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Breeding Return Times and Abundance in Capture–Recapture Models

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Summary. For many long-lived animal species, individuals do not breed every year, and are often not accessible during non-breeding periods. Individuals exhibit site fidelity if they return to the same breeding colony or spawning ground when they breed. If capture and recapture is only possible at the breeding site, temporary emigration models are used to allow for only a subset of the animals being present in any given year. Most temporary emigration models require the use of the robust sampling design, and their focus is usually on probabilities of annual survival and of transition between breeding and non-breeding states. We use lake sturgeon *(Acipenser fulvescens)* data from a closed population where only a simple (one sample per year) sampling scheme is possible, and we also wish to estimate abundance as well as sex-specific survival and breeding return time probabilities. By adding return time parameters to the Schwarz-Arnason version of the Jolly–Seber model, we have developed a new likelihood-based model which yields plausible estimates of abundance, survival, transition and return time parameters. An important new finding from investigation of the model is the overestimation of abundance if a Jolly–Seber model is used when Markovian temporary emigration is present.

Key words: Abundance; Breeding return times; Capture–recapture analysis; Lake sturgeon; Temporary emigration; Unobserved state.

1. Introduction

For many long-lived animal species the individuals do not breed every year, but when breeding they exhibit site fidelity, returning to the same breeding colony or spawning ground. If capture and recapture are only possible at the breeding site, temporary emigration (TE) models are used to allow for only a subset of the animals being present in any given year. If no information is available from other sites where the animals might be residing while not breeding, TE models are also known as multistate or multi-event models with unobservable states. Many models with TE have been developed (Arnason, 1973; Brownie et al., 1993; Kendall and Bjorkland, 2001; Lebreton and Pradel, 2002; Kendall and Nichols, 2002; Fujiwara and Caswell, 2002; Kendall, 2004; Schaub et al., 2004; Pradel, 2005; Bailey, Kendall and Church, 2009; Converse et al., 2009; Hunter and Caswell, 2009; Kendall, 2009; Bailey, Converse and Kendall, 2010). Most TE models require the use of Pollock's robust sampling design (Pollock, 1982) in which several secondary samples are taken during each primary sample (e.g., each year), or another specialized study design such as the robust gateway design (Bailey et al., 2004; Church et al., 2007; de Lisle and Grayson, 2011), or the less-invasive robust design (Converse et al., 2009). The focus of existing TE studies is usually on (annual) probabilities of survival and of transition between sites or between breeding and non-breeding states.

We have an 11-year capture–recapture data set from an isolated population of freshwater lake sturgeon *(Acipenser fulvescens)* with salient features (i) spawning (breeding) occurs annually in the sole tributary river, (ii) only one sample per year is possible, at spawning time in the river, (iii) individual fish do not spawn every year, and (iv) non-spawning fish stay in the lake at spawning time, where they are unobservable. Our objectives are to estimate the changing **abundance** (population size) over the years and the probability distribution for **breeding return times** (number of years until next breeding).

Some studies have addressed the problem of restriction to the simple sampling scheme with only one sample per year. Clobert et al. (1994) developed a model for age at first breeding for birds marked as fledglings but then unobservable until breeding. Kendall and Nichols (2002) listed general methods for dealing with restriction to the simple design, namely (i) reducing the order of Markovian transition probabilities between states, (ii) imposing a degree of determinism on transition probabilities, (iii) removing state specificity of survival probabilities, and (iv) imposing temporal constancy of parameters. Fujiwara and Caswell (2002) investigated redundancy of parameters for TE models with the simple sampling scheme, and quantified the overestimation of survival estimates if TE is present but unmodeled. Hunter and Caswell (2009) further developed the identification of redundant parameters using automatic differentiation to assess model rank. The principles in Kendall and Nichols (2002) have been used by Rivalan et al. (2005) to estimate breeding return rates and reproductive effort in leatherback sea turtles, and by

Barbraud and Weimerskirch (2012) to estimate survival and breeding success in the Wandering Albatross. However, these simple-design models have been based on the Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton et al., 1992), conditioning on first capture and estimating survival but not population size.

The major innovation in this paper is to estimate abundance and recruitment as well as survival and return times. Ecologists generally want estimates of population abundance or density, but models providing them are less tractable than those above. Schwarz and Arnason (1996) produced a fully likelihood-based version of the Jolly–Seber (JS) model (Jolly, 1965; Seber, 1965), which estimates abundance, recruitment and survival. We extend the Jolly–Seber Schwarz–Arnason (JSSA) model with parameters for transitions between breeding and non-breeding states. By making some plausible assumptions of the types (i)–(iv) above (Kendall and Nichols, 2002), we have been able to produce a suite of feasible, likelihood-based models which enable us to perform model selection, to estimate abundance, recruitment, survival and return time parameters, and to test hypotheses of importance in modeling the dynamics of the population.

Section 2 gives the model assumptions, formulations and methods of analysis. The real data example is in Section 3, and Section 4 contains simulations to evaluate and validate the chosen models. The discussion is in Section 5, and Web Appendix A gives details of a potential source of bias in early abundance estimates.

