# Hidden Markov Model for Dependent Mark Loss and Survival Estimation

Jeffrey L. LAAKE, Devin S. JOHNSON, Duane R. DIEFENBACH, and Mark A. TERNENT

Mark-recapture estimators assume no loss of marks to provide unbiased estimates of population parameters. We describe a hidden Markov model (HMM) framework that integrates a mark loss model with a Cormack–Jolly–Seber model for survival estimation. Mark loss can be estimated with single-marked animals as long as a sub-sample of animals has a permanent mark. Double-marking provides an estimate of mark loss assuming independence but dependence can be modeled with a permanently marked sub-sample. We use a log-linear approach to include covariates for mark loss and dependence which is more flexible than existing published methods for integrated models. The HMM approach is demonstrated with a dataset of black bears (*Ursus americanus*) with two ear tags and a subset of which were permanently marked with tattoos. The data were analyzed with and without the tattoo. Dropping the tattoos resulted in estimates of survival that were reduced by 0.005–0.035 due to tag loss dependence that could not be modeled. We also analyzed the data with and without the tattoo using a single tag. By not using.

Supplementary materials accompanying this paper appear on-line.

**Key Words:** Capture-recapture; Cormack–Jolly–Seber (CJS); Hidden Markov model; Mark loss; Tag loss.

## 1. INTRODUCTION

Mark-recapture estimators assume recaptures of marked individuals are always detected (Seber 1982), which is violated when animals lose marks. Current methods of marking many different species indicate that problems with mark retention occur with small mammals (Fokidis et al. 2006), large terrestrial mammals (Fosgate et al. 2006), aquatic mammals (Bradshaw et al. 2000), fish (Cowen and Schwarz 2006), and reptiles (Rivalan et al. 2005). Animals that lose all marks become part of the unmarked population and estimates of

Jeffrey L. Laake (✉) (E-mail: *jeff.laake@noaa.gov*) and Devin S. Johnson are in National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, USA. Duane R. Diefenbach is in U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA. Mark A. Ternent is in Pennsylvania Game Commission, Harrisburg, PA 17110-9797, USA.

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population parameters (e.g., survival and abundance) will be biased (Arnason and Mills 1981; Diefenbach and Alt 1998). Complete loss of all marks is equivalent to death in a survival analysis. Using natural markings can avoid the mark loss problem (Stevick et al. 2001), but not all species can be monitored in this manner. Likewise, permanent marks are often possible (e.g., hot brands; Merrick et al. 1996) but sometimes controversial even if they have no deleterious effects on survival (McMahon et al. 2006). Thus, methods of estimating mark loss will be necessary until new technologies are developed that eliminate loss.

Historically, animals have been marked with two marks of the same type and the status of marks upon recapture (none or one mark missing) has been used to estimate mark loss under the assumption that each mark is lost independently of the other mark (Beverton and Holt 1957; Seber 1982). This independence assumption is required because animals that lose both marks are not observable upon recapture. In recent studies, however, where the opportunity has occurred to observe loss of both marks, the independence assumption has been shown to be invalid (Siniff and Ralls 1991; Diefenbach and Alt 1998; Bradshaw et al. 2000; Rivalan et al. 2005; McMahon and White 2009). These studies undermine the credibility of mark loss evaluations for situations in which loss of both marks is not observable (Pistorius et al. 2000). However, using two different types of marks such as a passive integrated transponder (PIT) and wing tag with quail (Carver et al. 1999), flipper tags and a PIT tag for marine turtles (Braun-McNeill et al. 2007), or a PIT tag and a snout tag in fish (Knudsen et al. 2011) may be more likely to have independent loss and provide more reliable estimates.

An alternative approach is to mark each animal with one or two marks and permanently mark a sub-sample of animals with a brand (Merrick et al. 1996), lip tattoo (Diefenbach and Alt 1998) or use natural marks (Forcada and Robinson 2006) or genetics (Mackey et al. 2008; Hastings et al. 2012; Feldheim et al. 2002). While use of permanent marks eliminates the need for mark loss estimation, they can be expensive to apply, may require extra training, or the options for permanent marking may not allow an individually identifiable mark for each animal (e.g., limited area for application or not all animals are naturally marked). With a sub-sample of permanently marked animals, mark loss can be estimated for single-marked animals and dependence in mark loss can be estimated with double-marked animals.

Obtaining a valid estimate of mark loss is only part of the problem of obtaining accurate estimates of population parameters, because the estimates need to be adjusted for mark loss. Until relatively recently, survival estimates were obtained from mark-recapture models and then an adjustment was made to the survival estimate (Arnason and Mills 1981). However, the adjustment assumes homogeneity in mark loss and mark loss can be a function of age (Cameron and Siniff 2004), mark type (Carver et al. 1999), mark placement (Oosthuizen et al. 2010), habitat (Casale et al. 2007), and study area (Smout et al. 2011b). Thus, it is preferable to integrate mark loss and survival in a single model that can include variation in mark loss.

