The Jolly-Seber-Tag-Loss Model with Group Heterogeneity

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Abstract: Mark-recapture experiments are performed to estimate population parameters such as survival probabilities. Animals are captured, tagged, released, and recaptured at subsequent time periods in order to obtain parameter information. The Jolly-Seber-Tag-Loss (JSTL) model (Cowen & Schwarz, 2006) requires some individuals to be double tagged in order to account for the possibility of animals losing their tags. The Jolly-Seber-Tag-Loss model does not, however, consider the possibility of parameters being different among different groups of individuals, that is, group heterogeneity (for example, males may have higher capture probabilities than females). Our research extends the Jolly-Seber-Tag-Loss model to account for this possibility of group heterogeneity among parameters. We use a Newton-Raphson method to obtain maximum likelihood estimators and R software to create a program that estimates population parameters from tag histories. Our simulation study concludes that when group heterogeneity exists, accounting for this group heterogeneity results in more accurate parameter estimates than the original JSTL model. We present the group heterogeneous JSTL (g-hJSTL) for this purpose.

Key Terms: capture-recapture, tag loss, Jolly-Seber, heterogeneity, double tagging

Introduction

Mark-recapture experiments are designed to study animal populations and, in particular, to estimate their parameters, such as survival rates. Early tagging studies of waterfowl resulted in the development of the Lincoln-Peterson estimator used to estimate population size. Limitations of the Lincoln-Peterson estimator led to the development of models that dealt with studies with multiple sample times, dealt with death and immigration, and allowed for flexibility in model parameters (e.g. survival varying over time or age) (Cormack, 1964; Jolly, 1965; Seber 1965). In these studies, animals are marked with unique tags, released, and recaptured at discrete sampling times (Williams, Nichols, & Conroy, 2002). If tags are lost during such experiments, bias may occur in parameter estimates. Cowen and Schwarz (2006) developed the Jolly-Seber-Tag-Loss (JSTL) model to account for the possibility of tag loss, using double tagging experiments in open populations.

One of the important assumptions of the JSTL model is that there is a single population group; that is, all the population parameters are homogeneous across all individuals of the population. The limitations of the JSTL model are thus particularly significant when different population groups (for example, males and females) are heterogeneous in terms of their parameters. Otis, Burnham, White, and Anderson (1978) discuss statistical inference of biological hypotheses such as capture heterogeneity. Here, they found that mice that had been caught one or more times were "trap happy," thus the assumption of homogeneity among capture probabilities was violated, and so behaviour of the animals amounts to heterogeneity in population capture rates. The same is true for different groups of animals within a population, where, for example, females are more trap happy than males (for example, Chinook salmon in Cowen et al. (2007)). We extend the JSTL model to allow for heterogeneity of

parameters across multiple population groups. The group-heterogeneous JSTL (g-hJSTL) model allows for more accurate parameter estimation when these parameters vary across groups. These model improvements will benefit researchers for whom high precision regarding population information is essential. For example, if a disease affects only one gender of a species, it would be very important to be able to observe that gender's survival rates and other attributes vis-à-vis the other gender's parallel attributes.

Experimental Design

The study design is comparable to that outlined by Williams, Nichols, and Conroy (2002) and by Lebreton, Burnham, Clobert, and Anderson (1992). Briefly, animals are captured at an initial sample time, marked (some with single tags and some with double tags), released, and recaptured at subsequent sampling times. Untagged individuals may be captured, tagged, and released at any sampling time. The primary study area is chosen to cover most of the population's range, and sampling times cover the whole period of interest. Furthermore, the population group to which each observed animal belongs is identified and recorded.

Data are in the form of tag histories, a series of 1s and 0s, where a 1 indicates the tag was observed on a particular animal and a 0 indicates otherwise. For example, in a four-sample-time experiment, the tag history for a double-tagged individual with no tag loss, that is, captured only at the first and at the last sample times (but not in either the second or third sample time), is {11 00 00 11}. For a single-tagged individual with the same capture history and tag loss, the tag history would be {10 00 00 10}; the double identifier helps specify individual tags. An example of a double-tagged individual who loses a tag after the second sample time is {11 11 01 01}. Different tag histories may correspond to the same capture history. The capture history of an animal records a 1 for those sample times when the animal was observed and a 0 otherwise. Capture histories can be produced from the tag histories, but not vice versa. Finally, the number of animals with the same tag history and their group membership is required. Table 1 shows an example of data from a four-sample time experiment.

