The effect of recycled individuals in the Jolly-Seber model with tag loss.

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ABSTRACT:

1. In capture-recapture studies, recycled individuals occur when individuals lose all of their tags and are recaptured as though they were new individuals. Typically, the effect of these recycled individuals is assumed negligible.

2. Through a simulation-based study of double tagging experiments, we examined the effect of recycled individuals on parameter estimates in the Jolly-Seber model with tag loss (Cowen & Schwarz, 2006). We validated the simulation framework using long-term census data of elephant seals.

3. Including recycled individuals did not affect estimates of capture, survival, and tag-retention probabilities. However, with low tag-retention rates, high capture rates, and high survival rates, recycled individuals produced overestimates of population size. For the elephant seal case study, we found population size estimates to be between 8 and 53% larger when recycled individuals were ignored.

4. Ignoring the effects of recycled individuals can cause large biases in population size estimates. These results are particularly noticeable in longer studies.

KEY WORDS: Abundance; Capture-mark-recapture; Complete tag loss; Demography; Double-tagging; Elephant seal; Jolly-Seber; Recycled individual.

Introduction

Mark-recapture studies utilize statistical techniques to estimate population parameters. Over k sample times, individuals are captured, tagged with unique tags, released and potentially recaptured at subsequent sampling times. The Jolly-Seber model (Jolly, 1965; Seber, 1965) is 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 & Costa, 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 it's 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

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

In order to determine whether the simulation framework provided a reasonable approximation to the real world, we analyzed the effects of recycled individuals in long-term census data of elephant seals (*Mirounga leonina*). For this particular population, seals could be identified even if they lost both tags given that they had a permanent brand (McMahon & White, 2009).

Materials and Methods

The Jolly-Seber Model with Tag Loss (JSTL)

Full development of the JSTL model is given by (Cowen & Schwarz, 2006) and summarized in the Online Supplement including a table of notation.

Many different models can be specified for the JSTL model where parameters are homogeneous or heterogeneous with respect to time or group. We consider the case of the JSTL model where capture, survival, and tag retention probabilities are constant over time (Cowen & Schwarz, 2006).

Assumptions of the JSTL model with constant survival, capture, and tag retention probabilities and time-varying entry probabilities are as follows:

- The effect of recycled individuals is negligible

- All individuals (marked and unmarked) are equally catchable, and that capture probabilities for all individuals are the same for all individuals at all sample times

- All individuals (marked and unmarked) have equal survival probabilities between all sample times

- All individuals have equal entry (birth or immigration) probabilities, but entry probabilities can vary between sample times

- All marked individuals have equal tag retention probabilities between all sample times

- For double-tagged individuals, tag loss is independent between tags

- There is independence across all individuals

- The sampling period is relatively short compared to the interval between sampling times

Likelihood and Estimation

The JSTL model is developed under the idea of a superpopulation (the number of individuals that will enter population at some point during the study) (Schwarz & Arnason, 1996) and this allows the likelihood to be formulated into three parts: 1) a model for the observed number of unique tag histories given the superpopulation size (L_1^A), 2) a model for the recaptures given the observed number of unique tag histories (L_1^B), and 3) a model for the number of individuals lost on capture (L_3). The third component L_3, is typically used for harvest or fisheries data when known deaths occur. In this study and in the elephant seal application, we assume there is no possibility of loss on capture, thus the third component of the likelihood simplifies to 1. The full likelihood is given by the product of the components of the likelihood ($L = L_1^A \times L_1^B$) and can be found in the Online Supplement.

Maximum likelihood parameter estimates are found using a Newton-Raphson type method. Estimated standard errors are computed using the delta theorem. Models were implemented

using R software (R Core Team, 2014), and code can be obtained from the second author.