2. The Models

2.1. *Definitions, Assumptions and Parameters*

We use the words “breeding” and “animal” throughout, rather than “spawning” and “fish,” as our methods may well be applicable to animals other than fish, for example turtles (Nichols et al., 1994; Rivalan et al., 2005), birds (Clobert et al., 1994; Barbraud and Weimerskirch, 2012) and bats (Frick, Reynolds and Kunz, 2010).

Let **return time** be the number of years until next breeding, given the animal has bred this year, and let **current population size** be the total population at the time of each sample (whether breeding or not this year). **Recruitment** to the current population occurs at first breeding during the study, at which time the new recruits are first available for capture.

There are n distinct animals seen over K capture occasions (samples, years). The data form an $n \times K$ capture matrix $\boldsymbol{X}$, with $x_{ij} = 1$ if animal i is caught in sample (year) j ($j = 1, 2, \ldots, K$), otherwise $x_{ij} = 0$. The samples are equally spaced, in our case annually so that Sample 1 is Year 1. We start with the Jolly–Seber based Schwarz–Arnason (JSSA) model, and make most of their assumptions—that captures are independent, capture sessions are instantaneous, and marks are correctly identified and are not lost. However, the assumption that all emigration is permanent is relaxed in order to allow for TE. Any loss by permanent emigration is classed as death, and any entry by immigration is classed as recruitment to the breeding population. Our models perform best if there is no immigration (see the discussion, Section 5). The parameters follow:

JSSA parameters: (with our modifications shown in boldface)

N = superpopulation size, the number of animals available for capture (i.e., **breeding**) at least once during the study

β_{j-1} = proportion of N **first breeding in the study** (FBIS) at j, ($\sum_{j=1}^{K} \beta_{j-1} = 1$)

ϕ_j = Pr(survive to $j+1$ | alive at j)

p_j = Pr(caught at j | **alive and breeding** at j)

N_j = current population size at sample j (whether **breeding or not** at j)

B_{j-1} = $N\beta_{j-1}$, **number FBIS** at j

New parameters:

M = maximum number of non-breeding years before either death or returning to breed, assuming $M < K - 1$ for feasible model fitting

τ_r = Pr(first return to breed in year $j + r$ | breeding at j), for $r = 1, \ldots, M + 1$, ($\sum_{r=1}^{M+1} \tau_r = 1$)

R_j = number of retirees at sample j, $j = 1, \ldots, M$, with $R_j = 0$ if $j > M$

The retirees are adult individuals still alive in the lake over early samples, but they do not breed again during the study, and hence are not included in the superpopulation N. At most they survive until sample M.

Our basic model uses parameters $\{N, \beta_j, p_j, \phi_j, M, \tau_r\}$, but the alternative abundance and recruitment parameters N_j and B_j can replace the N and $\boldsymbol{\beta}$ parameters via the recursive relationship

$$N_j = \phi_{j-1} N_{j-1} + B_{j-1} + R_j \text{ for } j = 2, \ldots K \text{ with } N_1 = B_0 + R_1. \tag{1}$$

Setting the maximum M allows the specification of a sequence of non-breeding states, giving a first-order Markov chain. For example if $M = 3$ there are five states, $\mathcal{B}$ for breeding, $\mathcal{N}_1$, $\mathcal{N}_2$ and $\mathcal{N}_3$ for the first, second and third year non-breeding, and $\mathcal{D}$ for dead (Figure 1).

Breeding return times are assumed to depend only on years since last breeding, and not on calendar time (τ_r independent of j), and survival is assumed to be independent of breeding state, although it may vary temporally. We have thus employed methods (i) and (iii) proposed by Kendall and Nichols (2002) for enabling survival and transition probabilities to be estimated (Section 1).

2.2. *Likelihoods*

The multinomial likelihood for the parameters ($\boldsymbol{\Psi} = \{N, \boldsymbol{\beta}, \boldsymbol{\phi}, \boldsymbol{p}, M, \boldsymbol{\tau}\}$) given the observed data is

$$L\ (\boldsymbol{\Psi} \mid \boldsymbol{X}) \quad \propto \quad \frac{N!}{(N-n)!} \times \left(\prod_{i=1}^{n} L_i \right) \times \nu^{N-n} \tag{2}$$

where L_i is the likelihood for the i^{th} individual's capture history and ν is the probability an animal in the superpopulation is unseen.