Table 1: Sample Input Data: An example of data from a four-sample-time experiment including the tag and capture histories, the number of animals observed with each history (frequency), and an indicator variable for group membership when there are two possible groups.

Tag History	Capture History	Frequency	Group
11 11 11 11	1 1 1 1	12	1
10 00 10 00	1 0 1 0	107	2
00 00 01 01	0 0 1 1	119	2
11 01 00 01	1 1 0 1	28	1
11 11 00 10	1 1 0 1	82	1
11 01 00 00	1 1 0 0	97	2
⋮	⋮	⋮	⋮

Model

Model Design

The model is based on the proposal made by Schwarz and Arnason (1996) to consider a super-population, which includes all individuals that enter the population of interest during the experiment. We extend this model to more than one group by assuming G independent super-populations, where the super-population of N_g animals is assumed to enter the population through a multinomial distribution.

Model Assumptions

Important assumptions of this model are similar to those described by McDonald et al. (2003) but are modified to incorporate tag loss and heterogeneity of parameters across groups. They are outlined as follows:

- All animals in population group g enter the system between sample times j and j+1 with equal probability, but entry probabilities may vary across groups and/or across sample times.
- All animals in population group g are captured at sample time j with equal probability, but capture probabilities may vary across groups and/or sample times.
- All animals in population group g survive between sample times j and j+1 with equal probability, but survival probabilities may vary across groups and/or sample times.
- All animals in population group g that were first captured at sample time f retain their tag(s) between sample times j and $j+1$ with equal probability, but tag-retention probabilities may vary across groups and/or sample times.
- For double-tagged individuals, tag loss is independent between tags, and both tags have the same probability of being lost.
- Individuals who lose all their tags and are recaptured are either recognized when recaptured, or there are so few of these that even if they are mistaken as new individuals, they will have a small effect on overall estimates.
- The survival probabilities of any animal are independent of whether or not that animal has been previously captured.
- There is independence across animals and across groups of animals.
- Sampling occurs instantaneously. In practice, sampling occurs over a short period of time (a day for example) compared with the intervening sampling time (every month for example). This is a standard assumption for the Jolly-Seber type models as it discretizes the problem, simplifying the modelling process.

Notation

Statistics:

k number of sample times for the experiment

m number of unique tag histories

G number of population groups

i index for a tag history; $i = 0, 1, …, m$; $i = 0$ represents tag history for animals never caught, {00 00 … 00}

$nt_{g,j}$ number of tags on the individual i in group g at sample time j, $j = 1, 2, …, k$

$n_{g,j}$ number of individuals in group g captured at time j

n_{obs_g} total number of animals in group g observed during the experiment

$\boldsymbol{\omega_{gi}}^\star$ capture history vector $\boldsymbol{\omega_{gi}}^\star = (\omega_{gi1}^\star, \omega_{gi2}^\star, …, \omega_{gik}^\star)$, where

$$\omega_{gij}^{\square} = \begin{cases} 1 & \text{if individual } i \text{ from group } g \text{ was captured for the first time at sample time } j = f_i; \\ 1 & \text{if individual } i \text{ from group } g \text{ was captured at sample time } j > f_i \\ & \text{with at least one tag present;} \\ 0 & \text{if individual } i \text{ from group } g \text{ was not captured at sample time } j. \end{cases}$$

$\boldsymbol{\omega_{gi}}$ tag history vector $\omega_{gi} = (\omega_{g,i,1,1}, \omega_{g,i,1,2}, \omega_{g,i,2,1}, \omega_{g,i,2,2}, …, \omega_{g,i,k,2})$, $i = 0, 1, …, m$, where

$$\omega_{gijd} = \begin{cases} 1 & \text{if individual } i \text{ from group } g \text{ was captured and tag } d \text{ was present at time } j; \\ 0 & \text{if individual } i \text{ from group } g \text{ was captured at sample time } j \text{ without tag } d \text{ present;} \\ 0 & \text{if individual } i \text{ from group } g \text{ was not captured at sample time } j. \end{cases}$$