Experimental Design

To study the effect of recycled individuals on parameter estimates of this model, we conducted a simulation study. Data were simulated and analyzed using R 3.1.1 (R Core Team, 2014). Data sets varied both in super-population size, parameter values, and percent double tagged. We generated data for the JSTL model with constant survival, capture, and tag retention probabilities for a double-tagging experiment. Super-population sizes of 1000 and 100 000 were considered in order to study the effect of population size. For the super-population size of 100 000, experiments with ten sample times were considered. For the super-population size of 1000 we considered experiments with five, seven and ten sample times in order to determine the effect of the length of the study. For each population size, we tested different proportions of double-tagged versus single-tagged individuals (0.5 and 1). Survival, capture, and tag retention probability parameters were varied in a 3^3 experimental design with low (0.2), medium (0.5) and high (0.9) values for all parameters. The entry rates were fixed to be $1/k$ at each of the sampling times. No individuals were lost on capture.

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

132 loss in green nesting turtles to be as high as 0.38. Thus, we chose a wide range of tag loss

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

Simulation of Data

135 For all of the parameter combinations of super-population size ($N = 1000, 100\ 000$), fraction

136 double-tagged $(0.5, 1)$, survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p =$

137 $0.2, 0.5, 0.9$) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where

138 the simulated data met all the assumptions of the model.

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

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

141   2. For each sample time after entry (until death or first capture) determine if the individual

142   survives to that sample time (with probability ϕ). If they are still alive, determine if

143   they are first captured (with probability p). If they are captured, determine whether

144   they are single or double-tagged.

145   3. For each sample time after first capture (until death, loss of all tags or the end of the

146   study) determine if the individual survives to that sample time (with probability ϕ).

147   Then if they are still alive, determine if they lose any of their tags (with probability

148        $1 - \lambda$). If they still have at least one of their tags, determine if they are recaptured (with

149   probability p). If they have lost all of their tags, consider them as a new individual

150   entering the population at this sample time.

151 By keeping track of all the recycled individuals, this algorithm provides us with two data sets:

152 one that includes the recycled individuals (assumes individuals, who have complete tag loss,

153 are tagged again upon recapture and treated as new individuals) and one that doesn't include

154 recycled individuals (assumes that individuals, who have complete tag loss, can be recognized

155 upon recapture and are not re-tagged). The JSTL model was fit to the 100 simulated data

156 sets twice (once with and once without recycled individuals). We assumed that any difference

157 between the two analyses was due entirely to the recycled individuals. All data generated

158 during this study are included in this published article (and its supplementary information

159 files).

Evaluation Criteria

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161 To evaluate the resulting parameter estimates from each of the simulations, we looked at

162 several criteria including: average parameter estimate, relative bias of the estimates, the

163 average standard error of the parameter estimates, the standard deviation of the parameter

164 estimates, and root mean squared error (RMSE) of the parameter estimates.

165 Given that the $\hat{\theta}_i$'s are the parameter estimates from each of the 100 simulations and θ the

166 value of the parameter, we calculated:

167 - the mean parameter estimate as $\bar{\hat{\theta}} = \frac{1}{100} \sum_{i=1}^{100} \hat{\theta}_i$

168 - average standard error of the parameter estimate as $\mathrm{SE}(\hat{\theta}) = \frac{1}{100} \sum_{i=1}^{100} \mathrm{SE}(\hat{\theta}_i)$.

169 - the standard deviation of the parameter estimates as $\mathrm{SD}(\hat{\theta}) = \sqrt{\frac{1}{99} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.

170 - the RMSE of the parameter estimates as $\mathrm{RMSE} = \sqrt{\frac{1}{100} \sum_{i=1}^{100} (\hat{\theta}_i - \bar{\hat{\theta}})^2}$.

171 We compared the average parameter estimates to the true parameter values using relative

172 bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. We also compared the

173 relative bias from the analysis with the recycled individuals to the relative bias from the

174 analysis without the recycled individuals. We calculated the difference in the two relative

175 biases and consider this to be the relative bias that was contributed entirely by the recycled

176 individuals being tagged as "new" individuals.

