

<sup>1</sup> Complete tag loss in capture-recapture studies  
<sup>2</sup> affect abundance estimates: an elephant seal  
<sup>3</sup> case study.

<sup>4</sup>

<sup>5</sup> Emily Malcolm-White<sup>1</sup>, Clive R. McMahon<sup>2</sup>, Laura L.E. Cowen<sup>3\*</sup>,

<sup>1</sup> Mathematics and Statistics, Middlebury College, Middlebury, VT, USA

<sup>2</sup> Sydney Institute for Marine Science, Mosman, NSW, Australia

<sup>3</sup> Mathematics and Statistics, University of Victoria, Victoria, BC, Canada

<sup>6</sup>

<sup>7</sup> \*Corresponding author: Mathematics and Statistics, University of Victoria, PO Box 1700

<sup>8</sup> 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 (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 following tag history over three sampling occasions {11 01 00} was double tagged at sample time 1, lost a tag between times 1 and 2, and may have lost its last tag between sample times 2 and 3 and then have been recaptured at sample time 3 resulting in a new individual with capture history {00 00 11}. If the rate of tag loss is small, bias in the population estimate will also be small for the Peterson estimators (Seber & Felton, 1965). Typically in the Jolly-Seber and JSTL models, the effect of recycled individuals is assumed

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

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



71

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

## 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  $\omega_{ijd}$  denote the entries of the  
 77 tag history for individual  $i$  at time  $j$ , tag  $d$ ;  $i = 1, \dots, n_{obs}$ ,  $j = 1, \dots, k$ ,  $d = 1, 2$ ; with  $\omega_{ijd}$   
 78 equally 1 or 0 if the individual was seen with tag  $d$  or not. Capture histories  $\omega^*$  used in most  
 79 capture-recapture studies can be easily obtained from the tag histories  $\omega$  and are a series  
 80 of 1s and 0s depicting whether or not an individual was captured at each sample time. We  
 81 focus on the case with constant parameters as used in our simulation study. Let  $\phi$  denote  
 82 the survival probability,  $p$  the capture probability,  $\lambda$  the tag retention probability, and  $b_t$  the  
 83 entry probability for time  $t$ .  $\Psi$  and  $\chi$  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 superpopulation (the number of individuals  
 87 that will enter population at some point during the study) (Schwarz & Arnason, 1996) and  
 88 this allows the likelihood to be formulated into two parts: 1) a model for the observed number  
 89 of unique tag histories ( $n_{obs}$ ) given the superpopulation size ( $N$ ) and 2) a model for the  
 90 recaptures (in the form of capture history frequencies  $n_{\omega_i}$ ) 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:

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

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  $\Psi$  and  $\chi$  functions.

99 Assumptions of the JSTL model (under constant  $\phi$ ,  $p$ , and  $\lambda$  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. For  
124 the super-population size of 1000 we considered experiments with five, seven and ten sample  
125 times in order to determine the effect of the length of the study. 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. No 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% (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

<sup>141</sup> parameter values to try to capture the diversity among published tag loss rates.

<sup>142</sup> **Simulation of Data**

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

<sup>147</sup> For each individual, we simulated a capture history using the following algorithm:

<sup>148</sup> 1. Determine when the individual enters the population utilizing the entry probabilities.

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

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

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

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

<sup>168</sup> **Evaluation Criteria**

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

<sup>173</sup> Given that the  $\hat{\theta}_i$ 's are the parameter estimates from each of the 100 simulations and  $\theta$  the  
<sup>174</sup> value of the parameter, we calculated:

