The Effect of Recycled Individuals in the Jolly-Seber Tag Loss Model

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SUMMARY: In mark-recapture studies, the Jolly-Seber model assumes that individuals never lose their tags. In practice however, we know that tag loss does occur. Cowen and Schwarz (2006) developed the Jolly-Seber model with tag loss that relaxes this assumption and allows for estimation of tag retention and abundance in double-tagging experiments. Recycled individuals occur when individuals lose all of their tags and are recaptured as "new" individuals. Typically, the effect of these recycled individuals is assumed negligible. With low tag-retention rates, high capture rates, and high survival rates, recycled individuals can produce overestimates of population size. These results are particularly noticeable in longer studies. Through a simulation-based study, we examine the effect of recycled individuals on parameter estimates. We determine under what conditions recycled individuals have the most impact and offer advice for study designs.

KEY WORDS: Abundance; Complete tag loss; Double-tagging; Jolly-Seber; Mark-recapture; Recycling; Tag loss.

Introduction

Mark-recapture studies utilize statistical techniques to estimate numerical characteristics about populations. Over K sampling periods, individuals are captured, tagged, released and potentially recaptured at later sample times. The Jolly-Seber (JS) model (Jolly 1965, Seber 1965) is commonly 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 individuals never lose their tags. However, when this assumption is violated, serious bias can occur in the parameter and variance estimates (Arnason and Mills, 1981). Double-tagging, the placement of two tags on an individual, can be used to estimate tag retention rates. Often a mixture of single- and double-tagged individuals is used for practical purposes. Cowen and 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).

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 time 1, lost a tag between times 1 and 2, and may have lost it's last tag between sampling occasions 2 and 3. If recaptured at sample occasion 3 it would result in a new individual. If the rate of tag loss is small, bias in the population estimate will also be small for the Peterson estimators (Seber and Felton, 1981). Typically in the JS 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 purpose of this study was to investigate the effect of recycled individuals on parameter estimates in the JSTL model through simulation.

Methods

The Jolly-Seber Model with Tag Loss (JSTL)

Many different models can be specified for the JSTL model where parameters are homogeneous or heterogeneous with respect to time or group (Cowen and Schwarz, 2006; Xu et al, 2014). In the simplest form of the JSTL model, it is assumed that every individual present in the population at sampling occasion k has capture probability (p), tag retention probability (λ), and survival probability (ϕ) between sampling occasion k and $k+1$, that are homogeneous for all individuals in the population across all sampling occasions. For this study, we consider the homogeneous parameter form of the JSTL model with equal entry probabilities ($b_j, j = 0, , , , K-1$).

Likelihood and Estimation

The likelihood of the JSTL model can be divided into three parts: the probability of observing n_{obs}, the number of tag histories, given the super-population size N (L_1^A), the probability of observing recaptures given the number of tag histories (L_1^B), and the probability of observing the number of individuals lost on capture (L_3).

The probability of observing n_{obs} capture histories is given by a binomial distribution conditional on the super-population size N, the total number of individuals ever present in the population and available for capture during the study.

$$L_1^A = [n_{\text{obs}}|N] \sim \text{Binomial}(N, 1 - P_0), \text{ where } P_0 \text{ is the probability of never being seen.}$$

The probability of observing each unique tag history ω_i is modeled by a multinomial conditional upon being observed at least once.

$$L_1^B = [n_{\omega_i}|n_{obs}] \sim \text{Multinomial}(n_{obs}, \pi_{\omega_i}), \text{ where } \pi_{\omega_i} = P_{\omega_i}/(1 - P_0) \text{ and}$$

P_{ω_i} is the probability of observing tag history ω_i as described by Xu, Cowen and Gardner (2014). It is a function of the model parameters (β, ϕ, p, and λ) and the fraction double tagged. It is described in more detail in the Appendix. The fraction double tagged does not affect the likelihood for maximization (estimation) purposes, it does however affect the likelihood in situations such as considering goodness-of-fit.