Simulation Results

The relative bias of the survival estimates are biased for some parameter combinations of survival, capture, and tag retention probabilities. As an example, box plots of survival estimates for data with super-population size N=1000 and 100% double tagging are provided (Fig. 1). Box plots of survival estimates for other super-population sizes and double-tagging rates are provided in the Online Supplement (Figs A1-A4). Although there is bias in the survival estimates for several of the parameter combinations, the bias is similar between the analysis with and the analysis without the recycled individuals included for both super-population sizes ($N = 1000$ and 100 000) and for both double-tagging rates ($T_2 = 0.5, 1$). In fact, the differences in relative bias due to recycled individuals for the parameters ϕ, p and λ is small (<0.01) for all 108 parameter combinations considered. In general, the SE, SD and RMSE of the estimates of ϕ, p and λ are similar for both the analysis with and without recycled individuals for the parameter combinations considered. It seems that the treatment of recycled individuals has little effect, if any, on the accuracy of the JSTL estimators for survival, capture, and tag-retention probabilities. Box plots of capture and tag retention estimates for all models can also be found in the Online Supplement (Figs A5-A12).

Results are similar for both the super-population sizes of 1000 and 100 000 for all parameter combinations of survival, capture, and tag retention probabilities. There is slightly more bias due to recycled individuals for parameter combinations where the probability of double tagging (T_2) was only 0.5, compared to the parameter combinations where all individuals were double tagged. As an example, relative bias of the parameters are presented for the parameter combination where $\phi = 0.9, p = 0.9$ and $\lambda = 0.2$ for both the analysis with and without recycled individuals for varying population size and double-tagging probabilities (Table 1).
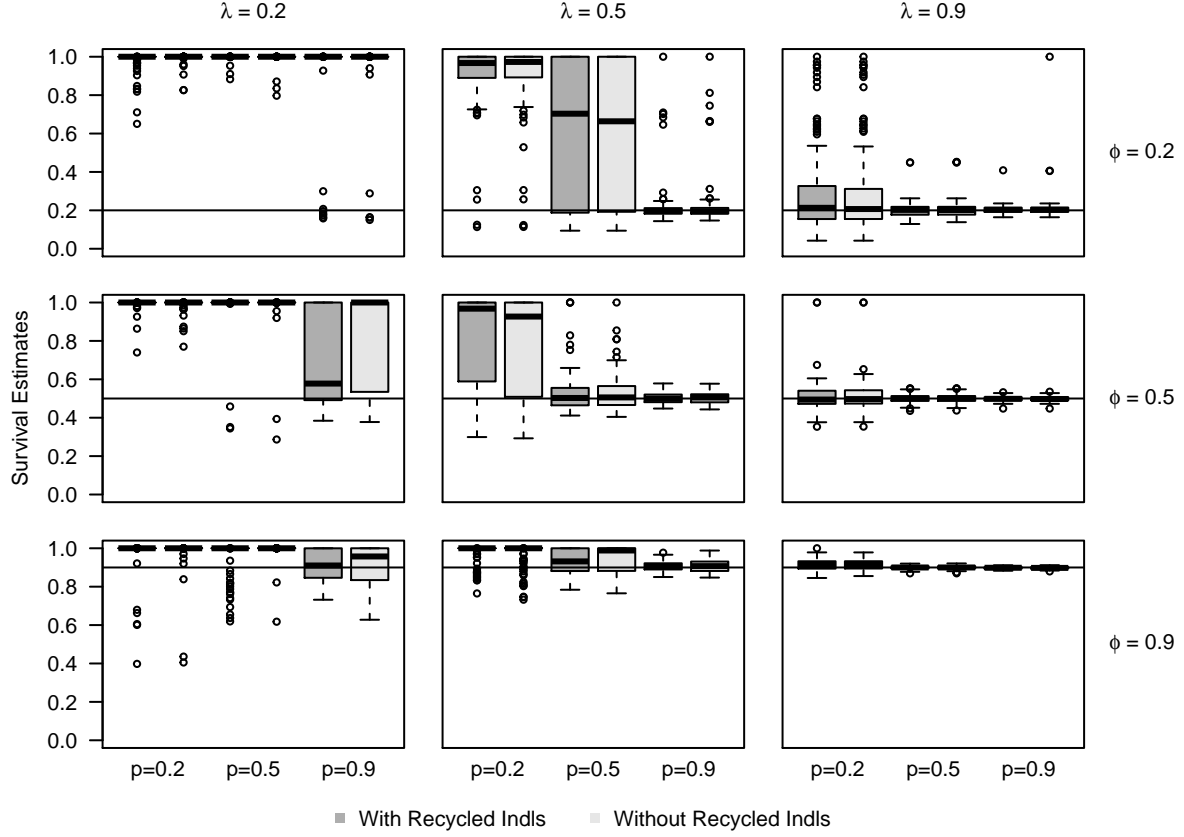
FIGURE 1: *Survival probability estimates for simulated data with super-population size $N = 1000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.2, 0.5, 0.9$), and different capture probabilities ($p = 0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study. Box plots of the estimates of ϕ for the model analyzed with and without 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 with (R) and without (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 different*