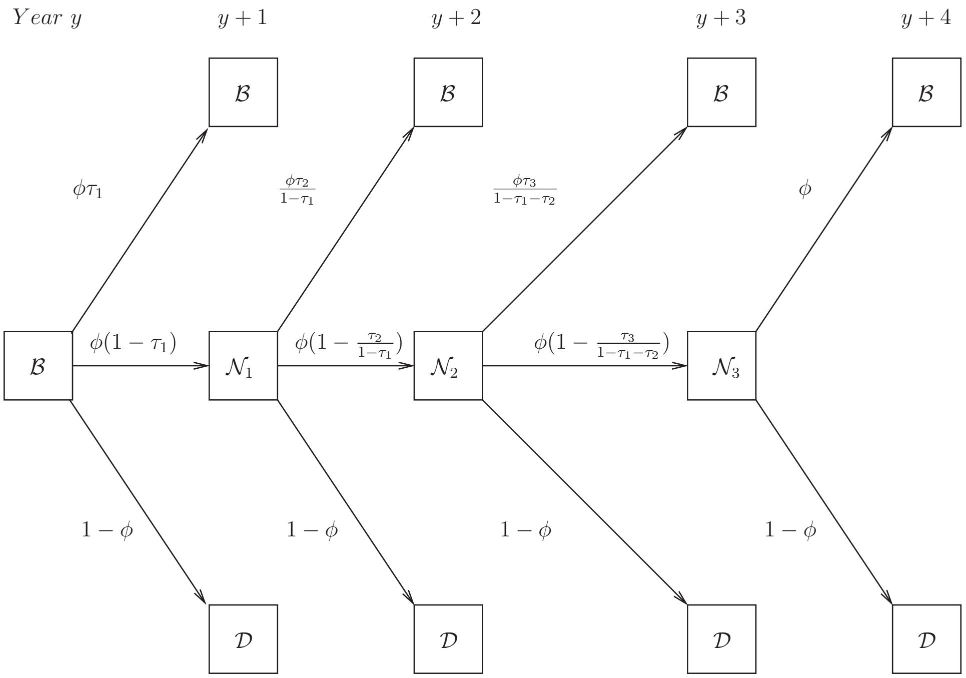

Figure 1. Branching diagram from breeding $\mathcal{B}$ to next breeding or death $\mathcal{D}$, with a maximum of 3 years between successive breeding years. Conditional annual transitional probabilities are shown on the branches. In this diagram $\boldsymbol{\phi}$ is constant over time, but it could be modified to ϕ_y, ϕ_{y+1}, etc.

We distinguish three types of segment in the observed capture histories:

S, starting segments, up to and including the first capture; A, alive adult segments, following a capture and up to and including the next capture; E, ending segments, after the last capture. These segments have respective probabilities γ_j, Pr(first captured at j | animal is in N); α_{jk}, Pr(next seen at k | seen at j), and; χ_j, Pr(not seen again | seen at j).

For example, a capture history $\boxed{0\ 0\ 1}$ $\boxed{0\ 1}$ $\boxed{1}$ $\boxed{0\ 0\ 1}$ $\boxed{0\ 0}$ has segments SAAAE as outlined and likelihood $L_i = \gamma_3\alpha_{35}\alpha_{56}\alpha_{69}\chi_9$. The following equations for γ_j, α_{jk} and χ_j are more complicated than their counterparts in the M-array of the CJS model and in the JSSA model, as they must take account of non-breeding states.

An animal first seen at j may have first bred in the study at any time up to j, indexed by $b = 1, 2, \ldots, j$. If $b < j$, it was breeding but not seen at b. If $b < j-1$, there are intermediate times between b and j when it was either not breeding, or breeding but not caught. The probability of an animal in the superpopulation first being seen at $j = 4$, say, is found by summing over $b = 1, 2, 3, 4$:

$$\begin{aligned}\gamma_4 = {} & \beta_0(1-p_1)\phi_1\phi_2\phi_3\{\tau_1(1-p_2)\tau_1(1-p_3)\tau_1 + \tau_1(1-p_2)\tau_2 \\ & + \tau_2(1-p_3)\tau_1 + \tau_3\}p_4 + \beta_1(1-p_2)\phi_2\phi_3\{\tau_1(1-p_3)\tau_1 \\ & + \tau_2\}p_4 + \beta_2(1-p_3)\phi_3 p_4 + \beta_3 p_4 \qquad (3)\end{aligned}$$

where the terms in { } sum over all possible intermediate combinations of breeding ($\mathcal{B}$) and not breeding ($\mathcal{N}$), for example, $\mathcal{BB}, \mathcal{BN}, \mathcal{NB}, \mathcal{NN}$ in the β_0 term.

Note that the probability of not being seen for an animal in the superpopulation N is

$$\nu = 1 - \sum_{j=1}^{K} \gamma_j. \qquad (4)$$

The probability for an A segment, $\alpha_{jk} = \Pr(\text{next seen at } k \mid \text{seen at } j)$, is given by (for example)

$$\begin{aligned}\alpha_{36} = {} & \phi_3\phi_4\phi_5\{\tau_1(1-p_4)\tau_1(1-p_5)\tau_1 + \tau_1(1-p_4)\tau_2 \\ & + \tau_2(1-p_5)\tau_1 + \tau_3\}p_6 \qquad (5)\end{aligned}$$

with probability paths in { } similar to those in Equation (3).

The probability for an E segment, $\chi_j = \Pr(\text{not seen again} \mid \text{seen at } j)$, is

$$\chi_j = 1 - \sum_{k=j+1}^{K} \alpha_{jk} \quad \text{for } j < K, \qquad (6)$$

with χ_K defined to be 1.

