



Tag loss can bias Jolly-Seber capture–recapture estimates

Trent L. McDonald, Steven C. Amstrup, and Bryan F. J. Manly

Abstract We identified cases where the Jolly-Seber estimator of population size is biased under tag loss and tag-induced mortality by examining the mathematical arguments and performing computer simulations. We found that, except under certain tag-loss models and high sample sizes, the population size estimators (uncorrected for tag loss) are severely biased high when tag loss or tag-induced mortality occurs. Our findings verify that this misconception about effects of tag loss and tag-induced mortality could have serious consequences for field biologists interested in population size. Reiterating common sense, we encourage those engaged in capture–recapture studies to be careful and humane when handling animals during tagging, to use tags with high retention rates, to double-tag animals when possible, and to strive for the highest capture probabilities possible.

Key words capture–recapture, Cormack marking, Jolly-Seber, open populations, population size, resight, survival rates, tagging

Use of the Jolly-Seber (Jolly 1965, Seber 1965) capture–recapture estimator to estimate size of an open population is common, even though the Jolly-Seber procedure is not useful in all situations and more efficient (and complex) estimators have been derived. Furthermore, a large number of modern open-population capture–recapture analyses are based on the Jolly-Seber method and its parameterization (e.g., Lebreton et al. 1992). The well-known assumptions of the Jolly-Seber estimator (see e.g., Pollock et al. 1990) are that 1) all animals in the population at the time of capture occasion j are captured with equal probability, 2) all animals survive from capture occasion j to capture occasion $j + 1$ with equal probability, 3) the survival and capture of an animal is independent of the survival and capture of all other animals, 4) captured animals and previously uncaptured animals survive equally well, and 5) all tagged animals retain their tags and are correctly identified. While a violation of any

one of these assumptions will limit utility of the Jolly-Seber estimator, we have noticed a misconception among biologists and statisticians regarding the severity of consequences in violating tag-induced mortality and tag-loss assumptions (assumptions 4 and 5).

Regarding tag loss, Arnason and Mills (1981: 1081) stated in their results section, “When homogeneous tag loss occurs in a population subject to birth and death, the Jolly-Seber full model estimates have the following properties: $\dots \hat{N}_j$ is unbiased for N_j, \dots ” They reiterated this finding in their abstract by stating, “We show that \hat{N} , $SE(\hat{N})$, and $SE(\hat{\phi})$ are not biased by tag loss, while $\hat{\phi}$, \hat{B} , and $SE(\hat{B})$ are biased.” While Arnason and Mills’ (1981) assumption of homogeneous tag loss was clearly indicated in their sections 1 and 2, and even in their abstract, these statements apparently have been taken out of context and interpreted, without qualification, to mean that size estimates in Jolly-Seber type open-

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population models are not affected by unknown tag loss. In their comprehensive description of statistical inferences available for capture-recapture analysis, Pollock et al. (1990:26) asserted, "The result [of animals losing their tags] is underestimation of survival rates but no influence on population size estimates." Pollock et al. (1990:25) extrapolated this conclusion to tag-induced mortality when they reported, "If marking decreases the animal's survival rate, serious bias can occur to the survival rate estimators.... Population size estimators are still unbiased." These unqualified conclusions seemed unintuitive and unlikely to hold in all situations, and, if untrue, could lead wildlife biologists to infer a higher degree of accuracy in their population size estimates than may be justified. Some scientists to whom we have spoken, especially those in fisheries, seem to know that tag loss can cause problems for the Jolly-Seber estimator of population size (because double tagging is common), but this knowledge is not clearly reflected in the wildlife literature.

The above statements by Arnason and Mills (1981) should not be taken out of context and their results should not be oversimplified. Arnason and Mills (1981:1080) clearly stated, "In this paper, we allow tag loss but assume that it is homogeneous, at rate $1 - \theta_i$, over all tagged animals alive at time t^+ . This is still a fairly restrictive assumption. It requires that tag-loss rate not depend on age or size of the animal, nor on the length of time it has borne the tag (retention time)." Homogeneous tag loss also requires that animals drop their tags at random times after they are initially tagged. A close reading reveals, as well, that Arnason and Mills (1981) computed asymptotic biases using the methods of Carothers (1973), whereby they evaluated the expected values of statistics and unobservable random variables, conditional on an initial population size and birth rates. Further examination shows that their asymptotic estimate of 0 bias becomes more accurate as the expected number of captures, expected number of marked animals at each trap occasion, and the expected recaptures from each release cohort become large. The expected number of marked animals and expected number of recaptures from each release cohort increase when population size is large and when capture probabilities increase. Hence, for practical purposes, Arnason and Mills' (1981) results are correct when tag loss is homogeneous and when capture probabilities are high.