A number of studies have incorporated mark loss in open and closed models but most have some limitations, such as assuming independence for double mark loss events (Cowen and Schwarz 2006), or double mark loss does not occur (Tavecchia et al. 2012), or the permanent mark does not uniquely identify individuals (Hyun et al. 2012). Conn et al. (2004) integrated a mark loss model with a resight-recovery model, which required recovery of the animal to record mark loss and Juillet et al. (2010) extended this model to account for heterogeneity

in reporting rates related to mark loss. Smout et al. (2011b) describe an integrated model in which individuals have different types of marks, including some with permanent brands, but the different types of marks are not applied to the same individual. Consequently, relative and absolute mark loss can be estimated only by assuming that survival rate is constant across individuals with different mark types. The models proposed by McMahon and White (2009), Chilvers and MacKenzie (2010), and Smout et al. (2011b) provide an integrated model for survival estimation that allowed dependence in mark loss using permanent marks. We improve on those models by using a a hidden Markov model (HMM) that integrates mark loss modeling into a Cormack–Jolly–Seber (CJS) model and allows a mixture of single- and double-marked animals with or without a permanently marked sub-sample. Also, we adopted the log-linear model framework described by Bradshaw et al. (2000) for mark loss which requires fewer parameters and easily incorporates covariates to explain heterogeneity in mark loss and dependence.

We apply our method to capture-recapture data on 298 yearling and older black bears (*Ursus americanus*) from Pennsylvania. Each bear was fitted with an ear tag in each ear and permanently marked with a tattoo on the inside lip. We randomly selected 50 % of the bears and ignored their lip tattoo using only the tags that were present (if any). For the remaining bears we used their tattoo and tags. We applied our models to those data with both ear tags to demonstrate and estimate dependence in mark loss. We also analyzed the data from the left ear tag to illustrate single-marking models with 50 % of the bears with a lip tattoo.

The models we propose can be fitted with program MARK (White and Burnham 1999), and we have added them to the package "marked" (Laake et al. 2013) for the R statistical environment (R Core Development Team 2012). Details for fitting mark loss models with the "marked" package and with MARK (White and Burnham 1999) using the RMark interface (Laake 2013b) are provided with an example using simulated data in the supplemental material. Also in the supplemental material we provide results from simulation. We demonstrate the model and code work using examples with large sample sizes. Also we show that negative bias in survival estimators occurs when mark loss events are dependent and no permanent marks are available to model the dependence and that the expected precision of survival is a function of the proportion of animals that are permanently marked and the average capture probability. The black bear data and code for fitting the models and generating the simulations also are provided as files with the supplemental material.

## 2. SINGLE-MARK LOSS CJS MODELS

We start with a situation in which each animal is given a single mark but a sub-sample also is given an additional permanent individual mark. We define the indicator variable $I_M$ to be 1 if the animal has a permanent mark and 0 if not. The animals are released and then recaptured at a set of occasions as in a standard CJS framework. We will assume that recapture of animals does not depend on their mark status (e.g., animals are physically caught and then examined for marks). At each occasion, the released animal can be in any one of $m = 3$ states: (1) state "1" where animal is alive and has retained its mark, (2) state "0" where the animal is alive but has lost its mark, and (3) state "Dead" where the animal is

dead. An encounter history string for each animal is constructed using one of 3 values: "+" when an animal is encountered alive with its mark, "−" when a permanently marked animal is encountered without its mark, and "0" for animals that are not encountered which would include a previously marked animal without a permanent mark that had lost its mark. We define $\phi$ to be the probability of surviving the interval between occasions, $\tau$ the probability of losing the mark during an interval, and $p$ to be the probability of encountering a live animal.

In specifying the HMM model we follow the notation used by Laake (2013a). At time $t$, the state is $C_t$ and the observation is $X_t$. For the single mark loss model, the states $C_t$ are "1" (alive with mark present), "0" (alive with mark missing) and dead. The observations $X_t$ are either "+," which means the mark was present, "−" when the mark was missing on a permanently marked animal, or "0" otherwise. For animals without a permanent mark, the only possible observations are "+" and "0." A HMM is fully specified with two matrices: (1) $\boldsymbol{\Gamma}$, the $m \times m$ one-step state transition probability matrix and (2) $\boldsymbol{D}$, the $s \times m$ state-dependent observation probability matrix. The elements of $\Gamma$, $\boldsymbol{\gamma}_{ij}$, are the probabilities of transitioning from state $i$ to state $j$.

| From state $C_{t-1}$ | To state $C_t$ | | |
|---|---|---|---|
| | 1 | 0 | Dead |
| 1 | $\phi(1-\tau)$ | $\phi\tau$ | $1-\phi$ |
| 0 | 0 | $\phi$ | $1-\phi$ |
| Dead | 0 | 0 | 1 |

The elements $d_{ik}$ of $\boldsymbol{D}$ are $Pr(X_t = i | C_t = k)$ where $i = 1, \ldots, s$ is a sequential index for the observations and $k = 1, \ldots, m$ is a state index.

| Observation $X_t$ | State $C_t$ | | |
|---|---|---|---|
| | 1 | 0 | Dead |
| + | $p$ | 0 | 0 |
| − | 0 | $pI_M$ | 0 |
| 0 | $1-p$ | $1-pI_M$ | 1 |

## 3. DOUBLE-MARK LOSS CJS MODELS

If each animal is given two marks and mark loss events are independent, then it is possible to estimate the probability that both marks are lost and the estimated survival can be corrected (Rotella and Hines 2005). However, recent studies have shown that mark loss events are likely to be dependent and models based on the independence assumption will underestimate double mark loss (Diefenbach and Alt 1998; McMahon and White 2009). We

can model the dependence in mark loss events if some of the animals that lose both marks are observable because they have a separate permanent mark.