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

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 estimated probability of never being seen. In the scenarios where many recycled individuals were recaptured and considered as "new" individuals, the number of observed individuals, n_{obs}, is larger than it should be and thus, $\hat{N}$ is biased upwards. This bias is corrected in the analysis without the recycled individuals considered. The relative bias in the super-population size ($\hat{N}$) due to recycled individuals is highest in the scenario with high survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$), as predicted (Fig. 2, Table 1). The relative bias is small for all scenarios where tag retention was high, but relative bias increases as tag retention decreases. The relative bias in $\hat{N}$ decreases as capture probability decreases, but recycled individuals appear to still have some effect on the estimates even when capture probabilities are low ($p = 0.2$). The relative bias in $\hat{N}$ is high for scenarios where survival probability is high, and decreases as survival probability decreases. In all scenarios where survival probability is low ($\phi = 0.2$) individuals are unlikely to survive long enough to be able to be tagged, lose tag(s) and be recaptured as "new" individuals. When survival probability is low, the relative bias due to the recycled individuals is small (less than 0.15) and hence not shown in Fig. 2. SE, SD, and RMSE of $\hat{N}$ varies, but remains similar between the analyses with and without recycled individuals included, across all scenarios.
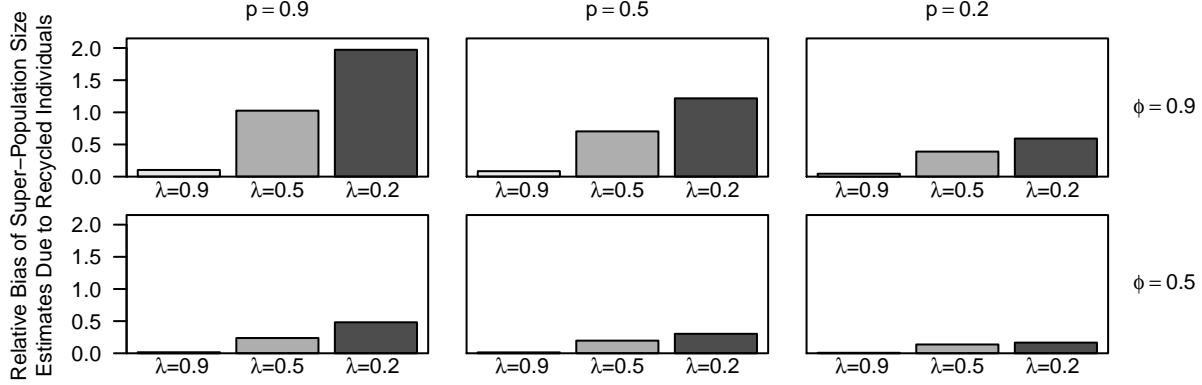
FIGURE 2: *The difference in mean relative bias of the super-population estimate ($\hat{N}$) between the model analyzed with and without the recycled individuals for data with super-population size $N = 100\,000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), 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.*
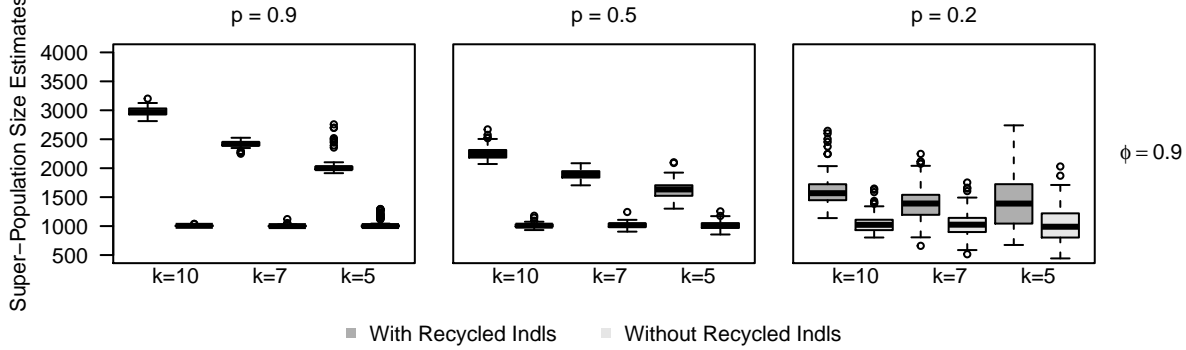