Even when capture-recapture studies meet all other assumptions of the Jolly-Seber method, many capture-recapture situations, including most large-mammal studies, do not meet the tag-loss assumptions of Arnason and Mills (1981). Many real-world capture-recapture studies have sighting or capture probabilities <50%, and sometimes <10% (Menkens and Anderson 1988, Bear et al. 1989, Lunn et al. 1997, Miller et al. 1997, Amstrup et al. 2001). Furthermore, many types of tags are lost immediately or soon after attachment, thus inducing a retention-time dependency in tag loss. Common sense dictates that tag loss and tag-induced mortality bias population size estimators when capture probabilities are low because fewer tags are at risk (available for recapture) in the population than the estimator believes. As an extreme example, suppose probability of capture was 10% and all animals lost their tags or died shortly after capture. In this example no tagged animals would be recaptured on subsequent occasions, and scientists conducting the study would have no choice but to conclude the population's size was very large because only "new" animals were observed.

We use 2 methods to correct the misconception that the Jolly-Seber size estimator is generally unbiased in situations where tag loss or tag-induced mortality occurs. First, we assume a realistic model for tag loss (and tag-induced mortality) and demonstrate effects of those losses on expected values of the estimators. We then derive a mathematical expression for relative bias in the size estimator. Second, we assume another model for tag loss and conduct a series of intuitive computer simulations to demonstrate that bias does occur when capture probabilities are low and tags are lost or tagging induces mortality.

Methods

Assume a capture-mark-recapture study has been conducted on an open population and k capture occasions were realized. Let n_j = total number of animals, marked plus unmarked, in the sample of animals at capture occasion j ($j = 1, 2, \dots, k$). Of the n_j , assume m_j of them were marked. Assume also that z_j animals were seen before occasion j , not seen at occasion j , and subsequently seen again after occasion j . Let s_j be the number of animals captured at occasion j that were returned alive to the population, and assume r_j of these s_j were resighted or captured sometime after occasion j . Under this notation, the Jolly-Seber (JS) estimator of

population size at trap occasion j is,

$$\hat{N}_j = \hat{M}_j n_j / m_j, \tag{1}$$

where

$$\hat{M}_j = (z_j s_j / r_j) + m_j. \tag{2}$$

for $j=2, \dots, k-1$ (Jolly 1965, Seber 1965, Pollock et al. 1990), and \hat{M}_j is an estimator for number of tags in the population at occasion j . Estimates of number of births and estimates of standard errors for \hat{N}_j are available but will not be considered here. We are only interested in documenting bias in the population size point estimator.

Tag-loss Model 1

Consider the population of N_j animals alive at time j . We model tag loss by splitting these N_j animals into 2 classes. Animals in 1 class always drop their tags immediately after initial release and all subsequent releases and will be called "tag losers." Animals in the other class always retain their tag and will be called "tag retainers." Assume further that the probability of 1 of the N_j animals being a tag loser is θ and, conversely, that the probability of 1 of the N_j being a tag retainer is $1-\theta$. The number of tag-losing animals in the population at time j is a binomial random variable with probability θ and expected value $N_j\theta$, provided the tag-losing or tag-retaining status of animals is independent of the status of other animals. Under these conditions, an animal must survive and be a tag retainer for that animal to be seen and identified after time j . The expected number of tag retainers in the population at occasion j is $(1-\theta)N_j$.

All tag losers and tag retainers alive at time j had the opportunity to be captured before, at, and after occasion j . Define α_{j-} to be the probability that one of the N_j animals alive at time j was seen before j . Define α_{j+} to be the probability that an animal alive at time j was seen after j , regardless of whether it was correctly identified. Here, the parameters α_{j-} are complex functions of survival and capture probabilities prior to time j . The parameters α_{j+} are complex functions of survival and capture probabilities after time j . Define p_j to be the probability of capture at time j and assume that all animals captured at time j were released alive (i.e., $n_j=s_j$). Under these mild definitions and assumptions, we can work out the expected values of all random variables in the JS estimator for N_j and derive an

approximate expression for bias.