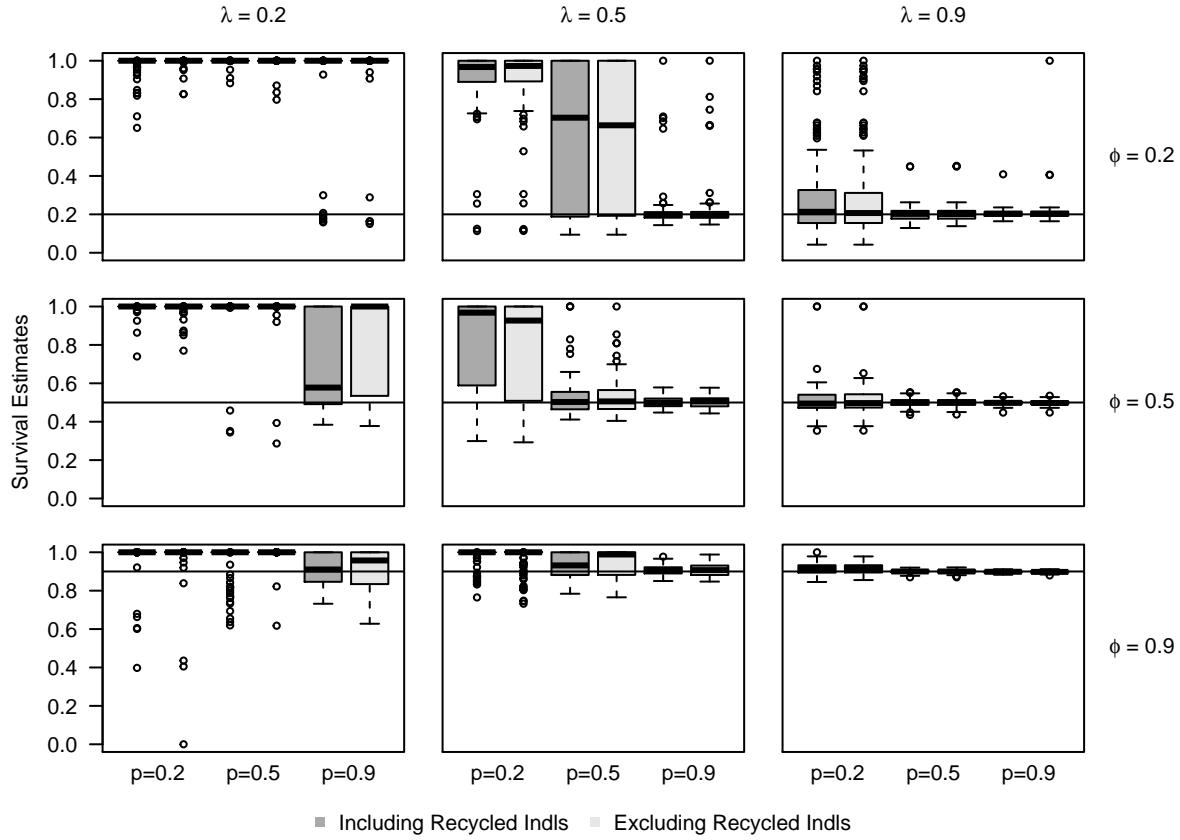
- <sup>175</sup> • the mean parameter estimate as  $\bar{\hat{\theta}} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$
- <sup>176</sup> • average standard error of the parameter estimate as  $SE(\hat{\theta}) = \frac{1}{100} \sum_{i=1}^{100} SE(\hat{\theta}_i)$ .
- <sup>177</sup> • the standard deviation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

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

**185 Simulation Results**

186 The survival estimates are biased for some parameter combinations of survival, capture, and  
187 tag retention probabilities. As an example, box plots of survival estimates for data with  
188 super-population size  $N=1000$  and 100% double tagging are provided (Fig. 2). Box plots of  
189 survival estimates for other super-population sizes and double-tagging rates are provided in  
190 the Online Supplement (Figs A1-A4). Although there is bias in the survival estimates for  
191 several of the parameter combinations, the bias is similar between the analysis including and  
192 the analysis excluding the recycled individuals for both super-population sizes ( $N = 1000$  and  
193 100 000) and for both double-tagging rates ( $T_2 = 0.5, 1$ ). In fact, the differences in relative  
194 bias due to recycled individuals for the parameters  $\phi$ ,  $p$  and  $\lambda$  is small ( $<0.01$ ) for all 108  
195 parameter combinations considered. In general, the SE, SD and RMSE of the estimates of  
196  $\phi$ ,  $p$  and  $\lambda$  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 are  
204 presented for the parameter combination where  $\phi = 0.9, p = 0.9$  and  $\lambda = 0.2$  for both the  
205 analysis with and without recycled individuals for varying population size and double-tagging  
206 probabilities (Table 1).



207

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  $\phi$  for the model analyzed including and excluding the recycled individuals are provided. The black line indicates the true value of  $\phi$  used to simulate the data for each model.