FIGURE 3: *Box plots of the estimates of N for the model analyzed with and without the recycled individuals for data with super-population size $N = 1000$ with 100% double-tagging for different capture probabilities ($p = 0.2, 0.5, 0.9$), and constant survival ($\phi = 0.9$) and tag retention ($\lambda = 0.2$) 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. 3). With a larger number of sampling occasions, there is more time for individuals to be captured and

249 tagged, lose their tags, and survive to be recaptured (be recycled). In shorter studies, there

250 are fewer numbers of recycled individuals and thus the bias in $\hat{N}$ due to recycled individuals is

251 lower although not unnoticeable in the worst case scenarios (low tag retention, high survival

252 and high capture probabilities). Box plots of super-population size (N) for all scenarios are

253 available in the Online Supplement (Figs A19-A24).
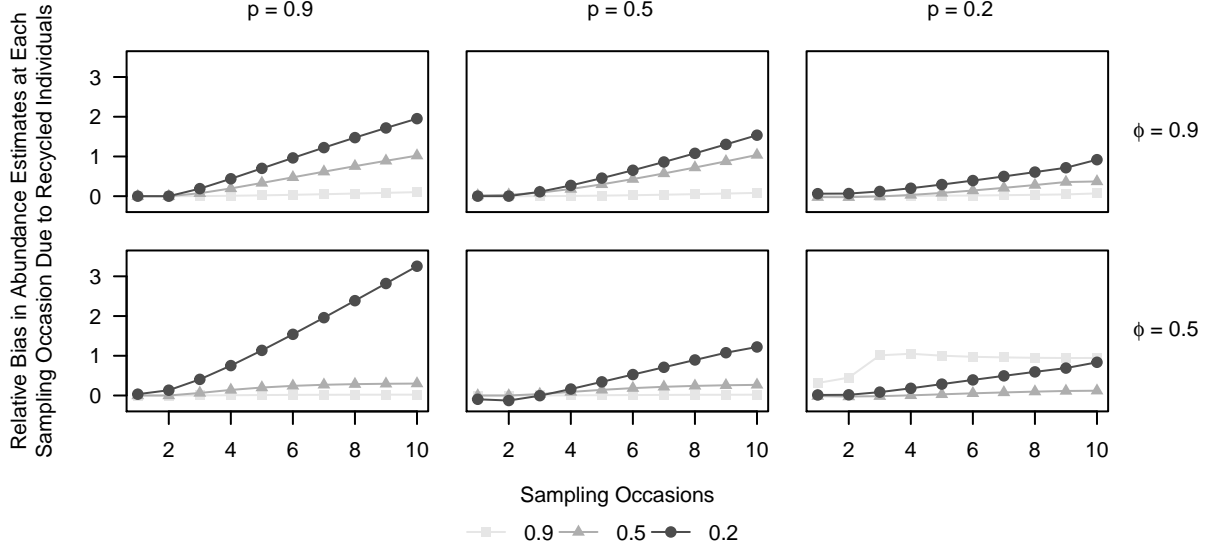

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FIGURE 4: *The difference in mean relative bias of the abundance estimates at each*

sample time ($\hat{N}_j$) between the model analyzed with and without the recycled indi-

viduals 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 different capture probabilities ($p = 0.2, 0.5, 0.9$) using the

JSTL model from a ten-sample-time study. Note that lines are added between

the points to emphasize the difference in values; no models were fit to generate

these lines.