To calculate the log likelihood $\ell = \log L$, we collate the S, A and E segments from the capture history matrix, giving the minimal sufficient statistics as the counts

g_j, no. S segments with first capture at j $\left(\sum_{j=1}^{K} g_j = n\right)$; a_{jk}, no. A segments with capture at j and next capture at k, and; c_j, no. E segments with last capture at j $\left(\sum_{j=1}^{K} c_j = n\right)$.

Then from Equation (2) the multinomial log likelihood is

$$\ell = \log N! - \log(N-n)! - \sum_{j=1}^{K} \log g_i! - \sum_{j=1}^{K-1} \sum_{k=j+1}^{K} \log a_{jk}!$$
$$- \sum_{j=1}^{K} \log c_j! + \sum_{j=1}^{K} g_j \log \gamma_j + \sum_{j=1}^{K-1} \sum_{k=j+1}^{K} a_{jk} \log \alpha_{jk}$$
$$+ \sum_{j=1}^{K} c_j \log \chi_j + (N-n) \log \nu, \tag{7}$$

using Equations (3)–(6) for γ_j, ν, α_{jk} and χ_j.

2.3. *Model Options*

The model specified above is the global model. A range of candidate models may be constructed by varying the assumptions about the basic parameters as follows.

1. The value of M may be set at different values over 1 to $K-2$. If (say) $M = 3$ the model is labeled $\tau(M3)$.
2. The parameters $\boldsymbol{\phi}$ and/or $\boldsymbol{p}$ may be made constant over time (labeled $\phi(c)$, $p(c)$) rather than varying from sample to sample (labeled $\phi(t)$, $p(t)$ as in Section 2.1).
3. The entry proportions $\boldsymbol{\beta}$ (for FBIS) will include accumulated older animals at samples $1, \ldots, M+1$, but from sample $M+2$ onwards only new breeders will be entering the superpopulation. To check if recruitment is constant over time, a useful model would have fluctuating $\boldsymbol{\beta}$s up to sample $M+1$ followed by constant $\boldsymbol{\beta}$ (labelled e.g., $\beta(t4c)$ if $M = 3$), or else constant $\boldsymbol{\beta}$ up to $M+1$ followed by a lower constant (labelled $\beta(c4c)$ if $M = 3$). (Note that the corresponding JSSA models are special cases of the return time models, in which breeding occurs every year, $M = 0$. Hence for JSSA only β_0 is likely to be larger than later $\boldsymbol{\beta}$'s, model $\beta(c1c)$, as all the accumulated older animals are present and enter the superpopulation at the first sample.)

A model with $\boldsymbol{\beta}$, $\boldsymbol{\phi}$ and $\boldsymbol{p}$ all varying over time, and with $M = 3$ maximum successive non-breeding years, may be labeled $\{\beta(t), \phi(t), p(t), \tau(M3)\}$; this is a return-time model extension to the JSSA model $\{\beta(t), \phi(t), p(t)\}$. If $\boldsymbol{\beta}$ is time-varying for the first three samples and constant thereafter, and $\boldsymbol{\phi}$ is constant over time, the model is labeled $\{\beta(t3c), \phi(c), p(t), \tau(M3)\}$.

A question of biological importance is whether all animals are returning at times selected from the same return time distribution, or whether there is **individual heterogeneity of return time**, with some animals on a faster return time distribution than others. This scenario is biologically relevant because the ability to acquire sufficient resources to allocate to future reproduction often varies among individuals (Van Noordwijk and de Jong, 1986) or over the lifetime on one individual (e.g., larger or older females breeding more often). Similarly the amount of resources allocated to reproduction may differ between females and males. This possible heterogeneity may also be of statistical importance, as fitting a homogeneous model to heterogeneous data may bias abundance estimates in a manner similar to the underestimation of abundance in JSSA in the presence of unmodeled individual heterogeneity of capture. We address this by using a finite mixture (cf. Pledger, Pollock, and Norris, 2010) to extend the models above by assuming the animals are in C classes, with each class having its own probability distribution of return times. There is now an $M+1$ by C matrix of return time probabilities, (τ_{rc}). Membership of the classes is unknown, but *a priori* any individual has probability π_c of belonging in class c ($c = 1, \ldots, C$, $\sum \pi_c = 1$). (After fitting the model, for each observed individual it is possible to calculate its *a posteriori* probabilities of belonging in each class, thus distinguishing fast and slow breeders. In future work, this will provide useful extra information for biologists investigating reproductive success.)

A model with individual heterogeneity of return times has two $K \times C$ matrices (γ_{jc}) and (χ_{jc}) and a $K \times K \times C$ array (α_{jkc}). Their values are derived class by class using equations similar to 3, 5, and 6. The likelihood in Equation 2 has

$$L_i = \sum_{c=1}^{C} \pi_c L_{ic} \quad \text{and} \quad \nu = 1 - \sum_{c=1}^{C} \pi_c \sum_{j=1}^{K} \gamma_{jc},$$

where L_{ic} uses the appropriate $\boldsymbol{\gamma}$, $\boldsymbol{\alpha}$ and $\boldsymbol{\chi}$ parameters for capture history i and class c.