With 2 marks, let $\mathbf{S} = (S_1, S_2)$ represent the state vector of the status of the 2 marks where $S_i$ is a "1" if the $i$th mark is present and "0" if the $i$th mark is absent (lost) (note: this is different from the convention of Diefenbach and Alt (1998), Bradshaw et al. (2000) and Rivalan et al. (2005) who use "1" to denote a mark loss event). Usually the marked animals can only be identified if one or more marks are retained and animals that have lost both marks ($\mathbf{S} = (0,0)$) are not observable. However, with a sample of permanently marked animals, the "00" state is observable for those animals. Instead of assuming independence, we cast a model motivated by Bradshaw et al. (2000) with a parameter that controls whether mark loss is dependent or independent.

We model the mark loss probability odds with a logit link function that enables use of covariates and incorporating dependence in mark fates. The conditional odds of losing the $i$th mark ($S_i = 0$) given the other mark is present ($S_{3-i} = 1$) is $e^{\beta_i}$ and the conditional odds of losing the $i$th mark ($S_i = 0$) given other mark is absent ($S_{3-i} = 0$) is $e^{\beta_i + \beta_3}$ where $\beta_3$ determines the amount of dependence. If $\beta_3 = 0$ we have independence. The joint probabilities for double mark status, $\tau_{s_1 s_2} = Pr(S_1 = s_1, S_2 = s_2)$ and the marginal probabilities ($i$th mark loss $\tau_i = Pr(S_i = 0)$, $i$th mark retention $1 - \tau_i = Pr(S_i = 1)$) are:

| Mark 1 status ($S_1$) | Mark 2 status ($S_2$) | | Marginal |
| | Present ($S_2 = 1$) | Absent ($S_2 = 0$) | |
| --- | --- | --- | --- |
| Present ($S_1 = 1$) | $\tau_{11} = 1/K$ | $\tau_{10} = e^{\beta_2}/K$ | $1 - \tau_1 = (1 + e^{\beta_2})/K$ |
| Absent ($S_1 = 0$) | $\tau_{01} = e^{\beta_1}/K$ | $\tau_{00} = e^{\beta_1 + \beta_2 + \beta_3}/K$ | $\tau_1 = e^{\beta_1}(1 + e^{\beta_2 + \beta_3})/K$ |
| Marginal | $1 - \tau_2 = (1 + e^{\beta_1})/K$ | $\tau_2 = e^{\beta_2}(1 + e^{\beta_1 + \beta_3})/K$ | |

where $K = 1 + e^{\beta_1} + e^{\beta_2} + e^{\beta_1 + \beta_2 + \beta_3}$. The mark loss odds can be constructed from the conditional probabilities $\tau_i^{(0)} = Pr(S_i = 0 | S_{3-i} = 0) = \frac{e^{\beta_i + \beta_3}}{1 + e^{\beta_i + \beta_3}}$ and $\tau_i^{(1)} = Pr(S_i = 0 | S_{3-i} = 1) = \frac{e^{\beta_i}}{1 + e^{\beta_i}}$. The odds of losing mark 2 ($S_2 = 0$) given mark 1 is present ($S_1 = 1$) is $\tau_2^{(1)}/(1 - \tau_2^{(1)}) = e^{\beta_2}$. The odds can also be constructed from the ratios of joint probabilities. The relationship between this model and the dependence model for dual observer mark-recapture distance sampling (Borchers et al. 2006) is described in the Appendix. The model we propose here for tag loss could also be used for mark-recapture distance sampling.

Diefenbach and Alt (1998) and Rivalan et al. (2005) specified the joint probabilities in a slightly different manner with $\tau_{01} = \tau_{10} = \tau(1 - \tau^*)$, $\tau_{00} = \tau \tau^*$ and $\tau_{11} = 1 - 2\tau + \tau \tau^*$, where $\tau$ is the marginal mark loss probability and $\tau^*$ is the conditional probability of losing a mark given the other mark was absent. Although not stated, their conditional probability of losing a mark given the presence of the other mark would be $\tau(1 - \tau^*)/(1 - \tau)$. In both papers the authors used separate functional forms for $\tau$ and $\tau^*$ and specified the independence model by using the same model for both ($\tau = \tau^*$). Their approach is viable but we believe it is preferable to have a model with a parameter that controls dependence

and with independence specified simply as $\beta_3 = 0$. Also, use of the logit link provides a way to model dependence as a function of covariates.