263 In general, the bias due to recycled individuals in the $\hat{N}_j$'s follows a similar pattern to

264 the bias due to recycled individuals in $\hat{N}$, with relative bias in the $\hat{N}_j$'s increasing as tag

265 retention decreases, survival increases, and capture probability increases (Fig. 4). For all

266 scenarios, the relative bias in the estimates of abundance at each sample time j is smaller for

₂₆₇ earlier sampling occasions and larger for later sampling occasions. Since the estimates of the

₂₆₈ 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

₂₆₉ in the earlier abundance estimates is magnified in the later sampling occasions abundance

₂₇₀ estimates. The scenario with $\phi = 0.5$, $p = 0.9$, and $\lambda = 0.2$ appears to have very high relative

₂₇₁ bias in the abundance estimates in later sampling occasions (>3 for $\hat{N}_{10}$), which is caused by

₂₇₂ a combination of more upward bias in the survival probability estimates for the analysis with

₂₇₃ recycled individuals than without (Fig. A14) as well as upward bias in the super-population

₂₇₄ size estimates. Plots of the mean abundance estimates for all scenarios are available in the

₂₇₅ Online Supplement (Figs A17-A28).

Case Study: Elephant Seals

₂₇₇ To validate the simulation framework, we analyzed data from a long-term mark-recapture

₂₇₈ study of elephant seals on Macquarie Island. The data used for the case study consists

₂₇₉ of 7 years between 1993 and 2000. Elephant seal pups were marked with two tags in the

₂₈₀ inter-digital webbing of their hind flippers and were given a permanent hot-iron branding with

₂₈₁ a unique identifier on their flank (McMahon *et al.*, 2009). This permanent branding allowed

₂₈₂ for individual elephant seals to be identified even if they lost both tags. Thus, recycled

₂₈₃ individuals could be easily identified.

₂₈₄ We considered two analyzes of the data:

₂₈₅ 1. We assumed that recycled individuals could not be recognized upon recapture (ignoring

₂₈₆ branding) and were re-tagged as if they were new individuals. This scenario simulates

₂₈₇ analysis ignoring the effects of recycled individuals.

₂₈₈ 2. Recycled individuals were recognized upon recapture (by branding) and were re-tagged

₂₈₉ with new tags identical to their lost tags.

₂₉₀ 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 excluded. For this analysis, we used the same model as the simulation study where capture, survival and tag retention rates were held constant.

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

Similar to the simulations, there is not much difference in the estimates of survival, capture, and tag-retention probabilities between the analysis with and without recycled individuals. For comparison to the previous simulations, we note that tag retention probability for the elephant seals was estimated to be ≈ 0.8 (high). Standard error estimates are also higher when recycled individuals are included in the analysis. The same pattern is seen in the simulation studies (see Web Appendix A).

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

	With Recycled		Without 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

Discussion

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

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324 the effects are reduced.

325 For longer term studies when survival and capture probabilities are low, the bias in abundance

326 estimates associated with recycled individuals is smaller. These are characteristics that might

327 be associated with small, endangered, or decreasing populations.

328 It is not surprising that survival estimates are not biased upwards when recycled individuals

329 are ignored. Survival estimates are essentially a relative measure of how many individuals

330 are around now versus the previous time step. Thus the bias in the numerator and the

331 denominator essentially cancels out (i.e. $\hat{\phi}_j \approx \hat{N}_j / \hat{N}_{j-1}$).

332 Although the case study of elephant seals validated some of the results from the simulation

333 study (recycled individuals bias abundance estimates upwards), some caution must be

334 taken when comparing simulation studies to the real world. There are many parameters

335 that may differ or be uncertain, such as entry probabilities, that may influence the results.

336 Simplifications of the individuals in the simulation studies may not take into account the

337 complexities that arise in real life scenarios.

338 Although our study provides some evidence that recycled individuals have an effect on

339 estimators of the JSTL model in particular situations, there is room for improvement in our

340 approach and questions remain for future work. We only examined three levels of survival,

341 capture, and tag-retention probabilities (Low=0.2, Medium=0.5 and High=0.9) which was

342 intended to simulate across a variety of scenarios that may exist in real life. Future work could

343 examine levels of survival, capture, or tag retention for scenarios of interest for particular

344 populations or could simulate across more levels to try to get a better sense of the relationship

345 between the parameters and the effect of recycled individuals. Additionally, future work

346 could examine the effect of recycled individuals in situations where survival, capture or

347 tag-retention probabilities are thought to be time- or group-varying.