The third component L_3 models the number of losses on capture as a binomial. In this simulation study we assume there is no possibility of loss on capture, this 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 Appendix. Numerical maximum likelihood parameter estimates are found using a Newton-Raphson type method. Estimated standard errors are computed using the delta theorem.

Experimental Design

To study the effect of recycled individuals on parameter estimates of this model, we conducted a simulation study 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 determine the effect that population size may have on the results. For the super-population size of 100 000, experiments with ten sampling occasions were considered. For the super-population size of 1000 we considered experiments with five, seven and ten sampling occasions in order to determine if the length of the study has any effect on the results. For each population size, we tested different proportions of double-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 each parameter. The entry rates were fixed to be the same at each of the sampling times. No individuals were lost on capture.

Simulation of Data

For all of the parameter combinations of super-population size ($N = 1000, 100000$), fraction double-tagged ($0.5, 1$), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p = 0.2, 0.5, 0.9$) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$), we generated 100 data sets where the simulated data met all the assumptions of the model.

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

1. Determine when the individual enters the population using the entry probabilities (b_j).
2. For each time period after entry (until death or first capture) we determine if the individual survives to the next sample time (with probability ϕ). If they are still alive, determine if they were first captured (with probability p). If they are captured, determine whether they are double-tagged.
3. For each time period after first capture (until death, loss of all tags or the end of the study) determine if the individual survives to that time period (with probability ϕ). Then if they are still alive, determine if they lose any of their tags (with probability $1 - \lambda$). If they still have at least one of their tags, determine if they were recaptured (with probability p). If they have lost all of their tags, consider them as a new individual entering the population at this time period.

By keeping track of all the recycled individuals, this algorithm provided two data sets: one that includes the recycled individuals (assumes individuals, who have lost their tags, are tagged again upon recapture and treated as new individuals) and one that doesn't include the recycled individuals (assumes that individuals, who have lost their tags, can be recognized upon recapture and are not re-tagged). We fit the JSTL model to the 100 simulated data sets twice (once with and once without recycled individuals). We assumed that any difference between the two analyses was due entirely to the recycled individuals.

Evaluation Criteria

We quantified the extent of the recycled individual problem by studying several example simulations. We calculated the fraction of recycled individuals (number of recycled individuals captured / total number of individuals captured) at each sample occasion for a 5, 7, and 10 occasion experiment with parameter values $\{\phi,\ p,\ \lambda\}$ set to $\{0.9{,}0.9{,}0.2\}$, $\{0.9{,}0.9{,}0.9\}$, $\{0.9,\ 0.5,\ 0.2\}$, $\{0.9{,}0.5{,}0.9\}$, and $\{0.5{,}0.5{,}0.5\}$. Out of over 100 possible parameter combinations, we choose parameter values that would represent high, medium, and low numbers of recycled individuals in the experiment.

To evaluate the 100 resulting parameter estimates from each of the 100 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.

We calculated the mean parameter estimate as $\bar{\hat{\theta}} = \frac{1}{100}\sum_{i=1}^{100}\hat{\theta}_i$, where the $\hat{\theta}_i$'s are the parameter estimates from each of the 100 simulations and θ is the true value of the parameter. We calculated average standard error of the parameter estimate as $\text{SE}(\hat{\theta}) = \frac{1}{100}\sum_{i=1}^{100}\text{SE}(\hat{\theta}_i)$. We calculated the standard deviation of the parameter estimates as $\text{SD}(\hat{\theta}) = \sqrt{\frac{1}{99}\sum_{i=1}^{100}(\hat{\theta}_i - \hat{\theta})^2}$. We calculated the root mean square error of the parameter estimates as $\text{RMSE} = \sqrt{\frac{1}{100}\sum_{i=1}^{100}(\hat{\theta}_i - \theta)^2}$.