First, we note the expected number of animals in the sample at time j is the probability of capture times the number of animals in the population,

$$E[n_j] = p_j N_j. \tag{3}$$

Second, we note that, to be included in the count z_j , an animal alive at time j must have been seen before time j , not seen at time j , seen after time j , and be a tag retainer. The expected value of z_j is then $\alpha_{j-}(1-p_j)\alpha_{j+}$ times the expected number of tag retainers in the population at time j , which is $(1-\theta)N_j$ so that

$$E[z_j] = \alpha_{j-}(1-p_j)\alpha_{j+}(1-\theta)N_j. \tag{4}$$

Third, we note the count r_j consists of tag-retaining animals seen at time j that were later recaptured. The expected value of r_j is, therefore, α_{j+} times the expected number of tag retainers captured at time j , i.e.,

$$E[r_j] = \alpha_{j+} p_j (1-\theta) N_j. \tag{5}$$

Finally, we note that, to be included in the count m_j , an animal must have been seen prior to time j and be a captured tag retainer. The expected value of m_j is therefore α_{j-} times the expected number of tag retainers captured at time j , i.e.,

$$E[m_j] = \alpha_{j-} p_j (1-\theta) N_j. \tag{6}$$

Using the fact that $E[ab] \cong E[a]E[b]$ and $E[a/b] \cong E[a]/E[b]$ for any random variables a and b , the approximate expected value of the JS estimator is

$$\begin{aligned} E[\hat{N}_j] &= E[\hat{M}_j n_j / m_j] \\ &= E\left[\frac{z_j n_j^2}{r_j m_j} \right] + E[n_j] \\ &\cong \frac{E[z_j]E[n_j^2]}{E[r_j]E[m_j]} + E[n_j] \\ &\cong \frac{(\alpha_{j-}(1-p_j)\alpha_{j+}(1-\theta)N_j)(p_j^2 N_j^2)}{(\alpha_{j+} p_j (1-\theta)N_j)(\alpha_{j-} p_j (1-\theta)N_j)} + p_j N_j \\ &\cong N_j \left(1 + (1-p_j) \frac{\theta}{1-\theta} \right). \tag{7} \end{aligned}$$

This expression for the expected value of \hat{N}_j implies that absolute bias in the JS estimator of

population size is approximately $N_j(1-p_j)(\theta/(1-\theta))$ when tag loss of the type we describe is occurring. The relative bias in \hat{N}_j is, therefore,

$$\text{relative bias}(\hat{N}_j) = \frac{E[\hat{N}_j] - N_j}{N_j} = (1-p_j) \frac{\theta}{1-\theta}. \quad (8)$$

This can be substantial. For example, if $p_j=0.1$ and $\theta=0.2$, then

$$\text{relative bias}(\hat{N}_j) = 0.9 \times \frac{0.2}{0.8} = 0.225. \quad (9)$$

Tag-loss Model 2

To investigate the bias in the JS estimator under a different tag-loss model, we conducted some simple computer simulations. Our Monte Carlo computer simulations investigated the bias of \hat{N}_j when a random fraction of captured animals lose their tags immediately after capture.

We conducted our simulations in 3 algorithmic steps. First, we constructed an artificial open population of animals such that survival probabilities, birth rates, and size at each trap occasion were known. Second, we sampled the artificial population with specified capture probabilities, and third, we computed the JS estimators \hat{N}_j . We repeated the second and third steps 500 times to assess bias. Each step in the simulation is described below.

To construct an open population of animals, we specified an initial number of animals in the population, true survival probabilities, and true birth rates. To satisfy assumptions of the JS model, survival rates between occasion j and $j+1$ (i.e., ϕ_j) were constant for all animals alive at time j but potentially varied across occasions (i.e., $\phi_j \neq \phi_{j+1}$). Given an initial number of animals in the population and all survival probabilities ϕ_j ($j=1, 2, \dots, k-1$), we generated a Bernoulli random variable with probability of success equal to ϕ_j for every animal alive at time j . If the outcome of the Bernoulli trial was 1 (“success”), the animal survived from time j to time $j+1$. The animal died during the interval of time between j and $j+1$ if the outcome of the Bernoulli trial was 0 (“failure”). To facilitate simulation of population growth or decline, we added animals to the population just prior to each occasion. The number of animals added prior to each occasion was controlled by birth rates. Assuming N_j animals were alive at occasion j and b_j was the birth rate for occasion j ($0 \leq b_j \leq 1$, $j = 1, 2, \dots, k-1$), we added $N_j b_j$ animals to the population just prior to

occasion $j+1$. Birth and immigration were not differentiated. The end result was a list of individual animals alive at each trap occasion. We computed the true number of animals in the population by adding up the number alive at each trap occasion.