215

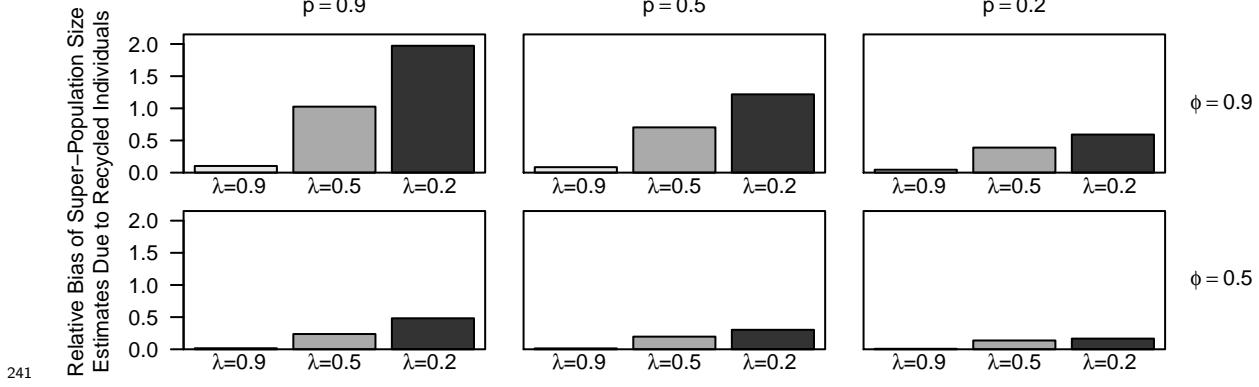
TABLE 1: The mean relative bias of the parameters from the model analyzed including ( $R$ ) and excluding ( $R'$ ) the recycled individuals for data with high survival probability ( $\phi = 0.9$ ), high capture probability ( $p = 0.9$ ), and low tag retention ( $\lambda = 0.2$ ) for different super-populations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

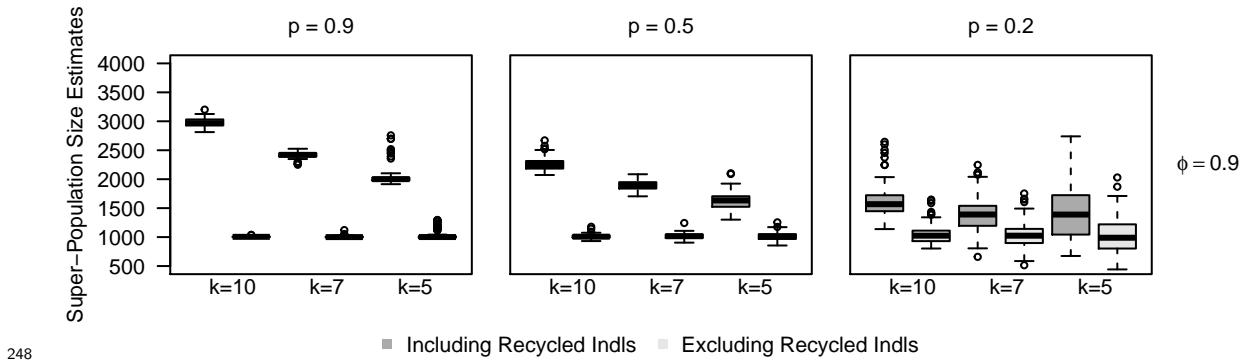
	N=1000				N=100 000			
	$T_2 = 1$		$T_2 = 0.5$		$T_2 = 1$		$T_2 = 0.5$	
	$R$	$R'$	$R$	$R'$	$R$	$R'$	$R$	$R'$
$\phi$	0.00	0.00	0.06	0.05	0.00	0.00	0.11	0.10
$p$	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\lambda$	0.00	0.00	0.00	0.00	0.00	0.00	-0.09	-0.08
N	1.98	0.00	2.13	0.00	1.98	0.00	2.12	0.00

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,  $n_{\text{obs}}$ , 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  
 232 as capture probability decreases, but recycled individuals appear to still have some effect on  
 233 the estimates even when capture probabilities are low ( $p = 0.2$ ). The relative bias in  $\hat{N}$  is  
 234 high for scenarios where survival probability is high, and decreases as survival probability  
 235 decreases. In all scenarios where survival probability is low ( $\phi = 0.2$ ) individuals are unlikely  
 236 to survive long enough to be able to be tagged, lose tag(s) and be recaptured as “new”  
 237 individuals. When survival probability is low, the relative bias due to the recycled individuals  
 238 is small (less than 0.15) and hence not shown in Fig. 3. SE, SD, and RMSE of  $\hat{N}$  varies, but  
 239 remains similar between the analyses with and without recycled individuals included, across  
 240 all scenarios.