The average parameter estimates are compared to the true parameter values using relative bias. We calculated the relative bias of the estimators as $(\bar{\hat{\theta}} - \theta)/\theta$. Often, we 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 relative bias that was contributed entirely by the recycled individuals being tagged as “new” individuals. We name this “relative bias difference” throughout the rest of the manuscript.

Results

Table 1 shows examples of the fraction of recycled individuals captured at each sample time for various parameter scenarios. For the simulation with high survival and capture probabilities and low tag retention probability, the fraction of recycled individuals captured at each occasion rose quickly. Whereas, when tag retention rates were high (0.9), the fraction of recycled individuals remained low. For a more extensive range of parameter scenarios, see Table X in the Appendix.

The survival estimates were biased for some parameter combinations of survival, capture, and tag retention probabilities. As an example, boxplots of survival estimates for data with super-population size N=1000 and 100% double tagging are provided (Figure 1). Boxplots of survival estimates for other super-population sizes and double-tagging rates are provided in the Appendix (Figures A1-A4). Although there was bias in the survival estimates for several of the parameter combinations, the bias was similar between the analysis with and without the recycled individuals included for both super-population sizes ($N = 1000$ and 100000) 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 was small ($<$0.01) for all 108 parameter combinations considered. In general, the SE, SD and RMSE of the estimates of ϕ, p and λ were similar for both the analyses with and without recycled individuals. It seems that, in general, the treatment of recycled individuals has little effect, if any, on the accuracy of the JSTL estimators for survival, capture, and tag-retention probabilities. Boxplots of capture and tag retention estimates for all models can also be found in the Appendix (Figures

A5-A12).

Results were 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) is only 0.5, compared to the parameter combinations where all individuals are 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 analyses with and without recycled individuals for varying population size and double-tagging probabilities (Table 2).

The estimate of super-population size ($\hat{N}$) was computed as $\hat{N} = n_{\text{obs}}/(1 - \hat{P}_0)$, where $\hat{P}_0$ was the estimated probability of never being seen. In the scenarios where many recycled individuals were recaptured and considered as "new" individuals, n_{obs} was larger than it should be and thus, $\hat{N}$ was biased upwards. This bias was corrected in the analysis without the recycled individuals considered. As predicted, the relative bias in the super-population size ($\hat{N}$) due to recycled individuals was the highest in the scenario of high survival rates ($\phi = 0.9$), high capture rates ($p = 0.9$) and low tag retention rates ($\lambda = 0.2$)(Figure 2, Table 2). The relative bias was small for all scenarios where tag retention was high, but relative bias increased as tag retention decreased. The relative bias in $\hat{N}$ decreased as capture probabilities decreased, but recycled individuals appear to still have some effect on the estimates even when capture probabilities were low ($p = 0.2$). The relative bias in $\hat{N}$ was high for scenarios where survival probabilities was high, and decreased as survival probabilities decreased. In all scenarios where survival was low ($\phi = 0.2$) individuals were unlikely to survive long enough to be able to be tagged, lose their tag(s) and be recaptured as a "new" individual. When survival was low, the relative bias due to the recycled individuals was small (less than 0.15) and hence not shown in Figure 2. The SE, SD, and RMSE of $\hat{N}$ varied, but remained similar between the analysis with and without recycled individuals included, across all scenarios.

When studies were conducted with more sample occasions, there was more bias in $\hat{N}$ due to the recycled individuals (Figure 3). With a larger number of sampling occasions, there is more opportunity for individuals to be captured and tagged, lose all of their tags, and survive to be recaptured (be recycled). In shorter studies, there were fewer numbers of recycled individuals (Table 1) and thus the bias in $\hat{N}$ due to recycled individuals is lower although noticeable in the worst case scenarios (low tag retention, high survival and high capture probabilities). Boxplots of super-population size (N) for all scenarios are available in the Appendix (Figures A19-A24).