We specified equal probabilities of capture for all animals alive in the population at a specified sampling occasion as part of the simulation. Equal probabilities of capture satisfied the within-occasion homogeneity assumption of the JS model. If an animal died sometime before trap occasion j , its true probability of capture at occasion j was zero. Given true probabilities of capture, p_j ($j=1, 2, \dots, k$), we generated a Bernoulli random variable with probability of success equal to p_j for each animal alive at occasion j . If the outcome of the Bernoulli random variable was 1 (“success”), the animal was captured at occasion j , otherwise (“failure”), the animal was not captured at occasion j . We released all captured animals alive back into the system (i.e., no deaths upon capture were simulated). The end result was a list of random capture histories, I_{ij} , equaling ‘1’ if animal i was captured at occasion j , and ‘0’ otherwise.

We simulated a predetermined amount of tag loss in the artificial population by deleting all captures after the initial one from a random fraction of the generated capture histories. We placed any captures that were deleted after initial tagging in a new capture history (with zeros appended on the front) and added them to the list of generated capture histories. This procedure mimicked real situations where an animal loses its tag after its initial capture and appears later as an unmarked or new animal. The animal was assumed to retain its second tag.

As an example of the procedure that imposed tag loss, suppose we generated 100 capture histories from a fluctuating population that was not experiencing tag loss, and that 20% tag loss was to be imparted upon the set of realized capture histories. In this situation, $20=100(0.2)$ capture histories were chosen at random from the generated histories and the animals associated with these histories were forced to “lose” their tags. Suppose 2 of the randomly chosen capture histories were ‘0100101’ and ‘0010000’. To force the animals associated with these histories to lose their tags, the first history was changed into 2 histories, ‘0100000’ and ‘0000101’, while the other history remained unchanged as ‘0010000’ because this animal was never seen after its first encounter.

After we imposed tag loss upon the generated capture histories, we computed the JS estimator of

population size at time j for all occasions where it was possible. As usual, due to conditioning of the JS likelihood upon first captures and confounding of parameters, JS estimates of population size were not available for the first and last capture occasions.

We repeated simulated sampling of artificial populations 500 times. The 500 resulting estimates of \hat{N}_j were then averaged separately for each value of j and compared to true population sizes, N_j . We calculated bias of the estimators as,

$$\text{bias}(\hat{N}_j) = \sum_{i=1}^{500} (\hat{N}_j - N_j) / 500. \quad (10)$$

We conducted 2 basic sets of simulations. We ran one set of 54 simulations (9 levels of p_j times 6 tag-loss proportions, and 500 iterations each) with a relatively constant population size of 500 individuals, $k=10$ occasions, tag-loss proportions equal to 0, 0.1, 0.2, 0.3, 0.4, and 0.5, and probabilities of capture equal to 0.1, 0.2, ..., 0.9. During these 54 simulations, true probability of survival was $\phi_j=0.9$ (for $j=1, 2, \dots, 9$) and birth rates were $b_j=0.1$ (for $j=1, 2, \dots, 9$). Probability of capture was constant across occasions within a simulation (i.e., $p_j=p_j$ in each simulation).

We conducted another set of simulations to investigate bias of \hat{N}_j when the true population size and capture probability varied during the course of a study. During this set of 6 simulations (1 for each tag loss proportion), $k=10$ and survival probabilities were set to $\phi_1=1, \phi_2=1, \phi_3=1, \phi_4=1, \phi_5=0.9, \phi_6=0.85, \phi_7=0.8, \phi_8=0.75$, and $\phi_9=0.70$. Birth rates were $b_1=0.1, b_2=0.1, b_3=0.1, b_4=0.1, b_5=0.05, b_6=0.05, b_7=0.05, b_8=0.05$, and $b_9=0.05$. This resulted in true population size increasing from 500 individuals at occasion 1 to 731 individuals at occasion 5, and then decreasing to 284 individuals at occasion 10. Probabilities of capture were set to $p_1=0.1, p_2=0.1, p_3=0.2, p_4=0.2, p_5=0.3, p_6=0.3, p_7=0.5, p_8=0.5, p_9=1.0$, and $p_{10}=1.0$. We again set the proportion of lost tags to 0, 0.1, 0.2, 0.3, 0.4, and 0.5. The computer simulation was written in the S-Plus (version 2000) computer language (Table 1).