For double-marked animals, the states for the HMM are "11," "10," "01," "00," and "Dead". The first four states describe the double mark status for live animals. The parameters for $\Gamma$ are $\phi$ for survival, and the vector $\beta$ for mark loss, which is used to compute the values for $\tau_1^{(0)}$, $\tau_2^{(0)}$ and $\tau_{11}, \tau_{01}, \tau_{10}, \tau_{00}$:

|  | To state $C_t$ | | | | |
|---|---|---|---|---|---|
| From state $C_{t-1}$ | 11 | 10 | 01 | 00 | Dead |
| 11 | $\phi\tau_{11}$ | $\phi\tau_{10}$ | $\phi\tau_{01}$ | $\phi\tau_{00}$ | $(1-\phi)$ |
| 10 | 0 | $\phi(1-\tau_1^{(0)})$ | 0 | $\phi\tau_1^{(0)}$ | $(1-\phi)$ |
| 01 | 0 | 0 | $\phi(1-\tau_2^{(0)})$ | $\phi\tau_2^{(0)}$ | $(1-\phi)$ |
| 00 | 0 | 0 | 0 | $\phi$ | $(1-\phi)$ |
| Dead | 0 | 0 | 0 | 0 | 1 |

We define $t_i = 1 - S_i$ which are 1 when the $i$th mark is lost and 0 when not lost. With data for each of the four combinations of $t_1$ and $t_2$ (00, 01, 10, 11), a design matrix $X$ can be constructed with a formula using $t_i$ for the joint probabilities ($\tau_{11}, \tau_{01}, \tau_{10}, \tau_{00}$) and $\tau_1^{(0)}$, $\tau_2^{(0)}$ can be computed from those joint probabilities. For example, using R formula notation $t_1 + t_2 + t_1 : t_2$ produces $X = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 1 & 1 & 1 \end{bmatrix}$ and $\exp(X\beta)/(1'\exp(X\beta))$ produces the joint probabilities shown above where $1'$ is a row vector of ones and $K = 1'\exp(X\beta)$. The formula $t_1 + t_2$ produces a model based on independence with loss rates varying by mark and $I(t_1 + t_2)$ is the independence model with equal mark loss rates.

McMahon and White (2009) used the number of marks present (2, 1, 0) as states and the transition probabilities were specified using a log link. With that structure they were forced to specify an additional unnecessary parameter in the independence model for the transition from 2 marks to 1 mark, which disadvantages the independence model in model selection. By switching to a model with 4 states and a 0/1 state for each mark, the design matrix for the joint probabilities with the independence model and the same loss rate for each mark ($I(t_1 + t_2)$) is $X = \begin{bmatrix} 0 \\ 1 \\ 1 \\ 2 \end{bmatrix}$ and $X = \begin{bmatrix} 0 & 0 \\ 1 & 0 \\ 1 & 0 \\ 2 & 1 \end{bmatrix}$ for the dependence model ($I(t_1 + t_2) + t_1 : t_2$). Note that McMahon and White (2009) specified the model parameter in terms of mark retention and our model specifies mark loss.

The observed data are specified as "++," "+−," "−+," "− −," and "0". The "+" indicates the mark was present for an animal that was observed and a "−" means the mark was missing. The observation "0" means the animal was not encountered on the occasion which includes those with double mark loss and no permanent mark. Only permanently marked animals

can have an observation of "− −". A mixture of single- and double-marked animals can be accommodated by setting the initial release state observation for single-marked animals as either "+−" or "−+" depending on which mark is treated as the single mark. If a variable in the data is named "double" and given the value 0 for animals with single marks and 1 for double-marked animals, then the dependence parameter(s) can be restricted to double-marked animals with an interaction (e.g. $I(t_1 + t_2) +$ double $: t_1 : t_2$).

We assume that the correct status is recorded for each mark of a sampled animal. Thus, no errors or partial observations are allowed. The parameters for $D$ are capture probabilities $p$ and $I_M$ is 1 for permanently marked animals and 0 otherwise:

| | State $C_t$ | | | | |
|---|---|---|---|---|---|
| Observation $X_t$ | 11 | 10 | 01 | 00 | Dead |
| ++ | $p$ | 0 | 0 | 0 | 0 |
| +− | 0 | $p$ | 0 | 0 | 0 |
| −+ | 0 | 0 | $p$ | 0 | 0 |
| − − | 0 | 0 | 0 | $I_M p$ | 0 |
| 0 | $1 - p$ | $1 - p$ | $1 - p$ | $1 - I_M p$ | 1 |

All of the parameters can be functions of covariates and do not have to be constant as shown.

## 4. BLACK BEAR EXAMPLE

We used data from 298 yearling and older black bears (*U. americanus*) from Pennsylvania that were captured and marked over a 12-year period, 2002-2013. Each newly-captured bear was given a metal tag, style 56-L, size $36.5 \times 9.5$ mm (Hasco Tag Company, Dayton, Kentucky) in each ear and a permanent tattoo on the inside upper lip; however, for our purposes we randomly selected one-half as permanently marked. Upon recapture, the status (present/missing) of each tag was recorded and the bear was released. If a bear was missing both tags and was not selected as part of the permanently marked sample, its capture history was modified (i.e., "− −" changed to "0") because it would have not been recognized if it had both ear tags missing. Additionally, to demonstrate single mark loss models with these data we used only the left tag status and ignored the right tag.

### 4.1. ETHICS STATEMENT

We obtained permission to capture bears on the Sproul State Forest managed by the Pennsylvania Department of Conservation and Natural Resources. Approval to capture, ear tag, and tattoo black bears was obtained from Pennsylvania State University's Institutional Animal Care and Use Committee (Protocols 35978, 27498, 20672, and 14572).