In general, the bias due to recycled individuals in the population size at each sample time ($\hat{N}_j$) follow a similar pattern to the bias due to recycled individuals in $\hat{N}$, with relative bias in the $\hat{N}_j$'s increasing as tag retention decreases, survival increases and capture probability increases (Figure 4). For all scenarios, the relative bias in the estimates of abundance at each sample time j was 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 $\lambda = 0.2$ had very high relative bias in the abundance estimates in later sampling occasions (>3 for $\hat{N}_{10}$), which was caused by a combination of more upward bias in the survival estimates for the analysis with recycled individuals than without (Figure A14) as well as upward bias in the super-population size estimates. Plots of the difference in mean abundance estimates for all scenarios are available in the Appendix (Figures A17-A28).

Discussion

We used the time-homogeneous JSTL model to produce simulated data from 108 different parameter combinations of super-population size (N=1000,100 000), fraction double-tagged ($T_2 = 0.5, 1$), survival probability ($\phi = 0.2, 0.5, 0.9$), capture probability ($p = 0.2, 0.5, 0.9$) and tag retention probability ($\lambda = 0.2, 0.5, 0.9$) for ten sampling occasions. For the super-population size of 1000, we also examined experiments with five and seven sampling occasions. While these models 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 rate, high capture rate, or both. This effect is especially noticeable in experiments with more sample occasions. This contradicts the previous 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.

For researchers interested in conducting mark-recapture studies, we stress the importance of using tags with high retention rates, especially in situations 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 grossly 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 could also improve a study's estimates where possible. If researchers are only interested in the survival estimation, they do not need to be concerned with the effect of recycled individuals regardless of the study's tag-retention rates.

Future work would include extending the JSTL model to incorporate recognizable recycled individuals thus removing the need for the assumption that recycled individuals have a negligible effect.

Acknowledgements

Simulation studies and analyses were run on WestGrid/Compute Canada with assistance from Dr. Belaid Moa. This work was supported by an NSERC discovery grant held by LLEC.

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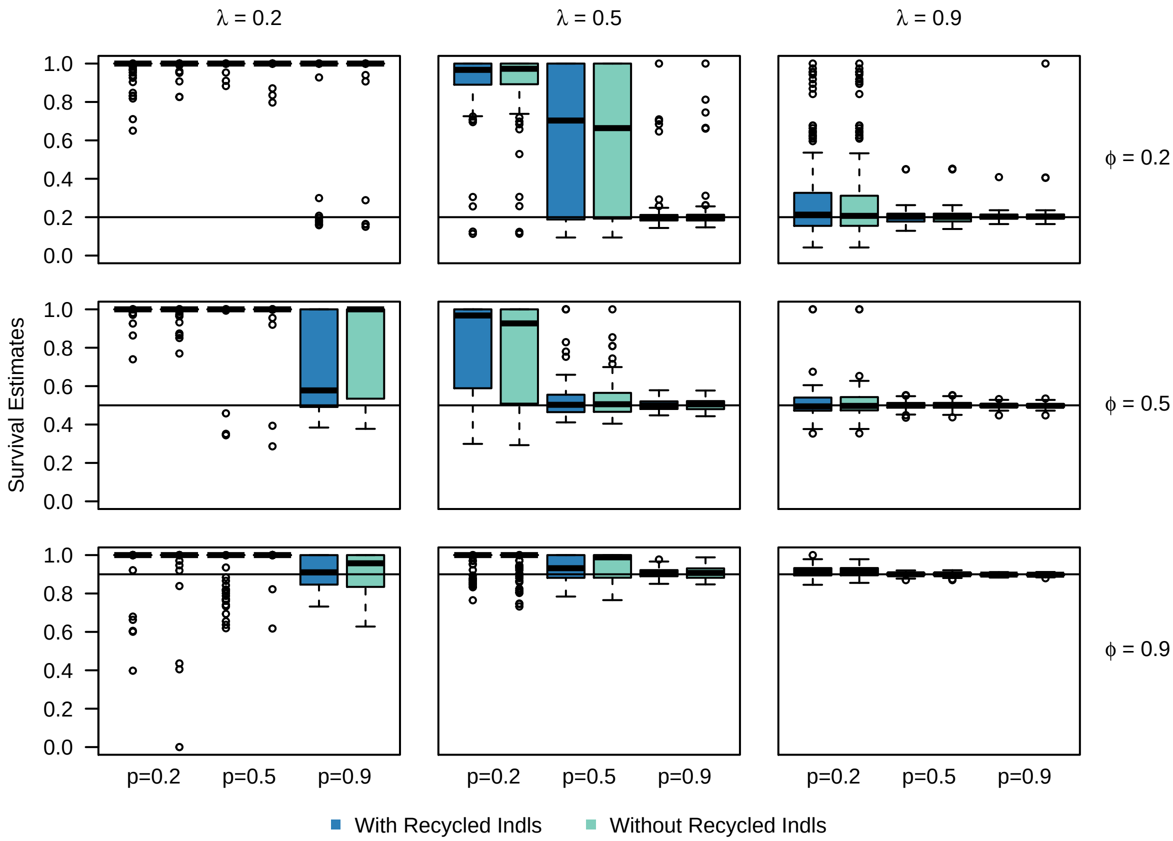