A model with $\boldsymbol{\beta}$ constant after three samples, $\boldsymbol{\phi}$ constant, $\boldsymbol{p}$ time-varying, a maximum of three successive non-breeding years, and heterogeneity with two classes is labeled (say) $\{\beta(t3c), \phi(c), p(t), \tau(M3H2)\}$.

The **alternative parameterization** in Section 2.1 replaces the N and $\boldsymbol{\beta}$ parameters with $N_1, N_2, \ldots, N_K$, the current population size at the time of each sample. This N_j sequence includes all adult animals, whether or not they are actually breeding that year. Note that Equations (2)–(7) do not include the retirees, which are present in the lake at the early stages but not counted in the superpopulation as they do not breed again during the study. If Equation (1) is used omitting R_j, the first M values of $\widehat{N}_j$ will be underestimates of the true value of the current (lake plus river) population. From sample $M+1$ onwards the retirees have gone and that particular source of bias in $\widehat{N}_j$ is removed. Failure to allow for retirees, because it underestimates the first few N_j values, may give rise to an apparent but spurious increase of estimated population size. An approximate method of estimating the number of retirees and correcting that bias is in Web Appendix A.

If different groups (e.g., sexes) are known, these models may be extended to include a group effect in population size, and survival, capture and return time probabilities. The vectors of N_j, ϕ_j, p_j, and τ_r are extended to matrices N_{jg}, ϕ_{jg}, p_{jg}, and τ_{rg} for groups $g = 1, \ldots, G$. The likelihood becomes the product of the likelihoods over the different groups.

2.4. *Analysis*

Model fitting by maximum likelihood estimation (MLE) yields parameter estimates and their asymptotic standard errors. Model selection may be effected using an information criterion such as AIC (Akaike, 1973), AICc (Burnham and Anderson, 2002) or BIC (Bayes' information criterion, Schwarz, 1978). Also, if one model is a submodel of another, the two models may be compared using a likelihood ratio test (LRT). If mixture models are used to allow for individual heterogeneity of return time, a comparison involving different numbers of classes has some parameters at the boundary of the parameters space. The LRT becomes non-standard but the tests are still possible (Self and Liang, 1987; Pledger, 2000).

We used "optim" in **R** (Version 2.12.1, R Development Core Team, 2010) to maximize the likelihood in Equation (7). For each possible M value, M was fixed in advance, and the input parameters were the transformed basic parameters, $\log N$ and the logits of parameters β_j, ϕ_j, p_j and τ_r (subject to $\sum \beta_j = 1$ and $\sum \tau_r = 1$). Equations (3) to (6) were used within the likelihood evaluation. Approximate asymmetric 95% confidence intervals were obtained by back-transforming from the endpoints of symmetric Wald intervals ($\pm z \times S.E.$) on the log or logit scale (with using standard errors from the hessian matrix). The R code, sample data and instructions for use are provided in Web Suuplementary Materials and on the first author's website: `http://www.victoria.ac.nz/smsor/about/staff/shirley-pledger` in the `personal home page` link.

3. Example

The lake sturgeon *(Acipenser fulvescens)* population in Black Lake, Michigan, USA has been the subject of ongoing study since 1997 (Baker and Borgeson, 1999; Smith and Baker, 2005; Forsythe et al., 2012). The population is closed to immigration by dams. Because of the lack of breeding habitats in the system, adults only breed in one tributary (Black River) which is shallow enough to allow access to all breeding adults annually. Lake sturgeon spend most of their life in Black Lake (~3,000 ha) but adults ascend the Black River to congregate and breed in spring (April–June). A detailed description of Black Lake and Black River can be found in Baker and Borgeson (1999) and Smith and Baker (2005).

Since 2001 breeding lake sturgeon have been sampled annually in the Black River. Breeding fish were captured using long-handled dip nets by personnel wading the river beginning at the upstream-most end of the breeding habitat and continuing to the downstream end of the breeding habitat; approximately 1.5 km of river. The breeding habitat was surveyed at least once daily and often several times each day during the breeding season. Lake sturgeon were easy to observe and capture in the breeding habitat and a capture attempt was made each time a lake sturgeon was observed. All captured lake sturgeon were tagged with a uniquely numbered passive integrated transponder (PIT) tag when initially captured and PIT tag numbers were recorded for all recaptured animals over the course of the study. Each breeding season was treated as a single sampling event because individual fish spend only a few days in the breeding habitat in any year. This resulted in eleven sampling occasions (years).

Data were collected from 356 unique females and 539 unique males. Because lake sturgeon spawn intermittently with an average interspawning interval of 2.3 years for males and 3.7 years for females (Forsythe et al. 2012), the total number of captures recorded for males was 1,370 and for females was 508 over the 11 year study period.