Referring to Table 1 for an example, we look at the fourth entry of the table. The individuals are from group $g = 2$, thus for each individual i which was observed with this tag history, we have the following capture history: $\boldsymbol{\omega_{2i}}^\star = (\omega_{2i1}^\star=1, \omega_{2i2}^\star=1, \omega_{2i3}^\star=0, \omega_{2i4}^\star=1)$, which is written in Table 1 as {1 1 0 1}. The tag history {11 01 00 01} in Table 1 is as follows:

$$\boldsymbol{\omega_{2i}} = (\omega_{2,i,1,1}=1, \omega_{2,i,1,2}=1, \omega_{2,i,2,1}=0, \omega_{2,i,2,2}=1, \omega_{2,i,3,1}=0, \omega_{2,i,3,2}=0, \omega_{2,i,4,1}=0, \omega_{2,i,4,2}=1).$$

$n_{\omega_{gi}}$ number of ω_{gi} tag histories

f_{gi} first sample time where $\omega_{gij}^\star = 1$

l_{gi} last sample time where $\omega_{gij}^\star = 1$

l_{gid} last sample time where tag d was present

q_{gid} first sample time where tag d was known to be missing for individual i in

group g; for example, for history {11 00 00 01}, q_{111} = 4 because tag 1 is not known to be missing

at sample time 2 or at sample time 3

Parameters:

$p_{g,j}$ the probability that an individual in group g is captured at sample time j, given the

individual is alive at that time, j = 1, 2, …, k

$\phi_{g,j}$ the probability that an individual in group g survives and remains in the population

between sample times j and $j+1$, given that it was alive and in the population at time j,

j = 2, 3, …, $k-1$

$b_{g,j}$ the probability that an individual in group g enters the system between sample

times j and $j+1$, j = 0, 1, …, $k-1$. Note that $b_{g,0}$ is the expected fraction of animals in group g alive

just prior to the first sample time and that $\sum_{j=0}^{k-1} b_{g,j} = 1.$

$\Lambda_{g,f_{gi},j}$ the probability that an individual in group g first tagged at sample time f_{gi} retains its tag

between sample times j and $j+1$ given that it is alive

N_g super-population size for group g (all individuals in group g that ever enter the population of

interest during the study)

Functions of Parameters:

$b^{\star}_{g,j}$ the expected fraction of the population in group g remaining to enter the

population that enters between sample times j and $j+1$, j = 0, 1, … , $k-1$. Note that this function is

defined as follows:

$$b^{\star}_{g,j} = \begin{cases} b_{g,0} & \text{if} \quad j = 0 \\[2mm] \dfrac{b_{g,j}}{\sum_{u=j}^{k-1} b_{g,u}} & \text{if} \quad j = 1, \ldots, k-2 \\[2mm] 1 & \text{if} \quad j = k-1 \end{cases}$$

$$\chi_{(g,f_{gi},l_{gi},nt)}$$

The probability that individual *i* in group *g*, first seen at f_{gi}, is not seen after sample time l_{gi} with *nt* tags.

This χ function is a recursive function of ϕ, *p*, and Λ. If $f_{gi} = 0$, this indicates individual *i* in group *g* has not yet been captured but is alive at time l_{gi}.

$$\chi_{(g,0,j,0)} = \begin{cases} 1 - \phi_{g,j} + \phi_{g,j}(1 - p_{g,j+1})\chi_{(g,f_{gi},j+1,0)} & \text{if } j < k \\[2mm] 1 & \text{if } j = k \end{cases}$$

$$\chi_{(g,f_{gi},j,1)} = \begin{cases} 1 - \phi_{g,j} + \phi_{g,j}(1 - p_{g,j+1})\Lambda_{g,f_{gi},j}(1 - \Lambda_{g,f_{gi},j})\chi_{(g,f_{gi},j+1,1)} \\ \quad + \phi_{g,j}(1 - \Lambda_{g,f_{gi},j}) \qquad\qquad\qquad \text{if } j < k \\[2mm] 1 \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{if } j = k \end{cases}$$

$$\chi_{(g,f_{gi},j,2)} = \begin{cases} 1 - \phi_{g,j} + \phi_{g,j}(1 - p_{g,j+1})\Lambda^2_{g,f_{gi},j}\chi_{(g,f_{gi},j+1,2)} \\ \quad + 2\phi_{g,j}(1 - p_{g,j+1})\Lambda_{g,f_{gi},j}(1 - \Lambda_{g,f_{gi},j})\chi_{(g,f_{gi},j+1,1)} \\ \quad + \phi_{g,j}(1 - \Lambda_{g,f_{gi},j})^2 \qquad\qquad\qquad\qquad \text{if } j < k \\[2mm] 1 \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\quad \text{if } j = k \end{cases}$$