FIGURE 1: *Boxplots of the estimates of ϕ for the model with and without the recycled individuals for simulated data with super-population size $N = 1000$ with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.2, 0.5, 0.9$), and different capture probabilities ($p = 0.2, 0.5, 0.9$) using the JSTL model from a ten-sample-time study. The black line indicates the true value of ϕ used to simulate the data for each model.*

Table 1: *Examples of the fraction of recycled individuals (number of recycled individuals captured / total number of individuals captured) at each sample occasion for a 5, 7, and 10 occasion experiment with parameter values {ϕ, p, λ} set to {0.9,0.9,0.2}, {0.9,0.9,0.9}, {0.9, 0.5, 0.2}, {0.9,0.5,0.9}, and {0.5,0.5,0.5} with super-population size* $N = 1000$ *with 100% double-tagging.*

	1	2	3	4	5	6	7	8	9	10
$\phi = 0.9, p = 0.9, \lambda = 0.2$	0.00	0.30	0.36	0.47	0.51	0.53	0.54	0.55	0.56	0.57
$\phi = 0.9, p = 0.9, \lambda = 0.9$	0.00	0.01	0.02	0.02	0.01	0.01	0.03	0.04	0.04	0.03
$\phi = 0.9, p = 0.5, \lambda = 0.2$	0.00	0.14	0.28	0.38	0.43	0.48	0.54	0.54	0.55	0.56
$\phi = 0.9, p = 0.5, \lambda = 0.9$	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.06	0.06
$\phi = 0.5, p = 0.5, \lambda = 0.5$	0.00	0.01	0.07	0.06	0.12	0.13	0.14	0.16	0.13	0.14

	1	2	3	4	5	6	7
$\phi = 0.9, p = 0.9, \lambda = 0.2$	0.00	0.32	0.40	0.49	0.50	0.53	0.55
$\phi = 0.9, p = 0.9, \lambda = 0.9$	0.00	0.01	0.01	0.02	0.02	0.02	0.02
$\phi = 0.9, p = 0.5, \lambda = 0.2$	0.00	0.12	0.30	0.35	0.42	0.47	0.50
$\phi = 0.9, p = 0.5, \lambda = 0.9$	0.00	0.01	0.00	0.02	0.02	0.03	0.04
$\phi = 0.5, p = 0.5, \lambda = 0.5$	0.00	0.05	0.04	0.05	0.09	0.11	0.12