In this study for females we set $\tau_1 = 0$, as no females were recorded breeding in successive years, and so no information was available to estimate τ_1. Assuming $\tau_1 = 0$ for females is biologically reasonable, as lake sturgeon females are known to spawn intermittently at intervals of 2–5 years (Forsythe et al., 2012).

3.1. *Model Selection Results*

Since combined models with grouping by sex showed big differences except in survival probability, we present here two separate analyses. If we wish to avoid overfitting BIC may be used, as this criterion tends to select simpler models than AIC when the data sets are large. This reduces the number of statistically-detected effects which are difficult to interpret biologically. For each sex, we fitted a global model $\{\beta(t), \phi(t), p(t), \tau(M)\}$ with M at its maximum of $K - 2 = 9$. Then M was reduced in steps to zero, and a reference model was selected using BIC ($M = 3$ for females and $M = 2$ for males). (If $M = 0$ the model reduces to the JSSA model $\{\beta(t), \phi(t), p(t)\}$, with animals breeding every year.) Starting from the reference model, candidate models were constructed by making $\boldsymbol{\beta}$, $\boldsymbol{\phi}$ and/or $\boldsymbol{p}$ constant, and trying individual heterogeneity of return times. The eight best BIC-selected models for each sex are shown in Table 1, followed by the reference model and the JSSA model for comparison. For males, AICc gave the same model selection as BIC, while for females AICc failed to distinguish clearly among the best few models but gave similar model selection to BIC.

For females the BIC-selected model was $\{\beta(c3c), \phi(c), p(c), \tau(M3)\}$. There was little evidence for more than three successive non-breeding years, for time-dependent entry, survival or capture probabilities, or for individual heterogeneity of return times. With at most $M = 3$ successive years without breeding, during the first four samples both older breeders first breeding during the study and new recruits were entering the superpopulation. After this only new breeders (recruits) were entering, and this was constant over time. Model $\beta(c3c)$ was actually chosen in preference to $\beta(c4c)$, probably because very few adult females spent the first 3 years not breeding.

For males there was little evidence for more than two successive non-breeding years ($M = 2$), and variable capture probability over time was detected. Over the first 3 years both older breeders and new recruits were entering the superpopulation, but from year 4 onwards there was constant recruitment to the breeding population. There was strong evidence of individual heterogeneity of return times, with the population including a mix of slow and fast breeders. This suggests that in the data matrix, the A segments were not randomly allocated over the individuals, but some fish specialized in short A segments, while others had longer ones. The finite mixture approach provides for each male the post-hoc probabilities of being in the fast- or slow-breeding group.

For both sexes the JSSA model and its variants with constant $\boldsymbol{\beta}$, $\boldsymbol{\phi}$, and/or $\boldsymbol{p}$ were fitted, to ascertain if the data could have arisen from populations which breed every year ($M = 0$). For females, all the JSSA models had BIC at least 107 higher than all the return-time models, and for males all JSSA models had BIC at least 45 higher than return-time models. We also noticed that the JSSA models were giving higher N estimates than the return-time models, which raised the question

Table 1

The best eight models for females and males, sorted by BIC, followed by the reference model $\{\beta(t), \phi(t), p(t), \tau(M)\}$ ($M = 3$ for females, $M = 2$ for males) and the JSSA model ($M = 0$) for comparison. BIC has a stronger penalty against too many parameters. Model selection is more clearcut for males, because of the larger data set

Sex	$\boldsymbol{\beta}$	$\boldsymbol{\phi}$	$\boldsymbol{p}$	$\boldsymbol{\tau}$	Max. ℓ	No. par.	Rel. AICc	Rel. BIC
Females	$c3c$	c	c	$M3$	−1734.1	6	2.8	**0.0**
	$t3c$	c	c	$M3$	−1733.3	8	6.2	7.1
	$t4c$	c	c	$M3$	−1731.4	9	5.0	7.7
	$c3c$	c	t	$M3$	−1721.2	15	1.8	13.4
	t	c	c	$M3$	−1721.5	15	2.4	14.0
	t	c	c	$M3H2$	−1715.3	18	0.0	14.7
	t	c	c	$M4$	−1721.5	16	5.7	18.4
	$c4c$	c	t	$M3$	−1724.5	15	8.4	20.0
	t	t	t	$M3$ (ref.)	−1717.2	32	67.9	79.2
	t	t	t	$M0$ (JSSA)	−1814.1	30	250.1	264.3
Males	$c2c$	c	t	$M2H2$	−5592.8	18	0.0	**0.0**
	$c1c$	c	t	$M2H2$	−5605.2	18	24.8	24.8
	$c2c$	c	t	$M2$	−5659.0	15	125.4	116.5
	$c2c$	c	c	$M2$	−5684.3	6	155.7	119.0
	$t2c$	c	c	$M2$	−5683.1	7	155.6	122.1
	$c1c$	c	t	$M2$	−5662.9	15	133.0	124.1
	$t3c$	c	c	$M2$	−5682.8	8	157.0	126.7
	$c1c$	c	c	$M2$	−5688.9	6	165.0	128.3
	t	t	t	$M2$ (ref.)	−5651.9	32	154.9	192.9
	t	t	t	$M0$ (JSSA)	−5706.6	30	258.5	291.5

of bias in the abundance estimates with each type of model. This was investigated by simulation (Section 4).