348 For researchers interested in conducting and analyzing mark-recapture studies, unsurprisingly

349 we stress the importance of using tags with high retention rates, especially in situations

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where survival and capture rates are suspected to be high. As long as tag-retention is high, the JSTL estimator of population size is not affected by recycled individuals. In situations where it is possible to recognize if an individual has been captured previously (by scarring, marking, etc), excluding these recycled individuals from the analysis can improve accuracy of the abundance estimates. Permanent marking should be used where possible. If researchers are only interested in the survival rates, they do not need to be concerned with the effect of recycled individuals regardless of the study's tag-retention rates.

Developing a model to incorporate recycled individuals is a similar problem to that of incorporating misidentification of individuals. Schwarz & Stobo (1999) developed a model to deal with tag-misreads in an open population capture-recapture setting. However most of the misidentification literature focusses on genetic or photographic identification errors. Here multiple identities can be assigned to the same individual leading to overestimates in population size if misidentification is ignored (Yoshizaki *et al.*, 2011). This is the same result that we see when recycled individuals are ignored. Link *et al.* (2010) introduced the notion of using a latent multinomial to model the latent capture histories for a closed population model. Others have extended Link *et al.*'s model to deal with multiple non-invasive marks (Bonner & Holmberg, 2013; McClintock *et al.*, 2013), heterogeneity in parameters (McClintock *et al.*, 2014) and open populations (Bonner & Holmberg, 2013). These latent multinomial models could be extended to include misidentification produced by complete tag loss.

Finally, the JSTL model we looked at did not include a component for loss on capture (when for example a fishery harvest occurs). It would be interesting for future work to include loss on capture to determine if recycled individuals are still problematic under this scenario. There remains a great deal more to study including testing some of the many assumptions that capture-mark-recapture analyses rely on, many of which we know are violated in the real world. Increasing computation power and a larger community applying themselves to these problems has the potential to answer and inform researchers and managers in a meaningful way, especially in terms of how we use imperfect observations to estimate vital rates (survival

377 and fecundity). Having more robust estimates of vital rates is especially important if we are
378 to manage efficiently an ever increasing list of endangered species.

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382 Authors' Contributions

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

386 Data Accessibility

387 The data can be obtained from CM.

388 References

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

391 Arnason, A. & Mills, K.H. (1981) Bias and loss of precision due to tag loss in Jolly-Seber
392   estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic*
393   *Science*, **38**, 1077–1095. Doi: 10.1139/f81-148.

Bellini, C., Godfrey, M.H. & Sanches, T.M. (2001) Metal tag loss in wild juvenile Hawksbill sea turtles (*Eretmochelys imbricata*). *Herpetological Review*, **32**, 172–174.

Bjorndal, K., Bolten, A.B., Lagueux, C.J. & Chaves, A. (1996) Probability of tag loss in green turtles nesting at Tortuguero, Costa Rica. *Journal of Herpetology*, **30**, 566–571. Doi: 10.2307/1565709.

Björnsson, B., Karlsson, H., Thorsteinsson, V. & Solmundsson, J. (2011) Should all fish in mark–recapture experiments be double-tagged? Lessons learned from tagging coastal cod *(Gadus morhua)*. *ICES Journal of Marine Science*, **68**, 603–610. Doi: 10.1093/icesjms/fsq187.

Bonner, S.J. & Holmberg, J. (2013) Mark-recapture with multiple, non-invasive marks. *Biometrics*, **69**, 766–775. Doi: 10.1111/biom.12045.

Cowen, L. & Schwarz, C.J. (2006) The Jolly-Seber model with tag loss. *Biometrics*, **62**, 699–705. Doi: 10.1111/j.1541-0420.2006.00523.x.

Diefenbach, D.R. & Alt, G.L. (1998) Modeling and evaluation of ear tag loss in black bears. *The Journal of Wildlife Management*, **62**, 1292–1300. Doi: 10.2307/3801993.