Tag-induced mortality

In the same way that we derived a bias estimate under our first tag-loss model, we can also derive a bias estimate when the process of catching and tagging an animal imparts additional mortality that researchers do not know about. To do so, we make the same assumptions that we did under our first

tag-loss model. In particular, we assume that 2 classes of animals are in the population. One class dies with probability 1 immediately after tagging. These animals are defined to be "diers." The other class lives with probability 1 after they are tagged and are defined to be "survivors." The population alive at time j consists solely of previously uncaught diers, plus survivors. We redefine θ of the previous section to be the probability that, unbeknownst to the researcher(s), a newly marked animal dies immediately after capture at occasion j .

Under these assumptions, $E[n_j]=p_j N_j$ as before, but

$$E[z_j] = \alpha_{j-}(1 - p_j)\alpha_{j+}N_j \quad (11)$$

because to be included in z_j , an animal must have been tagged before j . If an animal was tagged before j and has the possibility of being caught after j , it must have been a survivor. Thus, only survivors can contribute to z_j .

Under tag-induced mortality, the count r_j consists of survivors that have been seen at and after j . Any diers caught at j die and do not have a chance to be included in r_j . The expected value of r_j is therefore

$$E[r_j] = [\alpha_{j-} p_j \alpha_{j+} + (1 - \alpha_{j-}) p_j \alpha_{j+} (1 - \theta)] N_j. \quad (12)$$

The expected number of marks in the sample at time j is equal to the number of animals alive at time j , times the probability of being seen before, living, and being seen at time j . Thus,

$$E[m_j] = \alpha_{j-} p_j N_j. \quad (13)$$

The approximate bias of \hat{N}_j when unknown tag-induced mortality is taking place is

$$\begin{aligned} E[\hat{N}_j] &\cong \frac{E[z_j]E[n_j^2]}{E[r_j]E[m_j]} + E[n_j] \\ &\cong \frac{(\alpha_{j-}(1 - p_j)\alpha_{j+}N_j)(p_j^2N_j^2)}{(\alpha_{j+}p_j[\alpha_{j-} + (1 - \alpha_{j-})(1 - \theta)]N_j)(\alpha_{j-}p_jN_j)} \\ &\quad + p_j N_j \cong N_j \left(1 + (1 - p_j) \frac{\theta(1 - \alpha_{j-})}{1 - [\theta(1 - \alpha_{j-})]} \right). \quad (14) \end{aligned}$$

Results

Inspection of our mathematical expression for relative bias under our first model for tag loss (Eq. 8) reveals that bias in the JS estimator is positive

(i.e., an overestimate) because $(1 - p_j)(\theta / (1 - \theta))$ is >0 , whether tag loss is occurring or not. Regardless of tag loss, the JS estimator becomes less biased as capture probabilities increase. In order for the bias in \hat{N}_j to remain constant as θ increases, probability of capture must increase (Fig. 1). For example, when $\theta = 0.12$ and $p_j = 0.20$ bias is approximately 10%, but when θ increases to 0.20, p_j must increase to 0.78 in order for bias to remain 10%. Bias can become large ($>60\%$) when the proportion of tag losers in the population is $>50\%$ and $p_j < 0.5$ (Fig. 1).

Under the second tag-loss model implemented in our simulations, the JS estimator also was biased. When simulated population sizes were nearly constant at 500 ± 5 individuals for $k = 10$ capture occasions, and survival was 0.9 for each interval between capture occasions, the JS size estimator, \hat{N}_j , was biased by $>8\%$ when capture probabilities were $<30\%$ and tag loss was $>20\%$ (Fig. 2). With $p_j = 0.1$, the bias of \hat{N}_j was 17% without tag loss and reached 100% with 50% tag loss. When $p_j > 0.5$, the bias of \hat{N}_j was not substantial (bias $<8\%$) for any amount of tag loss (Fig. 2).

Bias of \hat{N}_j did not appear related to whether or not true population size varied over the course of the study. During the second set of simulations, when true population increased from 500 to 731 and then decreased to 284, the bias of \hat{N}_j was appreciable (bias $\geq 6\%$) when probability of capture was <0.5 and tag loss was >0.3 (Fig. 3). Bias became larger for smaller proportions of tag loss when probability of capture was low (Fig. 3).

