots of the estimates of N for the model analyzed including and excluding the recycled individuals for data with super-population size $N = 1000$ with 100% double-tagging for different capture probabilities ($p = 0.2, 0.5, 0.9$), and constant survival ($\phi = 0.9$) and tag retention ($\lambda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

There is more bias in \hat{N} due to recycled individuals in longer experiments (Fig. 4). With a 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, the
 272 relative bias in the estimates of abundance at each sample time j is **smaller for earlier sampling**

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

282 Case Study: Elephant Seals

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

290 We considered two analyses of the data:

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

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

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

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

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

312 TABLE 2 Estimates of survival probability (ϕ), capture probability (p), tag-
313 retention probability (λ), and annual population size (N_j) for the elephant seal
314 data analyzed with including and without the excluding recycled individuals.
315 Estimated standard errors (SE) are also presented.

	Including Recycled		Excluding Recycled	
Parameter	Estimate	SE	Estimate	SE
ϕ	0.759	0.006	0.744	0.006
p	0.682	0.006	0.741	0.006
λ	0.792	0.005	0.799	0.005
N_{1994}	1740	48	1601	36
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	

317 Discussion

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

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

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

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

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

355 Developing a model to incorporate recycled individuals is a similar problem to that of incorpo-
356 rating misidentification of individuals. ? developed a model to deal with tag-misreads in an
357 open population capture-recapture setting. However most of the misidentification literature
358 focusses on genetic or photographic identification errors. Here multiple identities can be
359 assigned to the same individual leading to overestimates in population size if misidentification
360 is ignored (?). This is the same result that we see when recycled individuals are ignored. ?
361 introduced the notion of using a latent multinomial to model the latent capture histories
362 for a closed population model. Others have extended ?'s model to deal with multiple non-
363 invasive marks (??), heterogeneity in parameters (?) and open populations (?). These latent
364 multinomial models could be extended to include misidentification produced by complete tag
365 loss.

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

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

376 For researchers interested in conducting and analyzing mark-recapture studies to determine
377 abundance estimates, we stress the importance of using tags with high retention rates,
378 especially in situations where survival and capture rates are suspected to be high. As long as
379 tag-retention is high, the JSTL estimator of population size is only weakly affected by recycled
380 individuals. Longer studies should be particularly concerned about recycled individuals
381 biasing ~~abundance~~ abundance estimates. In situations where it is possible, recognizing if an

382 individual has been captured previously (by scarring, marking, etc) can improve accuracy of
383 the abundance estimates. Permanent marking should be used where possible. If researchers
384 are only interested in the survival rates, they do not need to be concerned with the effect of
385 recycled individuals regardless of the study's tag-retention rates.~

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

391 Acknowledgements

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

394 Authors' Contributions

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

398 Data Accessibility

399 Data Accessibility:

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

402 **References**

- 403 Ainley, D.G. & DeMaster, D.P. (1980) Survival and mortality in a population of Adelie
404 penguins. *Ecology*, **61**, 522–530. Doi:10.2307/1937418.
- 405 Arnason, A. & Mills, K.H. (1981) Bias and loss of precision due to tag loss in Jolly-Seber
406 estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic
407 Science*, **38**, 1077–1095. Doi: 10.1139/f81-148.
- 408 Bellini, C., Godfrey, M.H. & Sanches, T.M. (2001) Metal tag loss in wild juvenile Hawksbill
409 sea turtles (*Eretmochelys imbricata*). *Herpetological Review*, **32**, 172–174.
- 410 Bjorndal, K., Bolten, A.B., Lagueux, C.J. & Chaves, A. (1996) Probability of tag loss in
411 green turtles nesting at Tortuguero, Costa Rica. *Journal of Herpetology*, **30**, 566–571. Doi:
412 10.2307/1565709.
- 413 Björnsson, B., Karlsson, H., Thorsteinsson, V. & Solmundsson, J. (2011) Should all fish in
414 mark-recapture experiments be double-tagged? Lessons learned from tagging coastal cod
415 (*Gadus morhua*). *ICES Journal of Marine Science*, **68**, 603–610. Doi: 10.1093/icesjm-
416 s/fsq187.
- 417 Bonner, S.J. & Holmberg, J. (2013) Mark-recapture with multiple, non-invasive marks.
418 *Biometrics*, **69**, 766–775. Doi: 10.1111/biom.12045.
- 419 Cowen, L. & Schwarz, C.J. (2006) The Jolly-Seber model with tag loss. *Biometrics*, **62**,
420 699–705. Doi: 10.1111/j.1541-0420.2006.00523.x.
- 421 Diefenbach, D.R. & Alt, G.L. (1998) Modeling and evaluation of ear tag loss in black bears.
422 *The Journal of Wildlife Management*, **62**, 1292–1300. Doi: 10.2307/3801993.
- 423 Fogarty, M.J., Borden, D.V.D. & Russell, H.J. (1980) Movements of tagged American
424 lobster, *Homarus americanus*, off Rhode Island. *Fishery Bulletin*, **78**, 771–780. Doi:
425 10.1139/f85-030.

