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Jointly estimating survival and mortality: integrating recapture and recovery data from complex multiple predator systems

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Abstract

Identifying where, when, and how many animals live and die over time is principal to understanding factors that influence population dynamics. Capture–recapture–recovery (CRR) models are widely used to estimate animal survival and, in many cases, quantify specific causes of mortality (e.g., harvest, predation, starvation). However, the restrictive CRR framework can inhibit the consideration and inclusion of some types of recovery data. We developed an extension to the CRR framework to allow for the incorporation of recoveries from indeterminate temporal or spatial origin. This model jointly estimates cause-specific mortality and survival probabilities across multiple spatial and temporal scales, while accounting for differences in mortality-specific reporting and recovery rates. We fitted the model to data on a group of juvenile steelhead trout (*Oncorhynchus mykiss*) marked with passive integrated transponder tags in the Columbia River basin, USA. Following tagging and release, fish were detected alive at up to six downstream locations and/or recovered dead on one of nine bird colonies during seaward migration. We estimated that, in aggregate, avian predators consumed 31% of juvenile steelhead during outmigration to the ocean (95% CRI: [27, 36]). Colony-specific predation rates ranged from <1 to 14% among river reaches, with avian predation accounting for $>95\%$ of all steelhead mortality within some reaches. This integrated modelling approach provides a flexible framework to integrate multiple recapture and recovery data sources, providing a more holistic understanding of animal life history, including direct comparisons of cause-specific mortality factors and the cumulative impact of multiple mortality factors across time or space.

Keywords Capture–recapture–recovery · Hierarchical Bayesian · Population dynamics · State-space models

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1 Introduction

Capture-recapture (CR) models have become a ubiquitous tool in the estimation of survival in populations with imperfect detection rates (Pollock et al. 1990; Barker 1997; Lebreton et al. 2009; McCrea and Morgan 2014; Bohning et al. 2017). More recent approaches have been developed that integrate both live animal recapture events and dead animal recovery events, referred to as capture–recapture–recovery (CRR) models (Burnham 1993; Barker 1997; Schaub and Pradel 2004; Colchero and Clark 2012). The use of recovery data can provide supplementary life history information and consequently facilitate greater precision and reduced bias in estimates of survival compared with the use of recapture data alone (Burnham 1993; Barker 1997; Catchpole et al. 1998; Schaub and Pradel 2004; Colchero and Clark 2012; Hostetter et al. 2018).

While CRR methods do well in providing estimates of survival probabilities, considerations of the various causes of mortality may be principal to developing a full understanding of the factors that influence survival (Schaub and Pradel 2004; Kendall et al. 2006; Michelot et al. 2015). However, dead-recoveries generally do not directly reflect the true or full impact of the mortality source. For instance, waterfowl band recoveries require that a (1) banded bird is shot, (2) recovered, and (3) reported (Burnham 1993). CRR methods to identify, separate, and quantify specific causes of mortality (e.g., harvest, predation, starvation) are of great interest and an area of active research (Schaub and Pradel 2004; McCrea and Morgan 2014; Hostetter et al. 2018). Furthermore, CRR models typically assume that the location or time of recovery (relative to recapture opportunities) are known and accurately reported. This assumption can inhibit the incorporation of many types of dead recoveries into a CRR framework (Catchpole et al. 2001; Hostetter et al. 2018), especially in complex, multi-predator systems.

CR studies are routinely used in the Columbia River, USA, to evaluate survival of multiple Endangered Species Act (ESA) listed salmonid species (*Oncorhynchus* spp.). Survival studies often focus on the seaward migration of tagged juveniles through a series of hydroelectric dams referred to as the Federal Columbia River Power System (FCRPS; Kareiva et al. 2000) using fish marked with passive integrated transponder (PIT) tags. In addition to recapture events, recoveries of PIT tags on piscivorous waterbird nesting colonies have been used to independently estimate mortality of tagged fish due to avian predation. To estimate true impacts of predation, studies often integrate auxiliary data to adjust raw recovery counts for fish that were consumed but not deposited on a bird colony, as well as imperfect recoveries of tags on bird colonies (i.e., reporting and recovery rates; Collis et al. 2001; Evans et al. 2012; Hostetter et al. 2015a). Predation models based on recovery data alone, however, are unable to incorporate uncertainty regarding where and when fish succumb to predation because birds commute long distances to forage on live tagged fish and because tag recovery efforts are not performed in real-time, but rather months after the fish were consumed (Evans et al. 2012; Osterback et al. 2013).

Herein, we develop a framework to quantify multiple mortality sources and survival by integrating live recapture data with mortality-specific recoveries, where the true location of mortality is only partially known. This method allows for the simultaneous modelling of survival and mortality, including the explicit identification of cause-specific mortality rates at different spatial- and temporal-scales. We present a concise construction of the likelihood function used in the model, which we refer to as the Joint Mortality and Survival (JMS) model. We demonstrate the utility of the JMS model through the analysis of a PIT-tagged steelhead trout (*Oncorhynchus mykiss*) dataset from the Columbia River. We conclude with a discussion of the overall effectiveness of the JMS model and ways the model can be further developed and applied to other research.

2 Methods

We first present a general construction of the JMS model in which there are K sequential capture/recapture opportunities of animals in a population, denoted $t_0, \dots, t_{K-1}$, followed by a single event of recovery, encompassing the recovery of animals from all sources of mortality, denoted t_K. We assume n_0 animals are individually marked and released at t_0 followed by $K-1$ opportunities for the attempted recapture of any previously marked animals and where an additional $n_1, \dots, n_{K-1}$ unmarked animals may also be newly captured, marked, and released. In the inter-event period between each t_k and t_{k+1}, $k = 0, \dots, K-1$, animals are assumed to be exposed to up to H mutually exclusive mortality hazard categories, $H-1$ from which they can be recovered, and a singular "other hazard" category encompassing all other mortality causes from which recoveries were not available. All recoveries of animals, dead from one of the $H-1$ recoverable hazards, are assumed to take place at t_K, some time/place after the last recapture event. Auxiliary information, specific to the probability of recovery from each of these hazards, is requisite in identifying the cause specific, inter-event hazard rates.