It is clear from Equation 14 that the bias of \hat{N}_j when tag-induced mortality occurs is similar in

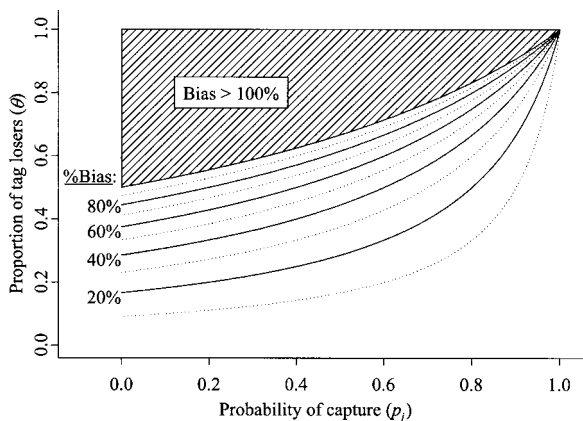


Figure 1. Contours of % bias in the Jolly-Seber estimator of population size as a function of probability of capture (p_j) and proportion of animals who lost their tags (θ). Percent bias was calculated as $(1 - p_j)\theta / (1 - \theta)$.

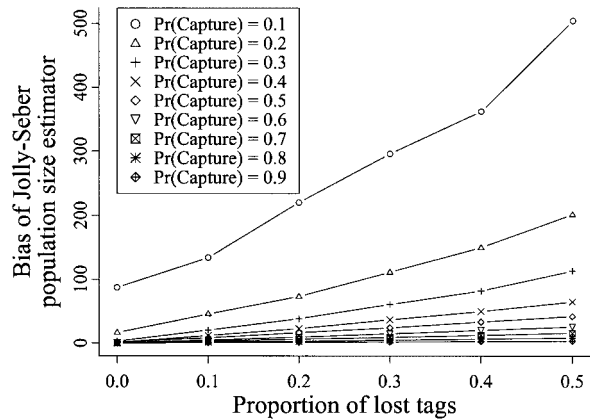


Figure 2. Bias of the Jolly-Seber estimator for population size when various proportions of tags are lost immediately after release. Simulated population size was nearly constant at 500 ± 5 individuals for $k = 10$ capture occasions. Simulated survival was 0.9 for each interval between $k = 10$ capture occasions. $Pr(\text{Capture}) = p_j$ was constant across all occasions and animals within a simulation.

form to the bias of \hat{N}_j when tag loss is occurring. Substituting $\theta^* = \theta(1 - \alpha_{j-})$ into Equation 14 shows it to be equivalent to Equation 7, except that the parameter measuring the degree of tag loss has been reduced by a factor <1 (i.e., $[1 - \alpha_{j-}]$). Tag-induced mortality of a certain level therefore causes less bias than tag loss of the same level. If α_{j-} = probability of seeing an animal before occasion j is high, bias caused by this type of tag-induced mortality is low because most animals have been seen before j and already had an opportunity to die. In

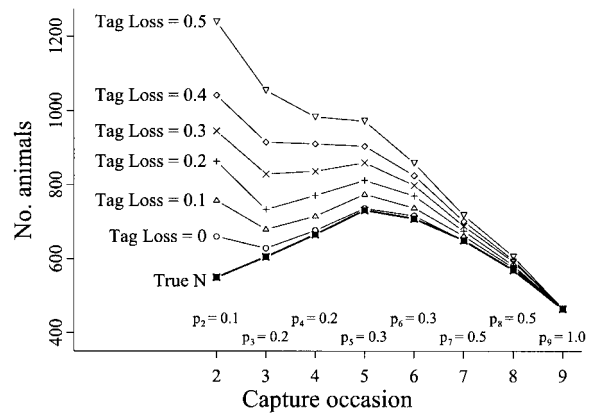


Figure 3. True population size and expected value of the Jolly-Seber estimator of population size when various proportions of tags are lost immediately after release. True probability of capture (p_j) listed along the bottom. Survival probabilities were 1, 1, 1, 1, 0.9, 0.85, 0.8, 0.75, and 0.70 for the 9 intervals between $k = 10$ capture occasions, respectively. Birth rates were 0.1, 0.1, 0.1, 0.1, 0.05, 0.05, 0.05, 0.05, and 0.05, respectively, for the same 9 intervals of time.