## 4.2. Single Mark Loss

Using only the left tag status, we used the black bear data to demonstrate an application of single mark loss models with one-half of the bears permanently marked and we then compared the results to an analysis without any permanent marks. If the left tag was not present and the bear was not permanently marked, then a "–" observation was changed to "0". To evaluate effects of age on survival, we binned ages into 2 classes (yearling and ages 2 and older) and 3 classes (yearling, age 2 and ages 3 and older). For capture probability, we used 2 classes (age 2 and ages 3 and older) because initial capture probability is not modeled for CJS models, so there was no yearling capture probability. We considered models for survival with effects of age, sex and their interaction. Capture probability was time-varying and we considered additional sex and age effects. We considered models with constant tag loss and variation due to sex and tag age (time at liberty). We fitted each combination of models and used Akaike's Information Criterion (AIC) for model selection.

Although there was no clearly best model (Table 1), models with most support included survival that varied by sex and 2 age classes and their interaction and capture probability with additive effects of time, age and sex. Models with constant tag loss had the most support (sum of weights = 0.497) and models with variation by tag age slightly less support (sum of weights = 0.308). There was little support for sex-variation in single mark loss.

Table 1. Model selection table with top 20 single mark loss models for black bear data with 50 % permanently marked.

| Model | $k$ | $\Delta$AIC | Weight |
|---|---|---|---|
| Phi(ageclass1 * sex)tau(1)p(time + sex + ageclass) | 18 | 0.000 | 0.167 |
| Phi(ageclass1 * sex)tau(tagAge)p(time + sex + ageclass) | 19 | 0.955 | 0.103 |
| Phi(ageclass1 + sex)tau(1)p(time + sex + ageclass) | 17 | 1.496 | 0.079 |
| Phi(ageclass1 * sex)tau(1)p(time + sex) | 17 | 1.872 | 0.065 |
| Phi(ageclass1 * sex)tau(sex)p(time + sex + ageclass) | 19 | 1.874 | 0.065 |
| Phi(ageclass1 * sex)tau(1)p(time) | 16 | 2.318 | 0.052 |
| Phi(ageclass1 + sex)tau(tagAge)p(time + sex + ageclass) | 18 | 2.440 | 0.049 |
| Phi(ageclass1 * sex)tau(tagAge)p(time + sex) | 18 | 2.834 | 0.040 |
| Phi(ageclass1 * sex)tau(tagAge)p(time) | 17 | 3.280 | 0.032 |
| Phi(ageclass1 + sex)tau(sex)p(time + sex + ageclass) | 18 | 3.368 | 0.031 |
| Phi(ageclass + sex)tau(1)p(time + sex + ageclass) | 18 | 3.440 | 0.030 |
| Phi(sex)tau(1)p(time) | 14 | 3.627 | 0.027 |
| Phi(ageclass1 * sex)tau(sex)p(time + sex) | 18 | 3.747 | 0.026 |
| Phi(ageclass1 + sex)tau(1)p(time) | 15 | 4.063 | 0.022 |
| Phi(ageclass1 * sex)tau(sex)p(time) | 17 | 4.193 | 0.020 |
| Phi(ageclass + sex)tau(tagAge)p(time + sex + ageclass) | 19 | 4.385 | 0.019 |
| Phi(ageclass1 + sex)tau(1)p(time + sex) | 16 | 4.497 | 0.018 |
| Phi(sex)tau(tagAge)p(time) | 15 | 4.582 | 0.017 |
| Phi(sex)tau(1)p(time + sex) | 15 | 4.828 | 0.015 |
| Phi(ageclass1 + sex)tau(tagAge)p(time) | 16 | 5.014 | 0.014 |

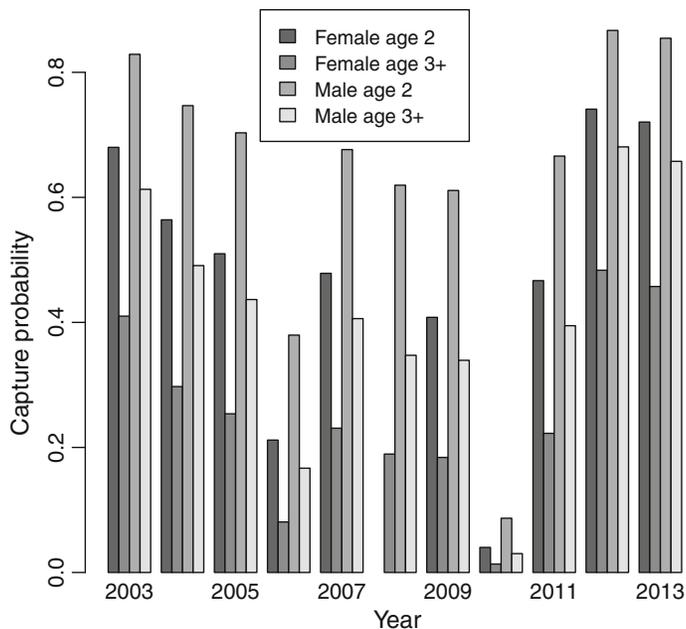The number of parameters is $k$ and weight is the AIC weight.

Figure 1.  Recapture probability estimates from single mark loss model for black bear data with 50 % permanently marked. Estimates are shown for each sex and ages 2 and 3 years and older for 2003–2013.