$\Psi_{g,j}$ the probability that an individual enters the population, is alive and is not seen before time *j*; *j = 1, 2, …, k.*

$$\Psi_{g,1} = b_{g,0}, \quad \text{and} \quad \Psi_{g,j+1} = \Psi_{g,j}(1 - p_{g,j})\phi_{g,j} + b_{g,j}$$

$B_{g,j}$ the number of individuals in group *g* who enter the population after sample time *j* and survive to sample time *j+1*; *j = 0, 1, …, k-1*. $B_{g,0}$ is the number of individuals alive just before

the first sample time. $E[B_{g,j}|N_g] = N_g b_{g,j}$.

$N_{g,j}$ total population size for group g at time j. Note that

$$N_{g,j} = \begin{cases} N_g b_0 & \text{if} \quad j = 1 \\ N_{g,j-1}\phi_{g,j-1} + N_g b_{g,j-1} & \text{if} \quad j = 2, \ldots, k. \end{cases}$$

Likelihood Development

Using a similar approach to Cowen and Schwarz (2006), we partition the likelihood by group as follows. The first part of the likelihood models the number of observed tag histories in group g as

$$L_{1,g}^A = [n_{obs_g}|N_g] \sim \text{Binomial}(N_g, 1 - P_{0_g})$$

where

$$P_{0_g} = \sum_{j=0}^{k-1} b_{g,j} \left(1 - p_{g,j+1}\right) \chi_{(g,0,j+1,0)}$$

and   .

$$n_{obs_g} = \sum_{i=1}^{m} n_{\omega_{gi}}$$

Here, $1 - P_{0_g}$ is the probability that a group g member is observed. The second part of the likelihood models the number of observed tag histories in each group conditional on being seen as

$$L_{1_g}^B = [\{n_{\omega_{gi}}\}|n_{obs_g}] \sim \text{Multinomial}\left(n_{obs_g}, \{\pi_{\omega_{gi}}\}\right)$$

where

$$\pi_{\omega_{gi}} = \frac{P(\omega_{gi})}{(1 - P_{0_g})}$$

and

$$P(\omega_{gi}) = \Psi_{g,f_{gi}} \left\{ \prod_{j=f_{gi}}^{l_{gi}} p_{g,j}^{\omega^\star_{gij}} (1 - p_{g,j})^{(1-\omega^\star_{gij})} \right\} \times \left\{ \prod_{j=f_{gi}}^{l_{gi}-1} \phi_{g,j} \right\}$$

$$\times \prod_{d=1}^{2} \left\{ \left(\prod_{j=f_{gi}}^{l_{gid}-1} \Lambda_{g,f_{gi},j} \right) \left(1 - \prod_{j=l_{gid}}^{q_{gid}-1} \Lambda_{g,f_{gi},j} \right)^{I(l_{gid} \neq l_{gi})} \right\}$$

$$\times \mathcal{X}_{(g,f_{gi},l_{gi},nt_{lgi})}$$

The complete likelihood for the model, therefore, is the product over all groups:

$$L = \prod_{g=1}^{G} L_{1,g}^{A} \times L_{1,g}^{B}$$

Note that in this model development, we have not included the possibility of loss on capture; this could also be developed following Cowen and Schwarz (2006) or Schwarz and Arnason (1996).

Parameter Estimation

We use a Newton-Raphson type estimator for estimating the model's parameters. Similar to Lebreton et al. (1992), we use a logit-link function (because it constrains the probabilities between 0 and 1) to transform the unknown probabilities $p_{g,j}$, $\phi_{g,j}$, $b^\star_{g,j}$ and $\Lambda_{g,f_{gi},j}$ to a reduced parameter set of β-parameters, and design matrices are used with this reduced parameter set to implement different, flexible models (for example, one design could have all parameters constant across sample times but varied across groups; another design may have all parameters varying across sample times and across groups).