2.1 Model parameterization

In general, CRR models rely on three categories of parameters describing the probabilities of survival/mortality, recapture, and recovery to construct likelihood statements about the fate of a marked animal. To fully parameterize this model, we first let

> $\boldsymbol{\phi}$ to be a K-sized vector where ϕ_k represents the probability an animal alive at t_{k-1} survives until t_k and
> $\boldsymbol{\Theta}$ be a $K \times H$ matrix where element $\Theta_{k,h}$ represents the probability an animal alive at t_{k-1} dies prior to t_k due to mortality cause h for $h = 1, \dots, H-1$. For $\Theta_{k,H}$, the probability an animal alive at t_{k-1} dies prior to t_k due to "other hazards", we avoid overparameterization by recognizing $\Theta_{k,H} = 1 - \phi_k - \Sigma_{h<H}\Theta_{k,h}$. Note that, since t_K does not involve live recapture, survival beyond the last recapture opportunity, ϕ_K, is necessarily confounded with death from "other hazards" after the last recapture opportunity, $\Theta_{K,H}$.
>
> We then also let
>
> $\mathbf{p}$ be a $(K-1)$-length vector where element p_k, $k = 1, \dots, K-1$, represents the probability that an animal alive at t_k is recaptured, and

> $\boldsymbol{\lambda}$ be a H-length vector where element λ_h represents the probability of recovery for an animal which dies due to mortality cause h at any time between t_0 and t_K. We assume $\lambda_h \in (0, 1]$ for $h = 1, 2, \ldots, H - 1$ and $\lambda_H = 0$, indicating the inability to recover animals from unspecified mortality causes. Here, we additionally assume $\boldsymbol{\lambda}$ to be independent of the inter-event opportunity period in which an animal dies.

2.2 Summary statistics

In addition to $\mathbf{n}$, the vector of newly captured, marked, and released animals defined above, we organize the statistics necessary to identify the survival/mortality and recapture probabilities with two matrices: $\mathbf{M}$, tabulating recaptures; and $\mathbf{D}$, tabulating recoveries. Specifically, we define

> $\mathbf{M}$ to be a K-sized upper-triangular square matrix where element $M_{k,k'}$ represents the number of animals released at t_{k-1} (both previously and newly marked) which are first recaptured again at opportunity $t_{k'}$, where $k' \geq k$, and
> $\mathbf{D}$ to be a $K \times H$ matrix where element $D_{k,h}$ represents the total number of animals released at opportunity t_{k-1} that are never recaptured again but later recovered from mortality cause h, for $h = 1, \ldots, H - 1$, and element $D_{k,H}$ represents the number of animals released at t_{k-1} that are never subsequently recaptured nor recovered. Note that, in contrast to the first $H - 1$ columns of $\mathbf{D}$, which correspond directly with the first $H - 1$ columns of $\boldsymbol{\Theta}$, the Hth column of $\mathbf{D}$ represents an accumulation of unrecovered animals from all mortality sources as well as animals who survive to t_K.

Finally, we define $\{\mathbf{U}\}$ to be a set of varying size encompassing all supplemental data used to inform recovery probabilities. In constructing the likelihood, we refer to the probability function relating $\{\mathbf{U}\}$ and $\boldsymbol{\lambda}$ as the "recovery information function" to be discussed in detail later.

2.3 Likelihood calculation

We define several notational parameters and statistics to help simplify the construction of the model. With these transformations we can express the likelihood function with five distinct products. The first product accounts for estimation of recapture probabilities using data from the recapture opportunities. The next three products address survival prior to an animal's last recapture and the continued survival, unsuccessful recapture, and eventual death that can be inferred from an animal's recovery or lack thereof. Lastly, we discuss the product dealing with auxiliary data addressing the identification of recovery parameters.

2.3.1 Recapture data

Noting the recapture of live animals and unsuccessful recapture of animals known to be alive provides a means to directly estimate the recapture probability throughout the system. The recapture of animals known to be alive at each recapture opportunity is assumed to be a binomial process with the elements of **p** representing the probability of successful recapture with the elements of **M** denoting the number of successful recaptures. For notational ease, we define

> $\mathbf{q} = 1 - \mathbf{p}$ to be a K-length vector representing the probabilities of unsuccessful recaptures and
> $\mathbf{V}$ to be a K-sized upper-triangular square matrix tabulating known failed recaptures. That is, $V_{k,k'}$ represents the number the animals released at t_{k-1} that were not recaptured at $t_{k'}$ but were encountered at one or more subsequent recapture opportunities (i.e. $V_{k,k'} = \Sigma_{j>k'} M_{k,j}$). Additional information about unsuccessful recapture can be inferred by recovery data which will be addressed shortly.