Table 2.  Estimates of survival from best single mark loss model fitted for black bear data with 50 and 0 % permanently marked.

|  | Age class | Sex | Estimate | SE | Lower 95 % CL | Upper 95 % CL |
|---|---|---|---|---|---|---|
| 50 % permanently marked | Yearling | F | 0.772 | 0.151 | 0.387 | 0.948 |
|  | Yearling | M | 0.099 | 0.051 | 0.035 | 0.250 |
|  | 2+ years | F | 0.806 | 0.030 | 0.741 | 0.858 |
|  | 2+ years | M | 0.396 | 0.066 | 0.276 | 0.530 |
| 0 % permanently marked | Yearling | F | 0.679 | 0.173 | 0.309 | 0.909 |
|  | Yearling | M | 0.089 | 0.044 | 0.032 | 0.222 |
|  | 2+ years | F | 0.728 | 0.041 | 0.640 | 0.801 |
|  | 2+ years | M | 0.331 | 0.069 | 0.212 | 0.477 |

Single tag loss from the constant model was 0.094 (SE = 0.021). From the best model with tag loss varying by tag age, tag loss increased with tag age from 0.077 (SE = 0.024) in the initial year to 0.219 (SE = 0.160) for a tag that had been applied 10 years earlier.

Capture probability (Fig. 1) was greater for males than for females and was greater for 2-year-old bears than bears aged 3 years or more. There was temporal variation in capture probability with the highest rate of 0.867 (SE = 0.071) in 2012 and the lowest rate of 0.013 (SE = 0.162) in 2010 when trapping began 3 months later than usual.

Survival for males was lower than females, especially yearling males (Table 2). These results are consistent with Diefenbach et al. (2004) who reported that harvest rates varied among sex-age classes with yearling males having the highest harvest rates and adult females

the lowest. The greatest cause of mortality in black bears in Pennsylvania is attributed to hunting (Diefenbach and Alt 1998). There was more support for a model with sex-age interaction (sum of weights = 0.572) than an additive model (sum of weights = 0.328). Survival estimates were sensitive to choice of survival model but were insensitive to choice of tag loss model when 50 % were permanently marked. However, when the data were analyzed without using permanent marks, the estimated survival was reduced by approximately the magnitude of the single tag loss rate (Table 2).

### 4.3. DOUBLE MARK LOSS

Using both tags, we fitted models with one-half of the bears permanently marked and we then compared the results to an analysis without any permanent marks. If both tags were not present and it was not permanently marked, then a "− −" observation was changed to "0". We fitted the same sequence of models for survival and capture probability that we did for the single mark loss example. However, because there were 2 tags we expanded the set of models for tag loss to include dependence between tag loss events and considered models in which dependence was a function of sex and tag age. We fitted each combination of models and used AIC for model selection.

For this example as well, there was no clearly best model (Table 3). However, as with the single mark loss analysis, the models with most support included survival that varied by sex and 2 age classes and their interaction and capture probability with additive effects of time, age and sex. The estimates of survival from the best model using both tags and 50 % permanently marked (Table 4) were nearly identical to the estimates from the equivalent best model from the single tag analysis. However, for the analysis with double tags and no permanently marked animals, the reduction in survival estimates was much less than the single tag analysis because the bear had to lose both tags and the loss of both tags was estimated assuming independence. Without permanently marked bears survival estimates were reduced because dependence in tag loss could not be estimated.

The dependence in tag loss events was well supported (Table 3) (sum of weights = 0.752) and there was some evidence that the dependence was a function of tag age (sum of weights = 0.355). However, there was less support for sex differences in tag loss rates or dependence (sum of weights = 0.21). From the best model, the probability of losing both tags in the first year was 0.012 (SE = 0.006) and the probability of losing one of the two tags was 0.119 (SE = 0.018). The comparable values from Diefenbach and Alt (1998) for males and females are 0.018 and 0.017, respectively, for double tag loss and 0.159 and 0.103 for loss of one of two tags in the first year.

## 5. DISCUSSION

We developed a HMM that integrates a mark loss model with the Cormack–Jolly–Seber model that provides estimates of survival that are not biased by mark loss. Our modeling approach can accommodate covariates that affect mark loss and survival which is not possible with the post-analysis adjustment of survival for mark loss (Arnason and Mills 1981). By

Table 3. Model selection table with top 20 double mark loss models for black bear data with 50 % permanently marked.