The parameters are modeled as logistic regressions on appropriate covariates; for example,

$$logit(\phi_{g,j}) = ln\left(\frac{\phi_{g,j}}{1-\phi_{g,j}}\right) = X_{ij}^{\phi}\beta^{\phi}$$

where *X* is the appropriate design matrix. The delta method is used to compute standard error estimates for the standard (p, ϕ, $b^\star$, and Λ) parameters. Note that the $b^\star$s are used in place of the b parameters because the former do not have the difficult constraint of the latter of adding up to 1 within a group. R 2.11.0 (R Development Core Team, 2009) was used in developing a program to obtain these results and is available from the authors.

We estimate the group *g* super-population size N_g as $\hat{N}_g = \frac{n_{obs_g}}{1-P_{0_g}}$. Using this estimated super-population size, we are able to estimate $N_{g,j}$ – the size of group *g* population at sample time *j* – using the formulae described above when we defined $N_{g,j}$ and replacing parameters with their estimates.

Goodness-of-fit

In testing the goodness-of-fit for a particular model, we calculate the log-likelihood, conditional on being observed,

$$l_{obs} = \sum_{g=1}^{G} \sum_{d=1}^{2} \sum_{j=1}^{k} l^* + ln(P(d|g,j)) + ln(P(g|j)) - ln(1 - P_{0_g})$$

where l^* is the log-likelihood for the model of interest. For each group and each sample time, we

calculate the probability that an individual is double tagged (versus single tagged) upon release, given

that it is in a particular group ($P(d|g,j)$). We then adjust the probability of occurrence for each tag

history for each group ($P(g|j)$). We then normalize the adjusted tag history probabilities by the

probability of being observed at any time during the experiment ($1 - P_{0g}$). Thus we obtain the fitted

model. We also calculate the log-likelihood for the saturated model, which has a multinomial

distribution for each group. Every tag history ω_{gi} in the multinomial distribution has probability

$n_{\omega_{gi}} / n_{obs_g}$. The test statistic is the difference between the conditional log-likelihood and the saturated

log-likelihood; it has a χ^2 distribution asymptotically. The degrees of freedom for this statistic are

calculated as the difference in the number of parameters for each model. The saturated model has

$\sum_{g=1}^{G} (n_{obs_g} - 1)$ parameters. The number of parameters for the conditional log-likelihood includes

catchability, survival, new entrants, and tag retention parameters plus (G x k) parameters for the double

tagging probabilities ($P(d|g,j)$), plus $k(G-1)$ parameters for the group membership ($P(g|j)$) probabilities.

Following Burnham and Anderson (2002), a variance expansion factor may be determined from

the goodness-of-fit statistic if overdispersion is deemed present.

Model Selection

Model design possibilities vary extensively for different sets of parameters. In accordance with the design specifications described by Lebreton et al. (1992), tag retention parameters may vary across release groups, any parameter may vary across sample times, and any or all parameters may vary across population groups. These different sets of parameters allow for extensive variability of model designs.

We follow Burnham and Anderson (2002) in applying the Akaike information criterion for model selection.

Simulation Study

In testing our g-hJSTL model, we generated a number of different datasets of various different population sizes and different parameter sets. Using notation akin to that of Lebreton et al. (1992), the following are some of the different designs we generated and estimated using our g-hJSTL model (and compared with the estimates of the JSTL model).

$b_i^\star p \phi \Lambda$ $\qquad$ = entry varies over time, but capture, survival, and tag retention are constant over time; no group heterogeneity.

$b_i^\star p_g \phi_g \Lambda_g$ $\qquad$ = entry varies over time but not across groups; capture, survival, and tag retention vary across groups but are constant across time.

$b_i^\star p_{g,t} \phi_{g,t} \Lambda_{g,t}$ = entry varies over time but not over groups; capture, survival, and tag retention vary across groups and over time.

For the more complicated models, we must take care to deal with non-identifiability of certain parameters. For instance, only the products $\phi_{k-1} p_k$ can be estimated. These parameters cannot be estimated individually. Similarly, $b_0 p_1$ can be estimated only as a product.

Table 2 shows the results for one dataset using the g-hJSTL model and also using the JSTL model for the model $b_i^\star p_g \phi_g \Lambda_g$. Percent bias of the estimates is calculated as $\frac{(\hat\theta - \theta)}{\theta} \times 100\%$.

Table 2: Simulation results to compare the JSTL model with and without group heterogeneity (g-hJSTL). Actual parameter values, parameter estimates (estimated standard errors) from the two models, and percent bias of the estimates are provided.