The contributions to the likelihood provided by **M** and **V** can be expressed

$$L_{recapture} \propto \prod_{k=1}^{K-1} p_k^{\sum_{i=1}^{k} M_{i,k}} q_k^{\sum_{i=1}^{k} V_{i,k}}.$$

2.3.2 Recovery data

The JMS model is constructed to describe complex systems with imperfect recapture rates, imperfect rates of recovery, and where recoveries are of uncertain spatial/temporal origin. The entries of **D** identify where an animal was last recaptured and then recovered, for columns $h = 1, \ldots, H - 1$, or never recovered for $h = H$. The information of **D** does not directly identify within which inter-event opportunity the individual died nor, in the case of $\mathrm{D}_{k,H} \forall k$, is the cause of death always known. Consequently, likelihood probabilities associated with entries of **D-**accounting for the full array of possible reaches survived, missed recaptures, and probable recovery- are most efficiently expressed with matrices. To enable these calculations, we first let

$$\mathrm{X} = \begin{bmatrix} 1 & \phi_1 q_1 & \phi_1 q_1 \phi_2 q_2 & \cdots & \prod_{\mathrm{k}=1}^{\mathrm{K}-1} \phi_k q_k \\ 0 & 1 & \phi_2 q_2 & \cdots & \prod_{\mathrm{k}=2}^{\mathrm{K}-1} \phi_k q_k \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 1 \end{bmatrix}$$

such that the entry at $\chi_{k,k+i}$ represents the probability that an individual released at t_{k-1} remains alive but is unsuccessfully recaptured for the next i consecutive opportunities. The product, $\mathbf{X}\boldsymbol{\Theta}$, is then be employed to describe the probabilities of individuals surviving subsequent their last recapture until death. Applying recovery probabilities, we can define

> $\mathbf{X}\boldsymbol{\Theta}\mathrm{diag}(\boldsymbol{\lambda})$, to be a $K \times H$ matrix where $\{\mathbf{X}\boldsymbol{\Theta}\mathrm{diag}(\boldsymbol{\lambda})\}_{k,h}$ represents the probability an individual last recaptured at t_{k-1} was never recaptured again but recovered from mortality cause h, for $h < H$, and

$\mathbf{X}\boldsymbol{\Theta}(1-\boldsymbol{\lambda})$ to be a K-length vector where $\{\mathbf{X}\boldsymbol{\Theta}(1-\boldsymbol{\lambda})\}_k$ represents the probability an animal last recaptured at t_{k-1} was never recaptured again nor ever recovered.

The contribution of $\mathbf{D}$ to the likelihood can then be expressed in three probability statements. We first define

$L_{\textit{survival to last recapture}} \propto \prod_{k=1}^{k-1} \phi_k^{\Sigma_{i=1}^{k}(n_{i-1}-\Sigma_h D_{k,h})}$ to account for the number of inter-event periods each animal was known to survive. We then define
$L_{\textit{dead recoveries}} \propto \prod_{k=1}^{K} \prod_{h=1}^{H-1} \{\mathbf{X}\boldsymbol{\Theta}\mathrm{diag}(\boldsymbol{\lambda})\}_{k,h}^{D_{k,h}}$ and
$L_{\textit{unrecovered animals}} \propto \prod_{k=1}^{K} \{\mathbf{X}\boldsymbol{\Theta}(1-\boldsymbol{\lambda})\}_k^{D_{k,H}}$ to account for the possible life paths an animal may have taken following its last recapture.

2.3.3 Recovery information function

The last portion of the likelihood equation encompasses the identification of the all the parameters describing recovery. Unless perfect recovery is assumed (i.e. $\lambda_h = 1 \forall h < H$), supplemental information is necessary to separately identify $\boldsymbol{\Theta}$ and $\boldsymbol{\lambda}$. In practice, we assume each λ_h to be a function of one or more additional parameters. These additional parameters are assumed identifiable through recovery information functions, $g_h(\mathbf{U}_h, \lambda_h)$, specific to each mortality source, where each $\mathbf{U}_h$ is a set of additional recovery data specific to mortality cause h (e.g., use of test tags, reward tags; Pollock et al. 2001; Hostetter et al. 2015a). We assume that, for each $h = 1, \ldots, H-1$, $\mathbf{U}_h$ is sufficient for the estimation of λ_h. Each $\mathbf{U}_h$ may summarize an array of information sources such as the probability of reporting of harvest by hunters or anglers, the probability of recovering a dead animal, the probability of recovering tags from fish on a bird colony, etc. The contribution of this information to the likelihood can be expressed generically as

$$L_{\textit{recovery information}} = \prod_{h=1}^{H-1} g_h(\mathbf{U}_{\mathrm{h}}, \lambda_h).$$

2.3.4 Likelihood

With these transformations we can express the likelihood function as follows:

$$L \propto \underbrace{\prod_{k=1}^{K-1} p_k^{\sum_{i=1}^{k} M_{i,k}} q_k^{\sum_{i=1}^{k} V_{i,k}}}_{\textit{recaptures}} \times \underbrace{\prod_{k=1}^{K-1} \phi_k^{\sum_{i=1}^{k}(n_{i-1}-\sum_h D_{k,h})}}_{\textit{survival to last recapture}}$$
$$\times \underbrace{\prod_{k=1}^{K} \prod_{h=1}^{H-1} \{\mathbf{X}\boldsymbol{\Theta}\mathrm{diag}(\lambda)\}_{k,h}^{D_{k,h}}}_{\textit{dead recoveries}} \times \underbrace{\prod_{k=1}^{K} \{\mathbf{X}\boldsymbol{\Theta}(1-\lambda)\}_k^{D_{k,H}}}_{\textit{unrecovered animals}} \times \underbrace{\prod_{h=1}^{H-1} g_h(U_h, \lambda_h)}_{\textit{recovery information}}.$$

2.3.5 Reparameterization as a single multinomial process

In a sequentially defined system, whereby simplexes of survival/mortality rates are uniquely defined for each inter-event period, each successive period's estimates are necessarily dependent on the cumulative estimate of survival through the preceding inter-event periods. Developing estimates of inter-event mortality rates can therefore become increasingly intractable as more recapture events are considered. This correlation among parameters creates interdependent prior distributions and complex likelihood geometries from which it is difficult to simulate draws using Monte Carlo algorithms (Gelman 2004; Papaspiliopoulos et al. 2007).