Table 1. S-Plus (version 2000) code used to estimate tag-loss-induced bias in the JS population size estimator. Inputs to the main function are: (1) n1 = number of animals alive at time 1, (2) ns = number of sample occasions, (3) surv.p = a (ns-1) vector of survival probabilities for time periods between j and $j+1$, constant across animals, (4) birth.p = a (ns-1) vector of birth proportions = proportions of the existing population added between time j and $j+1$, (5) iters = number of iterations in the simulation, (6) loss.p = vector of proportions of tagged population that lose their tags, and (7) cap.p = an (ns) vector of capture probabilities, constant across animals. An example call is `F.tag.loss.simu(n1=500, ns=10, surv.p=rep(.9,9), birth.p=rep(.1,9), iters=500, loss.p=c(0,.1,.2, .3, .4, .5), cap.p=rep(.1, 10))`.

```

F.tag.loss.simu _ function( n1, ns, surv.p,
birth.p, iters=500, loss.p, cap.p ){
  popln _ F.gen.popln( n1, ns, surv.p,
  birth.p )
  ans _ F.tag.loss.iterate( popln, iters, loss.p,
  cap.p, surv.p ); ans }
# -----
F.gen.popln _ function( nan, ns, surv.p,
birth.p ){
  pop _ matrix( 1, nrow=nan, ncol=1 )
  pop _ F.recursive.gen( pop, ns-1, surv.p,
  birth.p ); pop }
# -----
F.recursive.gen _ function( pop, ns,
surv.p, birth.p ){
  if( ns >= 1 ){mat.size _ nrow( pop )
  cur.gen _ ncol( pop )
  survivors _ rbinom( n=mat.size, size=1,
  prob=surv.p[1] )
  survivors _ survivors * pop[,cur.gen]
  n.babies _ round( sum( pop[,cur.gen] )
  * birth.p[1] )
  babies _ cbind( matrix( 0, nrow=n.babies,
  ncol=cur.gen ), 1 )
  pop _ cbind( pop, survivors )
  pop _ rbind( pop, babies )
  pop _ F.recursive.gen( pop, ns-1,
  surv.p[ 2:ns ], birth.p[2:ns] )
  dimnames(pop) _ list( NULL, NULL ) }
  return( pop ) }
# -----
F.sample.pop _ function( popln, cap.p ){
  ns _ ncol( popln )
  nan _ nrow( popln )
  tmp3 _ rbinom( nan*ns, size=1, prob=
  rep( cap.p, rep(nan, ns) ) )
  ans _ matrix(tmp3, nrow=nan)
  ans _ ans * popln
  ncap _ apply(ans, 1, sum)
  ans _ ans[ ncap >= 1, ]
  return(ans) }
# -----
F.impart.loss _ function( df, s ){
  orig.ch _ df[s,]
  ns _ ncol(df)
  na _ nrow(df)
  dim(orig.ch) _ c(length(s),ns)
  first _ col(orig.ch)
  first _ first * (orig.ch >= 1)
  get.loss.t _ function( ' ){fst _ min( x[x>0] )
  fst }
  loss.t _ apply( first, 1, FUN=get.loss.t )
  ans _ df
  for( i in 1:length(s) ){
  if(loss.t[i]<ns){ans[s[i],(loss.t[i]+1):ns]_0
  ch[ 1:loss.t[i] ] _ 0
  if(sum(ch)>=1){ans_rbind(ans,ch)}}}
}
# -----
F.cjs _ function( df ){
  m.array _ F.m.array( df )
  ans _ F.cjs.estim( m.array );ans }
# -----
F.cjs.estim_function( dat.list ){
  tt_dat.list$; marr_dat.list$m.array
  marr_dat.list$m.array*(row(marr)<
  col(marr))
  r _ c( apply( marr, 1, sum, na.rm=T), NA)
  m _ apply( marr, 2, sum, na.rm=T)
  s _ dat.list$s.array
  n _ dat.list$n.array; z _ 0
  for(i in (2:(tt-1))){
  j _ (row(marr) < i) & (col(marr) >= (i+1) )
  z _ c(z, sum( marr[j], na.rm=T) ) }
  z _ c(z, NA)
  mhat _ (s*z)/r + m
  alpha _ m/n
  n.hat _ mhat/alpha
  surv.hat_c(mhat[2:tt],NA) / (mhat-m+s)
  b.hat_c(n.hat[2:tt],NA)-surv.hat*(n.hat-n
  +s); p.hat _ n/n.hat
  return(n.hat, surv.hat, p.hat, b.hat) }
# -----
F.m.array_function( hist ) {
  n _ apply( (hist>=1), 2, sum )
  s _ apply( (hist==2), 2, sum )
  s _ n - s
  tt _ ncol(hist)
  marr_matrix(rep(NA,tt*(tt-1)),nrow=tt-1)
  for( i in (1:tt-1)){h _ hist[ hist[,i]>=1, ]
  for(j in ((i+1):tt)){k1 _ rep(0,tt)
  k2 _ rep(0,tt)
  k1 [c(i,j)]_1
  k2 [i:j] _ 1
  k3 _ apply( (t(h) == k1)*k2, 2, sum)
  marr [i,j] _ sum( k3 == sum(k2) ) } }
  return( list(m.array=marr, s.array=s,
  n.array=n, t=tt) ) }