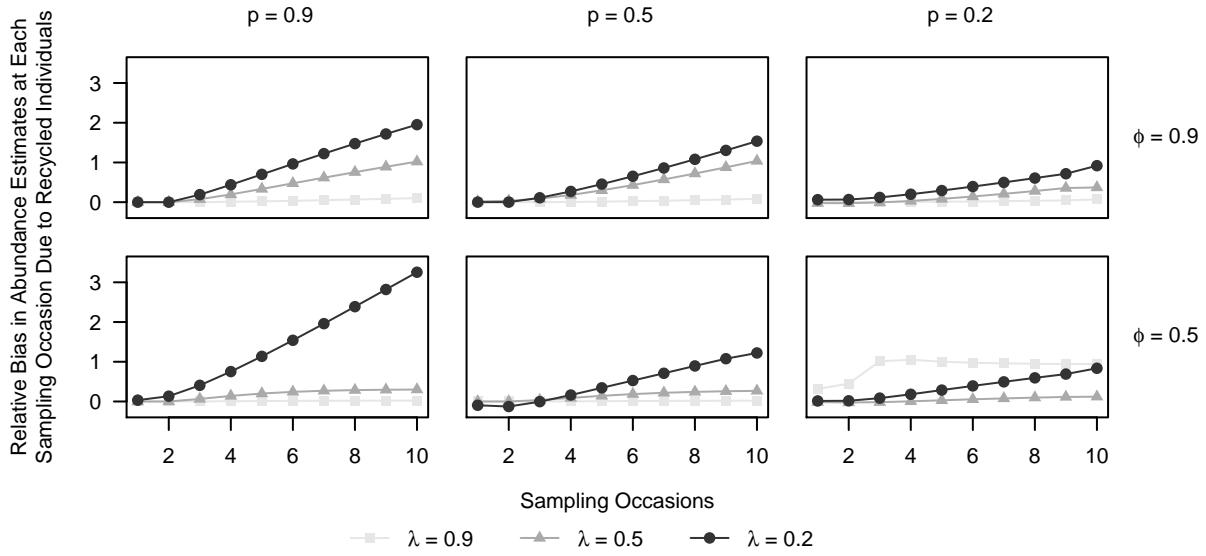
242 FIGURE 3: The difference in mean relative bias of the super-population estimate  
 243 ( $\hat{N}$ ) between the model analyzed including and excluding the recycled individuals  
 244 for data with super-population size  $N = 100\ 000$  with 100% double-tagging  
 245 for different tag retention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



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

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

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



261

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

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

earlier sampling occasions and larger for later sampling occasions. Since the estimates of the population sizes at each time  $j$  are computed iteratively as  $\hat{N}_{j+1} = \hat{\phi}(\hat{N}_j) + \hat{b}_j(\hat{N})$ , any bias in the earlier abundance estimates is magnified in the later sampling occasions abundance estimates. The scenario with  $\phi = 0.5$ ,  $p = 0.9$ , and  $\lambda = 0.2$  appears to have very high relative bias in the abundance estimates in later sampling occasions ( $>3$  for  $\hat{N}_{10}$ ), which is caused by a combination of more upward bias in the survival probability estimates for the analysis 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 data from a long-term mark-recapture study of elephant seals on Macquarie Island. The data used for the case study consists of 7 years between 1993 and 2000. Elephant seal pups were marked with two tags in the inter-digital webbing of their hind flippers and were given a permanent hot-iron branding with a unique identifier on their flank (McMahon *et al.*, 2009). This permanent branding allowed for individual elephant seals to be identified even if they lost both tags. Thus, recycled individuals could be easily identified.