We therefore suggest a re-parameterization allowing the system to be treated as a single multinomial process. We define a "life-path simplex", $\boldsymbol{\Omega} = \mathrm{diag}\left(\begin{bmatrix} 1 \\ \phi_1 \\ \phi_1\phi_2 \\ \vdots \\ \phi_1\phi_2 \ldots \phi_{K-1} \end{bmatrix}\right)\boldsymbol{\Theta}$, to be a $K \times H$ matrix, where $\Omega_{\mathrm{k,h}}$ represents the probability an animal released at t_0 survives until t_{k-1} then succumbs to hazard h prior to t_k. The elements of Ω then sum to one and represent all relevant outcomes possible for an animal released at t_0. Treating the system in this manner mitigates many of the concerns outlined above, most pragmatic of which, is the computational efficiency gained. Furthermore, this choice of re-parameterization facilitates several additional benefits including the simplifying of covariate introduction and the derivation of relationships among the mortality parameters. For instance, this parameterization readily allows for the modelling of serial correlation among weekly cohorts as demonstrated in the example dataset to follow.

3 Example application

3.1 Capture, recapture, and recovery data

To illustrate implementation of the JMS model, we analysed survival and cause-specific mortality of PIT-tagged juvenile steelhead trout outmigrating through the FCRPS to the Pacific Ocean. Over the course of 10 weeks in the spring (April–June) of 2014, 62 690 steelhead trout were captured at Lower Granite Dam (GRA), PIT-tagged (12-mm × 2-mm; 134.2 kHz), and released into the tailrace of the dam, 695 river kilometers {rkm} from the ocean. Following release at GRA, migrating steelhead encountered six potential live PIT-tag recapture locations downstream: (1) Little Goose Dam (LGO, rkm 635),(2) Lower Monumental Dam (LMO, rkm 589), (3) McNary Dam (MCN, rkm 470), (4) John Day Dam (JDA, rkm 348), (5) Bonneville Dam (BON rkm 234) and (6) a vessel towed pair-trawl net detection system in Columbia River Estuary (EST, rkm 75; Fig. 1). No unmarked fish were marked at subsequent recaptures (i.e. $n_k = 0 \forall k > 0$). In addition to recapture sites, some steelhead were consumed alive by avian predators and then recovered dead on one of nine bird colonies located downstream of GRA (Fig. 1). Researchers used hand-held PIT-tag antennas to recover tags on bird colonies following the breeding season (August–November; see Hostetter et al. 2015a for details). Waterbird colonies scanned for steelhead tags were identified by species and island location and included (1) Caspian terns (*Hydroprogne caspia*, hereafter CATE) nesting on Crescent Island (CSI, rkm 510), (2) Central Blalock Island (CBI, rkm 440), and (3) East Sand Island (ESI, rkm 8), (4) California and ring-billed gulls (*Larus californicus* and *Larus delewarensis*, hereafter LAXX) nesting on Island 20 (IS20, rkm 549) (5) CSI, (6) CBI, and (7) Miller Rocks Island (MRI, rkm 331), and double-crested cormorants (*Phalacrocorax auritus*, hereafter DCCO) nesting at (8) Foundation Island (FDI, rkm 518) and (9) ESI. As noted above, survival through the system and death beyond EST are necessarily confounded. We therefore refer to the life history represented by $\theta_{K,H}$ as "non-depredated survivors past EST".

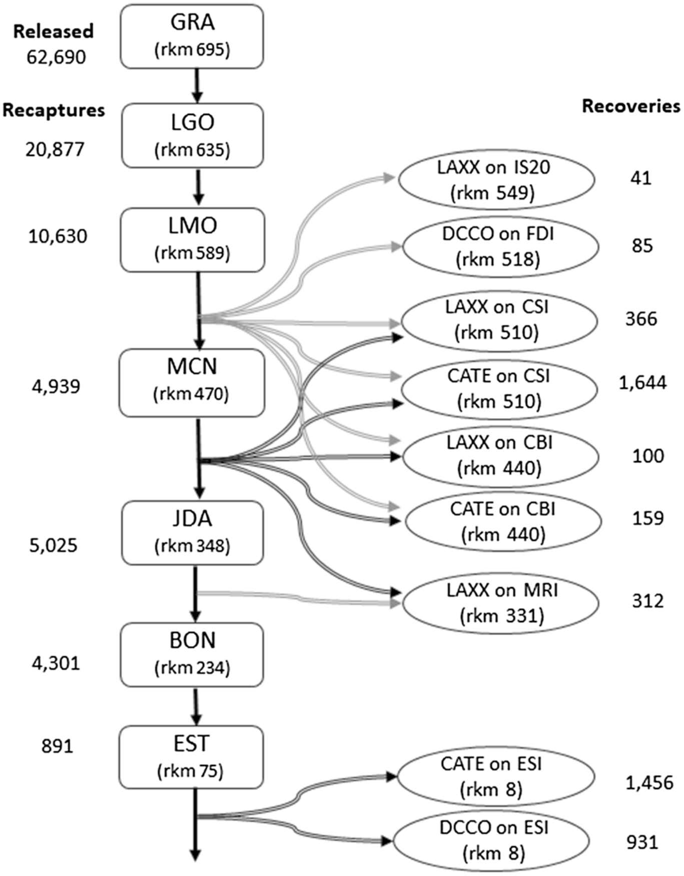

Fig. 1 Schematic of release, recapture, and recovery sites used in the study, along with the number of tagged steelhead detected at each site. Fish were released from Lower Granite Dam (GRA) and subject to live recapture events at downstream antennas or dead recovery events at bird colonies. Arrows depict colonies capable of consuming fish above and below live recapture sites

The flexible framework of the JMS model allowed for specialization to address several challenges and ecological hypotheses associated with the case study. Rates of survival, predation, recapture, and recovery were all assumed to vary over time, with rates from periods closer in time assumed to be more alike than those temporally further apart. To account for this variation, we grouped fish releases into weekly cohorts, defining recapture and recovery matrices accordingly ($\mathbf{M}_w$ and $\mathbf{D}_w$), and developed week-specific survival, recapture, and recovery rates ($\boldsymbol{\phi}_w$, $\mathbf{p}_w$, and $\boldsymbol{\lambda}_w$) with an assumption of serial correlation among weekly rates. Annual rates were calculated as an average of weekly rates weighted by weekly release counts.