Fogarty, M.J., Borden, D.V.D. & Russell, H.J. (1980) Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. *Fishery Bulletin*, **78**, 771–780. Doi: 10.1139/f85-030.

Gonzalez-Vicente, L., Diaz, D., Mallol, S. & Goni, R. (2012) Tag loss in the lobster *Palinurus elephas* (Fabricius, 1787) and implications for population assessment with capture-mark-recapture methods. *Fisheries Research*, **129**, 1–7. Doi: 10.1016/j.fishres.2012.05.014.

Griffiths, S.P. (2002) Retention of visible implant tags in small rockpool fishes. *Marine Ecology Progress Series*, **236**, 307–309. Doi: 10.3354/meps236307.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration– stochastic model. *Biometrika*, **52**, 225–247. Doi: 10.2307/2333826.

Link, W.A., Yoshizaki, J., Bailey, L.L. & Pollock, K.H. (2010) Uncovering a latent multinomial: Analysis of mark-recapture data with misidentification. *Biometrics*, **66**, 178–185. Doi: 10.1111/j.1541-0420.2009.01244.x.

McClintock, B.T., Bailey, L.L., Dreher, B.P. & Link, W.A. (2014) Probit models for capture-recapture data subject to imperfect detection, individual heterogeneity and misidentification. *The Annals of Applied Statistics*, **8**, 2461–2484. Doi:10.1214/14-AOAS783.

McClintock, B.T., Conn, P.B., Alonso, R.S. & Crooks, K.R. (2013) Integrated modeling of bilateral photo-identification data in mark-recapture analyses. *Ecology*, **94**, 1464–1471. Doi:10.1890/12-1613.1.

McMahon, C.R., Burton, H., van den Hoff, J., Woods, R. & Bradshaw, C.J.A. (2009) Assessing hot-iron and cyro-branding for permanently marking southern elephant seals. *Journal of Wildlife Management*, **70**, 1484–1489. Doi: 10.2193/0022-541X(2006)70[1484:AHACFP]2.0.CO;2.

McMahon, C. & White, G. (2009) Tag loss probabilities are not independent: Assessing and quantifying the assumption of independent tag transition probabilities from direct observations. *Journal of Experimental Marine Biology and Ecology*, **372**, 36–42. Doi: 10.1016/j.jembe.2009.02.006.

Pistorius, P.A., Bester, M.N., Kirkman, S.P. & Boveng, P.L. (2000) Evaluation of age- and sex-dependent rates of tag loss in southern elephant seals. *The Journal of Wildlife Management*, **64**, 373–380. Doi: 10.2307/3803235.

Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990) Statistical inference for capture-recapture experiments. *Wildlife Monographs*, **107**, 3–97.

R Core Team (2014) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Schwarz, C.J. & Arnason, A.N. (1996) A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, **52**, 860–873. Doi: 10.2307/2533048.

Schwarz, C.J. & Stobo, W.T. (1999) Estimation and effects of tag-misread rates in capture-recapture studies. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 551–559. Doi: 10.1139/f98-196.

Schwarz, L.K., H.M.M.C. & Costa, D. (2012) The implications of assuming independent tag loss in southern elephant seals. *Ecosphere*, **3**, 81. Doi: 10.1890/ES1812-00132.1.

Seber, G.A.F. (1965) A note on the multiple recapture census. *Biometrika*, **52**, 249–259. Doi: 10.2307/2333827.

Seber, G.A.F. & Felton, R. (1965) Tag loss and the Peterson mark-recapture experiment. *Biometrika*, **68**, 211–219. Doi: 10.1093/biomet/68.1.211.

Xu, Y., Cowen, L.L.E. & Gardner, C. (2014) Group heterogeneity in the Jolly-Seber-tag-loss model. *Statistical Methodology*, **17**, 3–16. Doi: 10.1016/j.stamet.2013.01.002.

Yoshizaki, J., Brownie, C., Pollock, K.H. & Link, W.A. (2011) Modeling misidentification errors that result from use of genetic tags in capture-recapture studies. *Environmental and Ecological Statistics*, **18**, 27–55. Doi: 10.1007/s10651-009-0116-1.