	1	2	3	4	5
$\phi = 0.9, p = 0.9, \lambda = 0.2$	0.00	0.29	0.34	0.45	0.52
$\phi = 0.9, p = 0.9, \lambda = 0.9$	0.00	0.01	0.01	0.02	0.02
$\phi = 0.9, p = 0.5, \lambda = 0.2$	0.00	0.14	0.27	0.33	0.38
$\phi = 0.9, p = 0.5, \lambda = 0.9$	0.00	0.00	0.01	0.01	0.02
$\phi = 0.5, p = 0.5, \lambda = 0.5$	0.00	0.03	0.09	0.10	0.12

TABLE 2: *The mean relative bias of the parameters from the model with (R) and without (R') the recycled individuals for simulated 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 ($N = 1000, 100000$) and different proportion double tagged ($T_2 = 0.5, 1$) using the JSTL model from a ten-sample-time study.*

	N=1000				N=100000			
	$T_2 = 1$		$T_2 = 0.5$		$T_2 = 1$		$T_2 = 0.5$	
	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

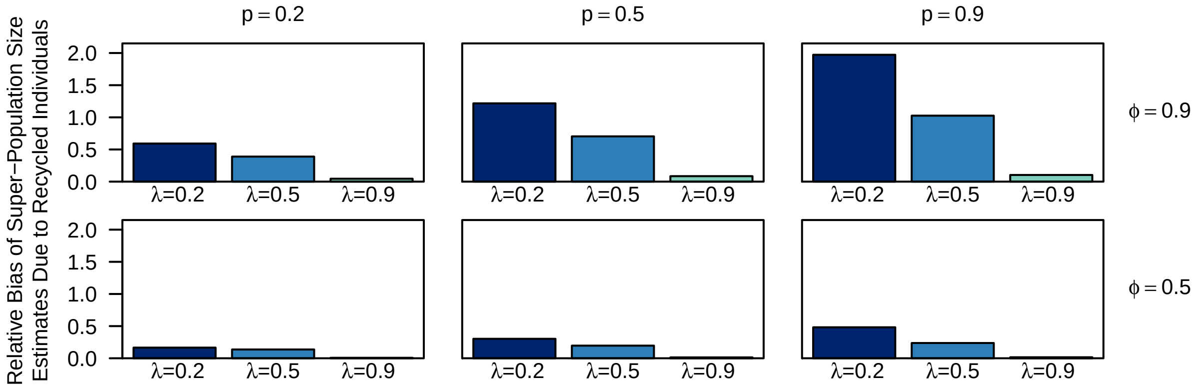

FIGURE 2: *The difference in mean relative bias of the super-population estimate ($\hat{N}$) between the model with and without the recycled individuals for simulated data with super-population size* $N = 100000$ *with 100% double-tagging for different tag retention probabilities* ($\lambda = 0.2, 0.5, 0.9$)*, survival probabilities* ($\phi = 0.5, 0.9$)*, and different capture probabilities* ($p = 0.2, 0.5, 0.9$) *using the JSTL model from a ten-sample-time study. .*