3.2 JMS adjustment for autocorrelation

Avian predation rates and survival rates were both assumed to vary weekly (Evans et al. 2014; Hostetter et al. 2015a) and Gaussian processes were employed to model this time-dependent variation. Noting vec($\boldsymbol{\Omega}_w$) as a simplex allows us to address autocorrelation with a logistic regression analogue. Using non-depredated survivors past EST as the reference level, we assume

$$\log\left(\frac{\Omega_{k,h,w+1}}{\Omega_{K,H,w+1}}\right) = \log\left(\frac{\Omega_{k,h,w}}{\Omega_{K,H,w}}\right) + \eta_{k,h,w}$$

where $\eta_{k,h,w} \sim \ Normal(0, \sigma^2_{k,h}) \forall k, h, w$ (excluding the reference level $k = K, h = H$).

Weekly differences in dam operations and river conditions (e.g., flows, spill percentage, etc.) were assumed to influence recapture probabilities of tagged fish across time at each dam (Sandford and Smith 2002; Hostetter et al. 2015b). Weekly variations in recapture rates were also modelled as an auto-regressive process,

$$\text{logit}(p_{k,w+1}) = \text{logit}(p_{k,w}) + \epsilon_{k,w}$$

where $\epsilon_{k,w} \sim Normal(0, \tau^2_k) \forall k, w$.

Using an amalgam of previous research, we can reduce the number of parameters to be estimated by recognizing the limited foraging range of the colonies under consideration (see Fig. 1; Evans et al. 2016). That is, cause-specific mortality rates for each colony were forced to equal zero (0) in river reaches in which we could assume they did not forage. Thus, we let

$$\boldsymbol{\theta} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \theta_{1,10} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \theta_{2,10} \\ \theta_{3,1} & \theta_{3,2} & 0 & \theta_{3,4} & \theta_{3,5} & \theta_{3,6} & 0 & \theta_{3,8} & 0 & \theta_{3,10} \\ 0 & \theta_{4,2} & 0 & \theta_{4,4} & \theta_{4,5} & \theta_{4,6} & \theta_{4,7} & 0 & 0 & \theta_{4,10} \\ 0 & 0 & 0 & 0 & 0 & 0 & \theta_{5,7} & 0 & 0 & \theta_{5,10} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \theta_{6,10} \\ 0 & 0 & \theta_{7,3} & 0 & 0 & 0 & 0 & 0 & \theta_{7,9} & \theta_{7,10} \end{bmatrix}$$

where river reaches and mortality causes are delineated as noted above and mortality cause $h = H = 10$ representing “other hazards” that were not under explicit consideration.

3.3 Recovery function form and data

The proportion of recovered steelhead tags does not account for all PIT-tagged fish consumed by a bird colony due to two probabilistic factors: (1) not all tags ingested by birds are subsequently deposited on the birds’ nesting colony (i.e., deposition probability is < 1.0; Hostetter et al. 2015a; Teuscher et al. 2015) and (2) not all tags deposited by birds on their nesting colony are subsequently found by researchers after the breeding season (i.e., detection probability < 1.0; Ryan et al. 2003; Evans et al. 2012). Furthermore, tags deposited later in the season are assumed to be more likely to be detected and thus inter-weekly variation must also be reflected in the construction of recovery rates and therefore into the construction of the recovery information function, $g_h(\mathbf{U}_{\boldsymbol{h},w}, \lambda_{h,w})$. The two processes comprising tag recovery are assumed to be statistically independent such that we can let $\lambda_{h,w} = \delta_h * \psi_h(w)$. While the detection probability, $\psi_h(w)$, is written as a function of week, the deposition rate, δ_h, is assumed constant across a breeding season (Hostetter et al. 2015a).

Predator-specific (CATE, DCCO, LAXX) deposition probabilities were estimated from an independent controlled feeding experiment (Hostetter et al. 2015a). Herein, we assume predator-specific deposition probabilities for each colony h, $\delta_h \sim Beta(a_h, b_h)$ where a_h and b_h are the Beta parameters suggested by Hostetter et al. (2015a) for the species of predator associated with colony h. Thus, δ_h is assumed identifiable from this information alone and is treated as an informed prior in the fitting of the model.

Estimates of detection probabilities were derived using repeated intentional sowing of a known number of PIT-tags on each colony that were then later recovered following the breeding season (Evans et al. 2012). We let

$U^n_{h,w}$ be the number of intentionally sown tags on colony h in week w and
$U^x_{h,w}$ be the number of $U^n_{h,w}$ subsequently recovered following the breeding/migration season.