| Model | Model | k | ΔAIC | Weight |
|---|---|---|---|---|
| 1 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time+sex+ageclass) | 20 | 0.000 | 0.115 |
| 2 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2:tagAge) p(time+sex+ageclass) | 20 | 0.416 | 0.093 |
| 3 | Phi(ageclass1+sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time+sex+ageclass) | 19 | 1.499 | 0.054 |
| 4 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time+sex) | 19 | 1.868 | 0.045 |
| 5 | Phi(ageclass1+sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2:tagAge) p(time+sex+ageclass) | 19 | 1.914 | 0.044 |
| 6 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2:tagAge) p(time+sex) | 19 | 2.284 | 0.037 |
| 7 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time) | 18 | 2.321 | 0.036 |
| 8 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)) p(time+sex+ageclass) | 19 | 2.531 | 0.032 |
| 9 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2:tagAge) p(time) | 18 | 2.738 | 0.029 |
| 10 | Phi(ageclass1*sex) tau(I(tag1+tag2)+male:I(tag1+tag2) +tagAge:I(tag1+tag2) +male:tagAge:I(tag1+tag2) +tag1:tag2:tagAge+male:tag1:tag2:tagAge) p(time+sex+ageclass) | 23 | 2.973 | 0.026 |
| 11 | Phi(ageclass1*sex) tau(I(tag1+tag2)) p(time+sex+ageclass) | 18 | 3.064 | 0.025 |
| 12 | Phi(ageclass+sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time+sex+ageclass) | 20 | 3.439 | 0.021 |
| 13 | Phi(sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time) | 16 | 3.624 | 0.019 |
| 14 | Phi(ageclass1*sex) tau(I(tag1+tag2)+male:I(tag1+tag2) +tagAge:I(tag1+tag2) +male:tagAge:I(tag1+tag2) +tag1:tag2+male:tag1:tag2) p(time+sex+ageclass) | 23 | 3.641 | 0.019 |
| 15 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2) +I(tag1+tag2):male+male:+tagAge:I(tag1+tag2)) p(time+sex+ageclass) | 21 | 3.817 | 0.017 |
| 16 | Phi(ageclass+sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2:tagAge) p(time+sex+ageclass) | 20 | 3.854 | 0.017 |
| 17 | Phi(ageclass1+sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)) p(time+sex+ageclass) | 18 | 4.030 | 0.015 |

Table 3.   (continued).

| Model | Model | k | ΔAIC | Weight |
|---|---|---|---|---|
| 18 | Phi(sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2:tagAge) p(time) | 16 | 4.040 | 0.015 |
| 19 | Phi(ageclass1+sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)+tag1:tag2) p(time) | 17 | 4.071 | 0.015 |
| 20 | Phi(ageclass1*sex) tau(I(tag1+tag2)+tagAge:I(tag1+tag2)) p(time+sex) | 18 | 4.399 | 0.013 |

The number of parameters is k and weight is the AIC weight.

Table 4.   Estimates of survival from best double mark loss model fitted for black bear data with 50 and 0 % permanently marked.

| | Age class | Sex | Estimate | SE | Lower 95 % CL | Upper 95 % CL |
|---|---|---|---|---|---|---|
| 50 % permanently marked | Yearling | F | 0.772 | 0.151 | 0.387 | 0.948 |
| | Yearling | M | 0.099 | 0.051 | 0.035 | 0.250 |
| | 2+ years | F | 0.806 | 0.030 | 0.741 | 0.858 |
| | 2+ years | M | 0.396 | 0.066 | 0.276 | 0.529 |
| 0 % permanently marked | Yearling | F | 0.754 | 0.170 | 0.337 | 0.948 |
| | Yearling | M | 0.094 | 0.048 | 0.033 | 0.239 |
| | 2+ years | F | 0.771 | 0.038 | 0.688 | 0.837 |
| | 2+ years | M | 0.363 | 0.067 | 0.244 | 0.502 |

using a sample of permanently marked animals, the model can account for dependence in mark loss events for animals with two marks. Mark loss events may be dependent either because of individual variation in tag strength or quality, tag application, or mechanistic reasons for tag loss (e.g., growth, aggression). If dependence cannot be estimated, survival rates will be negatively biased. The simulations in the supplemental material show that the bias is a function of the amount of unmodeled dependence. We also showed with simulation that bias in survival can be reduced or eliminated with a sample of permanently marked animals with a minor increase in the standard error as long as a sufficient proportion of animals have a permanent mark.

Dependence is also a problem for visibility surveys with two observers. One approach, called mark-recapture distance sampling (Borchers et al. 2006), uses auxiliary information from a distance sampling design to accommodate and estimate dependence. Unfortunately there is no equivalent for mark loss models. However, we can envision models that incorporate dependence only from double-marked individuals without a permanently marked sample, but such an estimator would be model-dependent without a robust means of evaluating model reliability. For example, California sea lions (*Zalophus californinanus*) have a tag applied to both fore-flippers as pups (Hernández-Camacho et al. 2008; Melin et al. 2012). Initial tag loss may be due to manufacturing or application defects, which may be independent between tags. However, growth of the fore-flipper may put pressure on the tag causing the tag to fail or may cause tissue damage that allows the tag to fall out. Furthermore, tag loss may not be independent because growth is symmetric and if one tag is lost the other

is also likely to be lost. Thus, we could develop a model in which $\beta_3 = 0$ initially for a few years but not subsequent years. If $\beta_i$ are age-invariant or can be expressed as a linear function of age, then the slope and intercept for tag loss could be estimated during the period in which $\beta_3 = 0$ and $\beta_3$ could be estimated for the other ages without a permanently marked sample. However, this approach would be very model-dependent with no means to evaluate model reliability. Inclusion of a permanently marked sample would be more reliable.