We considered two 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

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

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

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

313 TABLE 2 *Estimates of survival probability ( $\phi$ ), capture probability ( $p$ ), tag-*  
314 *retention probability ( $\lambda$ ), and annual population size ( $N_j$ ) for the elephant seal*  
315 *data analyzed with and without the recycled individuals. Estimated standard*  
316 *errors (SE) are also presented.*

	Including Recycled		Excluding Recycled	
Parameter	Estimate	SE	Estimate	SE
$\phi$	0.759	0.006	0.744	0.006
$p$	0.682	0.006	0.741	0.006
$\lambda$	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	

## 318 Discussion

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

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

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

335 It is not surprising that survival estimates are not biased upwards when recycled individuals  
336 are ignored. Survival estimates are essentially a relative measure of how many individuals  
337 are around now versus the previous time step. Thus the bias in the numerator and the  
338 denominator essentially cancels out (i.e.  $\hat{\phi}_j \approx \hat{N}_j / \hat{N}_{j-1}$ ). Although the case study of elephant  
339 seals validated some of the results from the simulation study (recycled individuals bias  
340 abundance estimates upwards), some caution must be taken when comparing simulation  
341 studies to the real world. There are many parameters that may differ or be uncertain, such  
342 as entry probabilities, that may influence the results. Simplifications of the individuals in the  
343 simulation studies may not take into account the complexities that 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 levels of survival, capture, or tag retention for scenarios of interest for particular  
350 populations or could simulate across more levels to try to get a better sense of the relationship  
351 between the parameters and the effect of recycled individuals. Additionally, future work  
352 could examine the effect of recycled individuals in situations where survival, capture or  
353 tag-retention probabilities are thought to be time- or group-varying.

354 Developing a model to incorporate recycled individuals is a similar problem to that of  
355 incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model

356 to deal with tag-misreads in an open population capture-recapture setting. However most  
357 of the misidentification literature focusses on genetic or photographic identification errors.  
358 Here multiple identities can be assigned to the same individual leading to overestimates in  
359 population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result  
360 that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of  
361 using a latent multinomial to model the latent capture histories for a closed population model.  
362 Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner  
363 & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*,  
364 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models  
365 could be extended to include misidentification produced by complete tag 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  
379 long as tag-retention is high, the JSTL estimator of population size is only weakly affected  
380 by recycled individuals. Longer studies should be particularly concerned about recycled  
381 individuals biasing 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 Acknowledgements

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

## 389 Authors' Contributions

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

## 393 Data Accessibility

394 Data Accessibility:

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

## 397 References

398 Ainley, D.G. & DeMaster, D.P. (1980) Survival and mortality in a population of Adelie  
399 penguins. *Ecology*, **61**, 522–530. Doi:10.2307/1937418.

- 400 Arnason, A. & Mills, K.H. (1981) Bias and loss of precision due to tag loss in Jolly-Seber  
401 estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic*  
402 *Science*, **38**, 1077–1095. Doi: 10.1139/f81-148.
- 403 Bellini, C., Godfrey, M.H. & Sanches, T.M. (2001) Metal tag loss in wild juvenile Hawksbill  
404 sea turtles (*Eretmochelys imbricata*). *Herpetological Review*, **32**, 172–174.
- 405 Bjorndal, K., Bolten, A.B., Lagueux, C.J. & Chaves, A. (1996) Probability of tag loss in  
406 green turtles nesting at Tortuguero, Costa Rica. *Journal of Herpetology*, **30**, 566–571. Doi:  
407 10.2307/1565709.
- 408 Björnsson, B., Karlsson, H., Thorsteinsson, V. & Solmundsson, J. (2011) Should all  
409 fish in mark–recapture experiments be double-tagged? Lessons learned from tagging  
410 coastal cod (*Gadus morhua*). *ICES Journal of Marine Science*, **68**, 603–610. Doi:  
411 10.1093/icesjms/fsq187.
- 412 Bonner, S.J. & Holmberg, J. (2013) Mark-recapture with multiple, non-invasive marks.  
413 *Biometrics*, **69**, 766–775. Doi: 10.1111/biom.12045.
- 414 Cowen, L. & Schwarz, C.J. (2006) The Jolly-Seber model with tag loss. *Biometrics*, **62**,  
415 699–705. Doi: 10.1111/j.1541-0420.2006.00523.x.
- 416 Diefenbach, D.R. & Alt, G.L. (1998) Modeling and evaluation of ear tag loss in black bears.  
417 *The Journal of Wildlife Management*, **62**, 1292–1300. Doi: 10.2307/3801993.
- 418 Fogarty, M.J., Borden, D.V.D. & Russell, H.J. (1980) Movements of tagged American  
419 lobster, *Homarus americanus*, off Rhode Island. *Fishery Bulletin*, **78**, 771–780. Doi:  
420 10.1139/f85-030.
- 421 Gonzalez-Vicente, L., Diaz, D., Mallol, S. & Goni, R. (2012) Tag loss in the lobster *Palinurus*  
422 *elephas* (Fabricius, 1787) and implications for population assessment with capture-mark–  
423 recapture methods. *Fisheries Research*, **129**, 1–7. Doi: 10.1016/j.fishres.2012.05.014.