The variation in the detection probability across time is modelled using logistic regression (Evans et al. 2012; Hostetter et al. 2015a). That is, we assume

$$U^x_{h,w} \sim Binomial\left(U^n_{h,w}, \psi_h(w)\right)$$

where

$$\psi_h(w) = \mathrm{logit}^{-1}(\alpha_h + \beta_h w).$$

For two of the colonies, researchers were unable to access the colonies prior to the breeding season to intentionally sow tags. We therefore incorporated information from other migration years to inform the estimate of $\psi_h(w)$. The colonies where these considerations were required were the LAXX colony on Island 20 (for which we incorporated information collected from the same colony in the years 2013, 2015, and 2016) and the CATE colony on Blalock Islands (for which we incorporated information collected from the same colony in the years 2008, 2009, 2011, 2013, 2015, and 2016). For these colonies, we assume the parameters defining the logistic relationship outlined above vary among years according to a multivariate-normal distribution. That is, we assume

$$\begin{bmatrix} \alpha_h^y \\ \beta_h^y \end{bmatrix} \sim \mathit{Normal}\left(\begin{bmatrix} \mu_{\alpha_h} \\ \mu_{\beta_h} \end{bmatrix}, \boldsymbol{\Sigma}_h \right).$$

Therefore, the recovery information function for this iteration of the JMS (omitting the requisite prior distributions) was

$$\prod_{h=1}^{H-1} g_h(\boldsymbol{U}_h, \lambda_h) \propto \prod_{h=1}^{H-1} \delta_h^{a_h-1}(1-\delta_h)^{b_h-1}$$
$$* \prod_{h=1}^{H-1} \prod_{w} \psi_h(w)^{U^x_{h,w}} [1-\psi_h(w)]^{U^n_{h,w}-U^x_{h,w}}.$$

There is substantial mortality on steelhead from sources with which recoveries were not possible (e.g., predatory fish, dam passage, disease, and other causes; Ward et al. 1995; Muir et al. 2001; Dietrich et al. 2011). All these other hazards are encompassed by mortality cause H and we therefore set $\lambda_H = 0$ (i.e. these animals cannot be recovered).

Non- or weakly-informative priors were employed for all parameters and hyperparameters, as suggested by Gelman et al. (2013). The initial week's recapture parameters, $\mathbf{p}_1$, and life path simplexes, $\boldsymbol{\Omega}_1$, exist in closed parameter spaces and were thus assigned uniform priors (i.e. $p_{k,1} \sim \mathit{Uniform}(0,1)$ and $[\mathrm{vec}(\boldsymbol{\Omega}_1)] \sim \mathit{Dirichlet}(\mathbf{1})$). The two variance parameters associated with the Gaussian processes, τ_i and $\sigma_{j,h}$, were assigned half-normal prior distributions with variance 25. Such distributions were selected primarily for the efficiency they provide in the MCMC process. The hyperparameters α_h and β_h were both assigned weakly-informative normal priors (mean of 0, variance of 25). The hyper–hyper parameters μ_{α_h} and μ_{β_h} were assigned similar weakly-informative normal priors (mean of 0, variance of 25). The parameters of $\boldsymbol{\Sigma}_h$ were assigned half-normal prior distributions with variance equal to 5.

Simulated samples from the posterior distribution were derived using the software Stan (Stan Development Team 2016), accessed through R version 3.1.2 (R Development Core Team 2014), using the rstan package (version 2.17.3; Stan Development Team 2016). We ran four parallel Hamiltonian Monte Carlo (HMC) simulations (Betancourt and Mark 2015). Each chain contained 2000 adaptation iterations, followed by 2000 posterior iterations. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2013). Chains were only considered valid given Gelman-Rubin statistics for all parameters valued less than

1.01 and zero (0) divergent transitions reported. Posterior predictive checks were used to assure model fit with respect to site-specific annual recapture counts and site-specific annual recovery counts (Gelman et al. 2013). Bayesian p values were all deemed to be of little concern (p values $\in (0.1, 0.9)$). We present estimate results as posterior medians along with 95% highest (posterior) density intervals (95% CRI).

4 Results

Well informed recovery probabilities were crucial to the identification of colony specific mortality rates and varied greatly across colonies. For instance, the probability of recovering a tag from a week 1 released fish consumed by LAXX nesting at CSI was estimated to be 0.08 (95% CRI: [0.05, 0.12]; Table 1). This suggests that for every week 1 released tag recovered from the CSI LAXX colony, approximately 11 other fish were consumed, but the tags were destroyed, lost, or otherwise rendered unrecoverable (see Hostetter et al. 2015a for additional details). Comparatively, the probability of recovering a tag from a week 10 released fish consumed by CATE nesting at CSI was estimated to be 0.52 (95% CRI: [0.29, 0.71]; Table 1). Thus, every recovery represented the consumption of approximately two fish by the CSI CATE colony.

We estimated high (>94%) annual survival rates of steelhead released from GRA in the first two downstream river reaches (GRA-LGO, LGO-LMO; Table 2), reaches that were outside of the foraging range of the colonies under consideration in this study (Fig. 1). Survival in the third reach (LMO-MCN), where steelhead first encountered predation from colonies included in the study, was estimated to be $\hat{\phi}_4 = 0.77$ (95% CRI: [0.73, 0.80]). We estimated aggregate predation by all birds ($\Sigma_{h<H}\hat{\theta}_{3,h}$) in this reach to be 0.14 (95% CRI: [0.11, 0.18]). The greatest colony-specific rate of predation in the LMO-MCN reach was due to CATE nesting on CSI, where an estimated 0.06 (95% CRI: [0.04, 0.10]) of steelhead alive at LMO were consumed by terns from this individual colony. The simultaneous estimation of cause-specific mortality and survival also provided a direct measure of the proportion of total mortality (compliment of survival) due to avian predation, which we estimated at 59.4% in this reach (95% CRI: [44, 82]; Fig. 2). This suggests that aggregate avian predation may have been this reach's greatest source of steelhead mortality.