3.2. *Parameter Estimates*

Estimates of the parameters from the selected model are shown in Table 2.

Fitting the models for a single population with two groups (sexes) showed that females and males had the same high annual survival probabilities, while males had higher and more variable capture probabilities. The return times were markedly different between the sexes, with 91% of males returning to breed within 1 or 2 years, compared with only 12% of females.

From the alternative parameterization, the estimated current population size N_j for $j = 1, \ldots, 11$ is shown in Figure 2. An increasing abundance is apparent.

For each sex, using the parameter estimates obtained from the chosen model and the methods in the Web Appendix A, the number of retirees was estimated and included in the estimates N_j of current breeding population size. There were fewer than ten retirees for each sex, as the high survival rates ensured most animals in the breeding population at the start of the study would survive to breed again, rather than die. This adjustment is only possible with a moderately stable population and no immigration (see Web Appendix A).

The rapid increase in lake sturgeon abundance over the period of study (Figure 2, confirmed in Section 4.4) was unexpected given the low rate of natural recruitment which is characteristic of the species biology. However, from 1982 to 88 11,512 lake sturgeon were stocked in Black Lake. A gillnet survey conducted in 1997 documented that immature stocked fish represented about 50% of the population (Baker and Borgeson, 1999). Stocked fish are presently reaching sexual maturity and recruiting into the spawning population at a rate much higher than natural recruitment observed for the species (Bruch, 1999). Therefore, the rapid increase in

Table 2

Parameter estimates and 95% confidence intervals using the best model for each sex. Confidence intervals are narrower for males, because of more data. Capture probability was constant for females, while for males $\hat{p}_j$ ranged from 0.374 to 0.724 over the 11 samples

Parameter		Females	Males	
Superpopulation	N	508 (465,555)	610 (588,634)	
Survival	ϕ	0.980 (0.874,0.997)	0.977 (0.962,0.987)	
Capture probability	p	0.399 (0.317,0.487)	Mean$(\hat{p}_j) = 0.553$	
Return time probabilities	τ_1	—	0.9999	0.1377
	τ_2	0.119	0.0001	0.6348
	τ_3	0.568	0.0000	0.2275
	τ_4	0.312	(16%)	(84%)

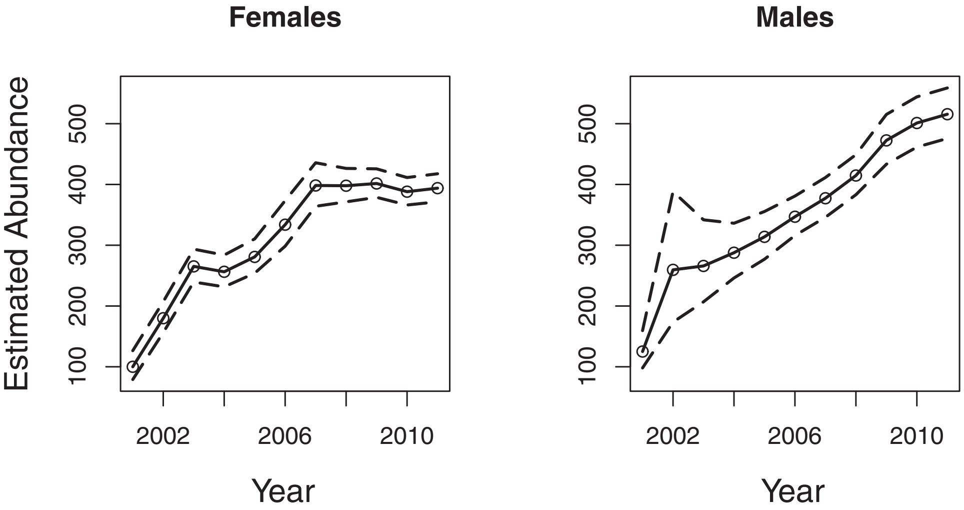

Figure 2. Abundance estimates ($\hat{N}_j$) and 95% confidence bands for female and male lake sturgeon over years 2001–2011. The confidence intervals are asymmetric as they were back-transformed from symmetric intervals on the log scale. The first two estimates for males and the first three for females are underestimates, as they do not include the retirees. However, the number of retirees is very small for both sexes.

abundance is largely attributed to the population's stocking history.

3.3. *Sensitivity of Abundance Estimates to Model Selection*

We checked the superpopulation abundance estimates to find if they are sensitive to the exact choice of model. The point estimates and 95% confidence intervals for N, from both return-time models and JSSA models, are plotted in Figure 3.