	Actual values	g-hJSTL model estimates	JSTL model estimates	Percent Bias: g-hJSTL model (%)	Percent Bias: JSTL model (%)
p	0.75	0.72 (0.03)	0.84 (0.02)	−4.00	12.00
	0.90	0.91 (0.01)		1.11	−6.67
ϕ	0.80	0.82 (0.04)	0.72 (0.02)	2.50	−10.00
	0.70	0.70 (0.01)		0.00	2.86
Λ	0.70	0.69 (0.02)	0.83 (0.01)	−1.42	18.57
	0.90	0.91 (0.01)		1.11	− 0.08
$b\ast$	0.200	0.20 (0.005)	0.20 (0.005)	0.00	0.00
	0.375	0.36 (0.007)	0.36 (0.006)	−2.93	−3.20
	1.000	1.00 (0.000)	1.00 (0.000)	0.00	0.00

The simulation dataset used to produce the estimation results tabulated in Table 2 included 10,000 individuals in the population, with 5,000 individuals in each of two groups in the population. Table 3 shows each $\hat{N}_{gj}$, which estimates the number of group *g* individuals in the entire population (observed and unobserved) at sample time *j*. Results show that these estimates are reasonably close to the actual total population numbers. Table 4 shows results calculated using the standard JSTL model. The super-population size is estimated ($\hat{N}$), and then the population size at each sample time *j* is calculated ($\hat{N}_j$). Results show that percent bias is smaller for all population-size related estimates when using the g-hJSTL model compared with the JSTL model.

Table 3: The g-hJSTL model estimates of number of group *g* individuals in population at sample time *j*, $\hat{N}_{gj}$. Actual group *g* super-population size *(N_g)*, estimated group *g* population size ($\hat{N}_g$), and percent bias of estimates are shown.

$\hat{N}_{gj}$	Sample Time			$\hat{N}_g$	N_g	Percent Bias (%)
	j = 1	*j* = 2	*j* = 3			
g = 1	1,014.86	2,334.30	4,542.92	5,137.05	5,000	2.74
g = 2	982.22	2,134.80	4,042.03	4,971.82	5,000	−0.56
Total	1,997.08	4,469.10	8,566.94	10,108.87	10,000	1.09

Table 4: The JSTL model estimates of number of individuals in population and sample time *j*. Actual super-population size (*N*), estimated population size ($\hat{N}$), and percent bias of estimates are shown.

	Sample Time			$\hat{N}$	N	Percent Bias (%)
	j = 1	*j* = 2	*j* = 3			
$\hat{N}_j$	1,815.33	4,034.71	7,679.94	9325.73	10,000	−6.74

Discussion

Heterogeneity often causes over-dispersion in data. For example, males in a population behaving differently than females would cause more variability in the data than a model ignoring sex differences accounts for; this extra variability is termed over-dispersion. Over-dispersion can be estimated, and estimated standard errors can be adjusted for over-dispersion; however, a more satisfactory approach would be to incorporate the source of over-dispersion directly in the model. One source of heterogeneity is the difference in behaviour of various groups.

By allowing parameters in the JSTL model to vary by group, we have extended the JSTL model to account for differences in group membership. Accounting for group heterogeneity, when it exists, improves the accuracy of parameter estimates. As observed in Table 2, percent bias is notably lower for the g-hJSTL model compared with the JSTL model. Similarly, derived estimates of population size are more accurate. These findings were confirmed with multiple simulated datasets.

Future applied work will involve using our group-heterogeneous JSTL model with real population data and estimating the population parameters using different model designs. Model selection will be determined using the Akaike Information Criterion. Further, we could extend our model to account for loss on capture (due to a fishery harvest for example), similar to Cowen and Schwarz (2006) and Schwarz and Arnason (1996). We could also relax the assumption of independent tag loss; that is, we could take into consideration the possibility that one tag's retention rate depends on the other tag's retention rate for double-tagged animals. For instance, tag loss may be due to a particular aspect of the individual – such as higher mobility leading to higher probability of tag loss – in which case, loss of one tag may suggest a higher probability of loss of a second tag as is the case with southern elephant seals (Pistorius, Bester, Kirkman, and Boveng, 2000). Finally, we could extend the model to work with more than two tags (for example, include a possibility of triple tagging certain individuals).

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