Despite the presence of multiple avian predators downstream of MCN (Fig. 1), estimated annual survival rates in both the MCN-JDA (0.94 (95% CRI: [0.89, 0.97]) and JDA-BON (0.92 (95% CRI: [0.87, 0.95]) reaches were high (Table 2). However, as with the LMO-MCN reach, the aggregate impact of avian predators in these river reaches was likely the dominate mortality factor, with aggregate avian predation accounting for an estimated 91% (95% CRI: [43, 100]) and 96% (95% CRI: [53, 100]) of all steelhead mortality sources in these two reaches, respectively. Of the individual colonies foraging in these reaches, predation rates were the highest by LAXX colonies, with gulls nesting on CBI and MRI consuming an estimated

Table 1 Comparison of estimated deposition (time independent), detection given deposition (shown for the first and final week of the migration season), and recovery (deposition *x* detection) probabilities along with 95% credible intervals

Colony	$p(deposition)$	$p(deposition)$		$p(recovery)$	
	$\hat{\delta}$	$\widehat{\psi(1)}$	$\widehat{\psi(10)}$	$\widehat{\lambda(1)}$	$\widehat{\lambda(10)}$
CATE on CSI	0.60 (0.33–0.81)	0.66 (0.53–0.77)	0.87 (0.81–0.92)	0.39 (0.21–0.56)	0.52 (0.29–0.71)
CATE on CBI	0.69 (0.48–0.86)	0.27 (0.03–0.69)	0.59 (0.31–0.83)	0.18 (0.02–0.48)	0.39 (0.19–0.59)
CATE on ESI	0.71 (0.53–0.88)	0.49 (0.41–0.57)	0.64 (0.59–0.70)	0.34 (0.24–0.45)	0.45 (0.33–0.57)
LAXX on IS20	0.15 (0.11–0.20)	0.60 (0.20–0.96)	0.81 (0.62–0.95)	0.09 (0.02–0.16)	0.12 (0.07–0.17)
LAXX on CSI	0.16 (0.12–0.21)	0.52 (0.31–0.71)	0.91 (0.83–0.98)	0.08 (0.05–0.12)	0.14 (0.11–0.19)
LAXX on CBI	0.15 (0.10–0.20)	0.81 (0.60–0.96)	0.95 (0.90–1.00)	0.12 (0.07–0.16)	0.14 (0.10–0.19)
LAXX in MRI	0.14 (0.10–0.19)	0.79 (0.63–0.92)	0.84 (0.77–0.91)	0.11 (0.07–0.16)	0.12 (0.08–0.16)
DCCO on FDI	0.49 (0.30–0.67)	0.19 (0.12–0.27)	0.19 (0.13–0.25)	0.09 (0.05–0.15)	0.09 (0.05–0.14)
DCCO on ESI	0.48 (0.31–0.67)	0.67 (0.60–0.73)	0.75 (0.70–0.79)	0.32 (0.19–0.44)	0.36 (0.22–0.49)

Bird species include Caspian terns (CATE), California and ring-billed gulls (LAXX), and double-crested cormorants (DCCO). Colony sites include Island 20 (IS20), Foundation Island (FDI), Crescent Island (CSI), Central Blalock Island (CBI), Miller Rocks Island (MRI), and East Sand Island (ESI)

Table 2 Annual estimates of reach-specific (inter-event) and cumulative survival probabilities, reach/colony-specific predation probabilities, reach-specific and cumulative predation probabilities, and recapture probabilities, along with 95% credible intervals

	GRA-LGO	LGO-LMO	LMO-MCN	MCN-JDA	JDA-BON	BON-EST	Beyond EST
Survival							
Reach	0.953 (0.94–0.97)	0.944 (0.92–0.97)	0.766 (0.73–0.80)	0.942 (0.89–0.97)	0.924 (0.87–0.95)	0.762 (0.63–1.00)	*NA*
Cumulative	0.953 (0.94–0.97)	0.899 (0.88–0.92)	0.687 (0.66–0.71)	0.647 (0.62–0.67)	0.597 (0.56–0.63)	0.450 (0.36–0.59)	*NA*
Colony specific predation by reach							
LAXX on IS20	< 0.01	< 0.01	0.007 (0.00–0.01)	< 0.01	< 0.01	< 0.01	<0.01
DCCO on FDI	< 0.01	< 0.01	0.017 (0.01–0.03)	< 0.01	< 0.01	< 0.01	<0.01
LAXX on CSI	< 0.01	< 0.01	0.050 (0.03–0.07)	0.009 (0.00–0.02)	< 0.01	< 0.01	<0.01
CATE on CSI	< 0.01	< 0.01	0.060 (0.04–0.10)	< 0.01	< 0.01	< 0.01	<0.01
LAXX on CBI	< 0.01	< 0.01	< 0.01	0.018 (0.01–0.03)	< 0.01	< 0.01	<0.01
CATE on CBI	< 0.01	< 0.01	< 0.01	0.013 (0.01–0.03)	< 0.01	< 0.01	<0.01
LAXX in MRI	< 0.01	< 0.01	< 0.01	0.002 (0.00–0.02)	0.067 (0.04–0.09)	< 0.01	<0.01
CATE on ESI	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.140 (0.10–0.20)
DCCO on ESI	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.095 (0.06–0.15)
Aggregate predation							
Reach	< 0.01	< 0.01	0.139 (0.11–0.18)	0.048 (0.03–0.07)	0.067 (0.04–0.09)	< 0.01	0.239 (0.16–0.33)
Cumulative	< 0.01	< 0.01	0.125 (0.10–0.17)	0.157 (0.13–0.20)	0.201 (0.16–0.24)	0.201 (0.16–0.24)	0.310 (0.27–0.36)
Recapture							
Reach	0.350 (0.34–0.36)	0.192 (0.19–0.20)	0.116 (0.11–0.12)	0.124 (0.12–0.13)	0.124 (0.12–0.13)	0.033 (0.03–0.04)	*NA*