```

fact, if $\alpha_{j-} = 1.0$, the JS estimator of size is approximately unbiased. As with tag loss, the JS estimator of size becomes less biased as capture probabilities increase.

Discussion

We considered 2 heterogeneous models for tag loss. Arnason and Mills (1981) considered the homogeneous model for tag loss. The first heterogeneous tag-loss model postulated a population of tag losers and tag retainers. The second heterogeneous tag-loss model postulated a study where a fraction of the captured animals lose their first tag immediately after initial release. Tag loss under this second model is heterogeneous across animals and is temporarily affected by trapping (trap response). While these models mimic only 2 of many possible realistic tag-loss situations, our calculations and simulations are sufficient to show that the JS estimator of population size can be substantially biased by unknown tag loss, especially when capture probabilities are low. The tag-loss bias we found in \hat{N}_j contradicts the assertion of Pollock et al. (1990) that estimates of \hat{N}_j are not affected by tag loss or tag-induced mortality. We conclude that Arnason and Mills' (1981) result of 0 bias in the JS size estimator is correct, provided tag loss is homogeneous and sample sizes are large. We speculate that Arnason and Mills' (1981) results were inappropriately extrapolated to other situations and that this led to the misconception that the JS estimator of size is unbiased under tag loss. While we examined the JS model specifically, it is clear our findings extrapolate to more modern modeling approaches including those employing covariates. In fact, depending on the covariates chosen, and individual or class heterogeneity in tag loss, resulting bias could be magnified.

For biologists interested in conducting and analyzing capture-recapture studies, we reiterate the common-sense notion that tags with high retention rates should be used and that probabilities of capture should be as high as possible. If, however, tag loss is occurring, capture probabilities are the determining factors in deciding whether population size estimates are being affected. If capture probabilities are high, the JS estimator of size is reasonably accurate if any amount of tag loss is occurring. Unfortunately, it appears the level of capture probability necessary for the size estimator to be unbiased varies according to the way in which tags are lost.

If, as in the first tag-loss model we considered, a certain fraction of animals always lose their tags immediately after release, capture probabilities need to be greater than ~90% for the size estimator to always be approximately unbiased. If, as in the second model we considered, a fraction of captured animals lose their tags once after their initial capture, capture probabilities need to be greater than ~50% for JS size estimator to be approximately unbiased. If a fraction of captured animals lose their tags at random times, we suspect the bias caused by tag loss would be less than that reported for our second tag-loss model. Under this last model for tag loss, capture probabilities could be <50% and the size estimator could still be reasonably unbiased.

If tag loss is known or suspected in a population, it is imperative the effects of that tag loss on size estimates be investigated. Rates of tag loss can be assessed and adjusted for with multiple tagging (Robson and Regier 1966, Seber 1982, Nichols and Hines 1993, Alisauskas and Lindberg 2002). Multiple tags and other field assessments of tag loss, however, may be logistically or financially prohibitive. If assumptions of the Jolly-Seber procedure are satisfied, our S-Plus code (Table 1) can be easily modified to perform investigations of the effects of a variety of tag-loss scenarios. In particular, different models for tag loss can be implemented by modifying our `Fimpart.loss` function. This function requires that it be called with a data frame of capture histories and a list of the histories to be modified. The function returns a data frame of modified capture histories after some type of tag loss has been imposed. If the tag-loss model were the only aspect of the situation that deviated from the assumptions of our simulation, no other functions would require modification.

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