- 424 Griffiths, S.P. (2002) Retention of visible implant tags in small rockpool fishes. *Marine*  
425      *Ecology Progress Series*, **236**, 307–309. Doi: 10.3354/meps236307.
- 426 Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and  
427      immigration– stochastic model. *Biometrika*, **52**, 225–247. Doi: 10.2307/2333826.
- 428 Link, W.A., Yoshizaki, J., Bailey, L.L. & Pollock, K.H. (2010) Uncovering a latent multinomial:  
429      Analysis of mark-recapture data with misidentification. *Biometrics*, **66**, 178–185. Doi:  
430      10.1111/j.1541-0420.2009.01244.x.
- 431 McClintock, B.T., Bailey, L.L., Dreher, B.P. & Link, W.A. (2014) Probit models for capture-  
432      recapture data subject to imperfect detection, individual heterogeneity and misidentification.  
433      *The Annals of Applied Statistics*, **8**, 2461–2484. Doi:10.1214/14-AOAS783.
- 434 McClintock, B.T., Conn, P.B., Alonso, R.S. & Crooks, K.R. (2013) Integrated modeling of  
435      bilateral photo-identification data in mark-recapture analyses. *Ecology*, **94**, 1464–1471.  
436      Doi:10.1890/12-1613.1.
- 437 McMahon, C.R., Burton, H., van den Hoff, J., Woods, R. & Bradshaw, C.J.A.  
438      (2009) Assessing hot-iron and cyro-branding for permanently marking southern ele-  
439      phant seals. *Journal of Wildlife Management*, **70**, 1484–1489. Doi: 10.2193/0022-  
440      541X(2006)70[1484:AHACFP]2.0.CO;2.
- 441 Pistorius, P.A., Bester, M.N., Kirkman, S.P. & Boveng, P.L. (2000) Evaluation of age-  
442      and sex-dependent rates of tag loss in southern elephant seals. *The Journal of Wildlife*  
443      *Management*, **64**, 373–380. Doi: 10.2307/3803235.
- 444 Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990) Statistical inference for  
445      capture-recapture experiments. *Wildlife Monographs*, **107**, 3–97.
- 446 R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation  
447      for Statistical Computing, Vienna, Austria.

- 448 Schwarz, C.J. & Arnason, A.N. (1996) A general methodology for the analysis of capture-  
449 recapture experiments in open populations. *Biometrics*, **52**, 860–873. Doi: 10.2307/2533048.
- 450 Schwarz, C.J. & Stobo, W.T. (1999) Estimation and effects of tag-misread rates in capture-  
451 recapture studies. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 551–559. Doi:  
452 10.1139/f98-196.
- 453 Schwarz, L., Hindell, M., McMahon, C. & Costa, D. (2012) The implications of assuming  
454 independent tag loss in southern elephant seals. *Ecosphere*, **3**, 81. Doi: 10.1890/ES12-  
455 00132.1.
- 456 Seber, G.A.F. (1965) A note on the multiple recapture census. *Biometrika*, **52**, 249–259. Doi:  
457 10.2307/2333827.
- 458 Seber, G.A.F. & Felton, R. (1965) Tag loss and the Peterson mark-recapture experiment.  
459 *Biometrika*, **68**, 211–219. Doi: 10.1093/biomet/68.1.211.
- 460 Xu, Y., Cowen, L.L.E. & Gardner, C. (2014) Group heterogeneity in the Jolly-Seber-tag-loss  
461 model. *Statistical Methodology*, **17**, 3–16. Doi: 10.1016/j.stamet.2013.01.002.
- 462 Yoshizaki, J., Brownie, C., Pollock, K.H. & Link, W.A. (2011) Modeling misidentification  
463 errors that result from use of genetic tags in capture-recapture studies. *Environmental and  
464 Ecological Statistics*, **18**, 27–55. Doi: 10.1007/s10651-009-0116-1.