Fish were released from Lower Granite Dam (GRA) and subject to live recapture events at Little Goose Dam (LGO), Lower Monumental Dam (LMN), McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and the trawl mounted array in the estuary (EST). Reach-specific rates are measured from the immediately preceding recapture opportunity, aggregate predation rates are measured within a reach, and cumulative rates are measured from release at GRA

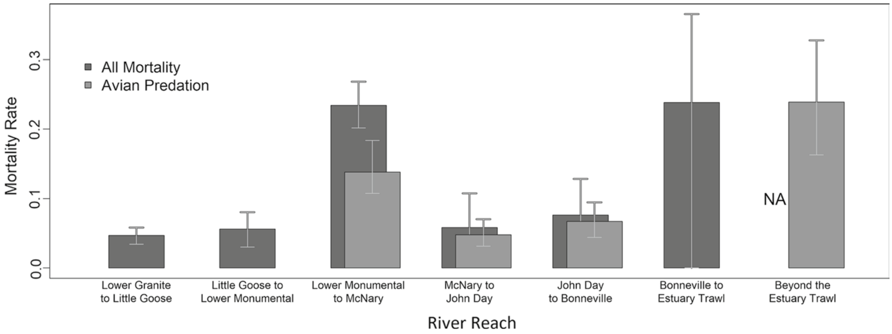

Fig. 2 Estimated total mortality (dark grey) and total avian predation mortality (light grey) of tagged steelhead released at Lower Granite Dam during 2014. Error bars represent 95% creditable interval. An estimate of total mortality downstream of estuary trawl is not available (NA). Avian predation only includes colonies listed in Table 1

0.02 (95% CRI: [0.01, 0.03]) and 0.07 (95% CRI: [0.04, 0.09]) of available steelhead within the MCN-JDA and JDA-BON reaches, respectively (Table 2).

Downstream of EST we estimated an aggregate avian predation rate in the estuary of 0.24 (95% CRI: [0.16, 0.33]), with predation probabilities of 0.14 (95% CRI: [0.10, 0.20]) for ESI CATE and 0.09 (95% CRI: [0.06, 0.15]) for ESI DCCO (Table 2). The recovery of tags from bird colonies on ESI additionally allowed for the estimation of survival through the BON-EST reach, an estimate otherwise unidentifiable from recapture data alone. We estimated cumulative steelhead survival from GRA to EST to be 0.45 (95% CRI: [0.36, 0.59]). It follows, that the rate of non-depredated survivors past EST was estimated to have been 0.34 (95% CRI: [0.24, 0.47]). This also represents the estimated upper limit of steelhead survival from GRA to the Pacific Ocean. The cumulative steelhead predation rate from release at GRA by all avian predators (CATE, DCCO, LAXX) was estimated to be 0.31 (95% CRI: [0.27, 0.36]). It follows that we estimate, for every three steelhead released at GRA in 2014, approximately at most one made it to the ocean, one was depredated by the colonies in this study, and one succumbed to some other unidentified cause. Collectively, these results indicate that, in aggregate, the nine avian colonies included in our study were likely one of greatest sources of steelhead mortality during outmigration to the Pacific Ocean in 2014.

5 Discussion

Information provided by recovery data can significantly increase precision and reduce bias in survival probabilities in CR models (Burnham 1993; Barker 1997; Catchpole et al. 1998). Also, CRR models, and the JMS model specifically, allow for survival estimation to the final recapture opportunity when there are subsequent recoveries opportunities. This was particularly evident in our example dataset, as there were substantially more tags recovered downstream of the final recapture site than were seen at the final recapture site (2387 recovered tags compared with 891 recaptured tags). The consideration of all available data (recapture and recovery) relevant to the life-cycle of an animal can also be beneficial, regardless of researchers' driving motivation, whether that be survival or cause-specific mortality rates. Further, the simultaneous or joint estimation of survival and mortality (in this case avian predation) provided a more holistic interpretation of results.

This example dataset demonstrates the numerous benefits of using the JMS model as an alternative to the independent survival and predation models currently in use. The JMS model allows for direct comparison of individual and aggregate mortality factors at various spatial and temporal scales. We note that previous avian predation studies in the Columbia River basin have estimated predation separate from survival using all fish detected (i.e., "released") at the nearest upstream dam (Evans et al. 2012; Hostetter et al. 2015a). While not incorporated into our example dataset, these newly detected fish can readily be included into the JMS model, resulting in larger sample sizes for both survival and mortality estimation.

While the benefits of the JMS are numerous, the added assumptions underlying the model must be carefully considered. Specifically, the JMS model assumes mortality rates are independent of the probability of recapture or recovery. This is a potential source of contention in the case study as recovery probabilities may be dependent on the physical condition of the fish, with poor condition fish (injured or sick fish) potentially more susceptible to predation by birds than good condition fish (Hostetter et al. 2012). Fish of different sizes (e.g., fork-lengths) and fish of poor condition may also have different recapture probabilities during migration (Zabel et al. 2005; Hostetter et al. 2015b). Thus, a disproportionate number of detections (recaptures and recoveries) may be made by fish with lower survival probabilities and higher predation rates. It may be difficult to prove such a relationship though, and additional research into the independence of these parameters could be valuable.

In conclusion, we have presented a comprehensive method for jointly estimating survival and cause-specific mortality rates based on recapture and recovery data with indeterminate time or place of death. This method allows the use of dead recoveries to increase knowledge about the fate of animals otherwise unknown from encounter histories alone. We are additionally able to model survival and multiple causes of mortality within one all-encompassing model, which leads to a more cohesive understanding of the factors influencing population dynamics with greater accuracy and precision.

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