We demonstrated the usefulness of the model with an application to black bears. The example illustrated negatively biased survival estimates that are obtained because of dependence with two tags and greater bias if bears had only a single tag and no permanent marks. The example dataset we used in this paper, and findings from other studies, indicated that models that incorporate mark loss need to be able to address dependence in mark loss (McMahon and White 2009), interaction effects among sex-age classes (Diefenbach and Alt 1998), differences in mark types (Smout et al. 2011a), and variation among study areas (Smout et al. 2011b). Whereas the difference between our estimates of tag loss and those of Diefenbach and Alt (1998) were within the range of estimation error, the difference in sex variation from the studies also highlights the potential for variation in tag loss rates. Thus, the advantage of the model we developed is that variation in tag loss can be easily incorporated directly into the CJS model, without bias due to dependence in tag loss, as long as a sub-sample of permanently marked animals is available.

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## 6. APPENDIX

The probability structure for mark loss is equivalent to capture-recapture (mark-recapture) for two occasions with a closed population, which has been used with two observers to measure detection probability in visual surveys. When detection probability is measured solely with the mark-recapture data, it is necessary to assume independence between the detections by the two observers because those missed by both observers ($n_{00}$) are obviously not included in the sample (Borchers 1996). Recently, the independence assumption was weakened (Laake 1999; Laake and Borchers 2004; Borchers et al. 2006) in the combined mark-recapture and distance sampling by including a dependence measure $\delta(x)$ which was estimated as the discrepancy between the detection probability at distance $x$ measured by the mark-recapture (double observer) data (based on independence) and the distance sampling data. If $\delta(x) = 1$ then independence at all distances is achieved. Because detection probability at $x = 0$ cannot be measured from the distance sampling data, the

independence assumption for the mark-recapture data was required for $x = 0$ ($\delta(0) = 1$) but not for the other distances.

The dependence structure we have defined for mark loss can be expressed in terms of the $\delta$ dependence of Borchers et al. (2006). Under the independence model, the probability that an animal would retain at least one mark is:

$$1 - \tau_{00}^* = \frac{1 + e^{\beta_1} + e^{\beta_2}}{1 + e^{\beta_1} + e^{\beta_2} + e^{\beta_1 + \beta_2}}$$

Likewise for the dependence model:

$$1 - \tau_{00} = \frac{1 + e^{\beta_1} + e^{\beta_2}}{1 + e^{\beta_1} + e^{\beta_2} + e^{\beta_1 + \beta_2 + \beta_3}}$$

The dependence measure of Borchers et al. (2006) is a ratio that measures the distortion between the joint probabilities from the independence model ($\beta_3 = 0$) and the dependence model ($\beta_3 \neq 0$) which can be expressed as:

$$\delta = \frac{1 - \tau_{00}^*}{1 - \tau_{00}} = \frac{K}{K^*} = 1 + \frac{e^{\beta_1 + \beta_2}(e^{\beta_3} - 1)}{1 + e^{\beta_1 + \beta_2} + e^{\beta_1} + e^{\beta_2}} = 1 + (e^{\beta_3} - 1)\tau_{00}^*$$

The same relationship can be obtained using conditional and marginal probabilities. Defining $\tau_i^{(s_{3-i})}$ to be the conditional probability that the $i$th mark is lost given the other mark status is $s_{3-i}$:

$$\tau_i^{(s_{3-i})} = Pr\left(S_i = 0 | S_{3-i} = s_{3-i}\right) = \frac{e^{\beta_i + \beta_3(1 - s_{3-i})}}{1 + e^{\beta_i + \beta_3(1 - s_{3-i})}}.$$

If $q_i^{(s_{3-i})} = 1 - \tau_i^{(s_{3-i})}$ and $q_i = 1 - \tau_i$ is the marginal mark retention rate, then $\delta = q_i^{(1)}/q_i = \frac{K}{K^*}$. Likewise the same ratio for any of the joint probabilities based on independence and dependence other than for the (0,0) event which is not used in the independence model. The dependence measure can also be expressed in terms of covariance (Borchers 1996):

$$\delta = 1 + \frac{\text{cov}(S_1, S_2)}{q_1 q_2} = 1 + \frac{\frac{1}{K} - q_1 q_2}{q_1 q_2} = 1 + \frac{\frac{1}{K}}{\frac{K^*}{K^2}} = 1 + (e^{\beta_3} - 1)\tau_{00}^*$$

In general there will likely be positive dependence in mark loss which means $\beta_3 > 0$ and $\delta > 1$ but negative dependence ($\beta_3 < 0$) is possible with a lower bound of $\delta > 1 - \tau_{00}^*$.

The joint probabilities can be rewritten in terms of $\delta$ as: $\tau_{11} = \delta q_1 q_2$, $\tau_{10} = q_1(1 - \delta q_2)$ and $\tau_{01} = q_2(1 - \delta q_1)$ or as $\tau_{11} = q_1^{(1)} q_2^{(1)}/\delta$, $\tau_{10} = q_1^{(1)} \tau_2^{(1)}/\delta$ and $\tau_{01} = q_2^{(1)} \tau_1^{(1)}/\delta$. The latter form makes it obvious that once you exclude $n_{00}$ and condition on the observed data, the $\delta$ will cancel from the rescaled joint probabilities which will only be functions of the $q_i^1$. This is also obvious by noting that the joint probabilities for the observed set of data ($n_{11} n_{10} n_{01}$) would only be functions of $\beta_i$ after conditioning on the exclusion of $n_{00}$. The same result was shown by Borchers et al. (2006) for mark-recapture distance sampling but in that case $\delta$ could be estimated from the observed distances.

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