- 426 Gonzalez-Vicente, L., Diaz, D., Mallol, S. & Goni, R. (2012) Tag loss in the lobster *Palinurus*
427 *elephas* (Fabricius, 1787) and implications for population assessment with capture-mark-
428 recapture methods. *Fisheries Research*, **129**, 1–7. Doi: 10.1016/j.fishres.2012.05.014.
- 429 Griffiths, S.P. (2002) Retention of visible implant tags in small rockpool fishes. *Marine*
430 *Ecology Progress Series*, **236**, 307–309. Doi: 10.3354/meps236307.
- 431 Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and
432 immigration– stochastic model. *Biometrika*, **52**, 225–247. Doi: 10.2307/2333826.
- 433 Link, W.A., Yoshizaki, J., Bailey, L.L. & Pollock, K.H. (2010) Uncovering a latent multinomial:
434 Analysis of mark-recapture data with misidentification. *Biometrics*, **66**, 178–185. Doi:
435 10.1111/j.1541-0420.2009.01244.x.
- 436 McClintock, B.T., Bailey, L.L., Dreher, B.P. & Link, W.A. (2014) Probit models for capture-
437 recapture data subject to imperfect detection, individual heterogeneity and misidentification.
438 *The Annals of Applied Statistics*, **8**, 2461–2484. Doi:10.1214/14-AOAS783.
- 439 McClintock, B.T., Conn, P.B., Alonso, R.S. & Crooks, K.R. (2013) Integrated modeling of
440 bilateral photo-identification data in mark-recapture analyses. *Ecology*, **94**, 1464–1471.
441 Doi:10.1890/12-1613.1.
- 442 McMahon, C.R., Burton, H., van den Hoff, J., Woods, R. & Bradshaw, C.J.A.
443 (2009) Assessing hot-iron and cyro-branding for permanently marking southern ele-
444 phant seals. *Journal of Wildlife Management*, **70**, 1484–1489. Doi: 10.2193/0022-
445 541X(2006)70[1484:AHACFP]2.0.CO;2.
- 446 McMahon, C. & White, G. (2009) Tag loss probabilities are not independent: Assessing
447 and quantifying the assumption of independent tag transition probabilities from direct
448 observations. *Journal of Experimental Marine Biology and Ecology*, **372**, 36–42. Doi:
449 10.1016/j.jembe.2009.02.006.

- 450 Pistorius, P.A., Bester, M.N., Kirkman, S.P. & Boveng, P.L. (2000) Evaluation of age-
451 and sex-dependent rates of tag loss in southern elephant seals. *The Journal of Wildlife
452 Management*, **64**, 373–380. Doi: 10.2307/3803235.
- 453 Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990) Statistical inference for
454 capture-recapture experiments. *Wildlife Monographs*, **107**, 3–97.
- 455 R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation
456 for Statistical Computing, Vienna, Austria.
- 457 Schwarz, C.J. & Arnason, A.N. (1996) A general methodology for the analysis of capture-
458 recapture experiments in open populations. *Biometrics*, **52**, 860–873. Doi: 10.2307/2533048.
- 459 Schwarz, C.J. & Stobo, W.T. (1999) Estimation and effects of tag-misread rates in capture-
460 recapture studies. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 551–559. Doi:
461 10.1139/f98-196.
- 462 Schwarz, L., Hindell, M., McMahon, C. & Costa, D. (2012) The implications of assuming
463 independent tag loss in southern elephant seals. *Ecosphere*, **3**, 81. Doi: 10.1890/ES12-
464 00132.1.
- 465 Seber, G.A.F. (1965) A note on the multiple recapture census. *Biometrika*, **52**, 249–259. Doi:
466 10.2307/2333827.
- 467 Seber, G.A.F. & Felton, R. (1965) Tag loss and the Peterson mark-recapture experiment.
468 *Biometrika*, **68**, 211–219. Doi: 10.1093/biomet/68.1.211.
- 469 Xu, Y., Cowen, L.L.E. & Gardner, C. (2014) Group heterogeneity in the Jolly-Seber-tag-loss
470 model. *Statistical Methodology*, **17**, 3–16. Doi: 10.1016/j.stamet.2013.01.002.
- 471 Yoshizaki, J., Brownie, C., Pollock, K.H. & Link, W.A. (2011) Modeling misidentification
472 errors that result from use of genetic tags in capture-recapture studies. *Environmental and
473 Ecological Statistics*, **18**, 27–55. Doi: 10.1007/s10651-009-0116-1.