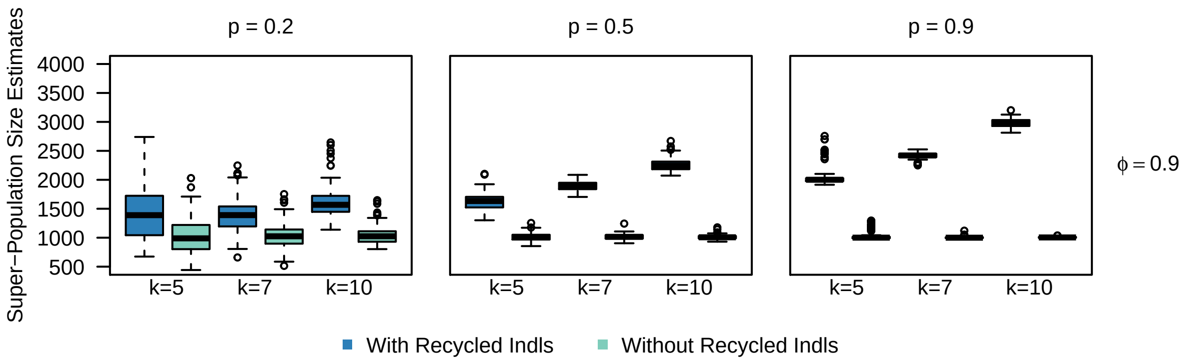

FIGURE 3: *Boxplots of the estimates of N for the model with and without the recycled individuals for simulated data with super-population size $N = 1000$ with 100% double-tagging for different capture probabilities ($p = 0.2, 0.5, 0.9$) and constant survival ($\phi = 0.9$) and tag retention probabilities ($\lambda = 0.2$) using the JSTL model from experiments with $k = 10, 7,$ and 5 sample-times.*

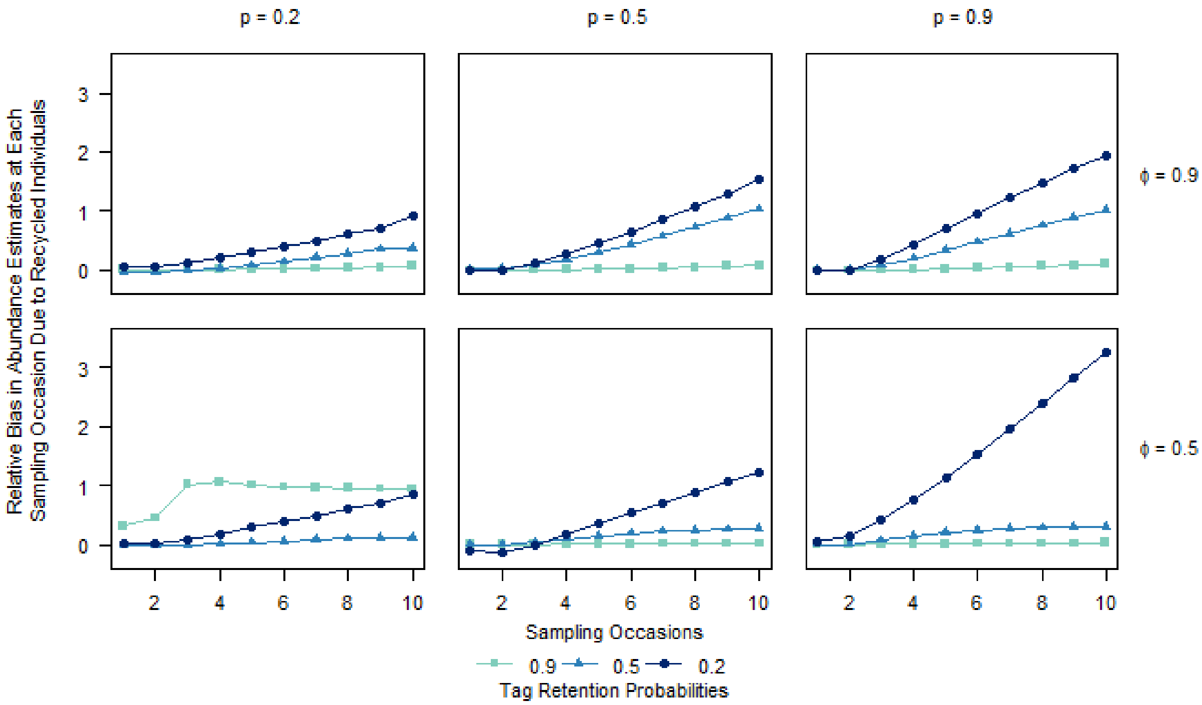

FIGURE 4: *The difference in mean relative bias of the abundance estimates at each time period ($\hat{N}_j$) between the model with and without the recycled individuals for simulated data with super-population size N=100 000 with 100% double-tagging for different tag retention probabilities ($\lambda = 0.2, 0.5, 0.9$), survival probabilities ($\phi = 0.5, 0.9$), 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.*