For both sexes, the point estimates and 95% confidence intervals for N were similar over the different return-time models, indicating that as far as abundance estimation is concerned, the exact choice of return-time model was not important. The males' data set showed that although there was strong individual heterogeneity in the return times, the abundance estimates were similar to those for the homogeneous model. However, an important finding was that abundance estimates were highly sensitive to return-time versus JSSA models, with $\hat{N}$ being distinctly lower if return times were modeled. This had a flow-on effect on all the N_j estimates; the same pattern of overestimation by JSSA occurs throughout the current population estimates, giving estimated profiles through time which are systematically above the true profiles.

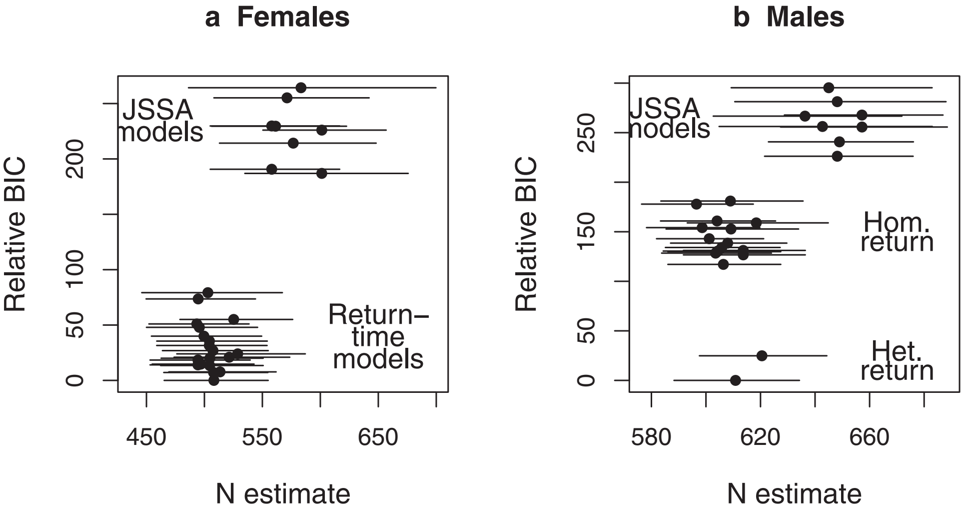

Figure 3. Superpopulation N point estimates and 95% confidence intervals for (a) females and (b) males using return-time and JSSA models. Models with lowest BIC are best, and all the return-time models were preferred to all the JSSA models. For males, individual heterogeneity of return times is selected, while for females the heterogeneous models were embedded among the homogeneous ones. For both sexes, the JSSA models give higher N estimates.

3.4. *Goodness of Fit*

We evaluated the goodness of fit of the selected models using a Pearson's χ^2 test on the counts a_{jk} and c_j. (Inclusion of the first-capture counts was not possible as N is unknown.) Expected values were calculated using estimated parameters from the fitted model, with a loss of one degree of freedom for each estimated parameter. Minimal pooling of adjacent cells was done to bring all expected values up to at least five. For females a good fit was found ($\chi^2 = 11.048$, 15 df, $p = 0.7492$). Males showed a poorer fit ($\chi^2 = 54.304$, 37 df, $p = 0.0330$). With larger counts in the males' data set, there was substantially less pooling, giving the lower p value; we note that large data sets generally lead to rejection with these goodness-of-fit tests.

4. Simulation

4.1. *Procedures*

We ran simulations in order to evaluate (i) the model selection procedure, (ii) the estimation of abundance of the superpopulation N, and (iii) the estimation of return times.

For each sex we generated two sets of data matrices over $K = 11$ years, 100 populations with homogeneous return times and 100 with individual heterogeneity. All parameter settings approximated the estimates from the sturgeon data. Constant $\boldsymbol{\phi}$ and $\boldsymbol{p}$ were used; females had $N = 500$, $M = 3$ and $\tau_1 = 0$, while males had $N = 600$ and $M = 2$. Females had model $\beta(c3c)$ with β_0 to $\beta_2 = 0.15$ and β_3 to $\beta_{10} = 0.55/8$, and males had $\beta(c2c)$ with β_0 and $\beta_1 = 0.2$ and β_2 to $\beta_{10} = 0.6/9$. The females' $\boldsymbol{\tau}$ inputs (from the sturgeon analysis) were $(0.000, 0.119, 0.568, 0.313)$ for the homogeneous case. Since the females did not exhibit heterogeneity of return times, we made an arbitrary choice of heterogeneous return time parameters for data generation: we chose $(0.000, 0.200, 0.568, 0.232)$ for fast return times and $(0.000, 0.038, 0.568, 0.394)$ for slow returns, and during simulation each female was assigned fast or slow return with probability 0.5 each. These return times average out to match the homogeneous case. For males, the heterogeneous return times came from the sturgeon analysis, with 16% fast returns, $\boldsymbol{\tau} = (0.9998, 0.0001, 0.0001)$ and 84% slow, $\boldsymbol{\tau} = (0.1377, 0.6348, 0.2275)$. Homogeneous return times were generated using the weighted average, $\boldsymbol{\tau} = (0.275636, 0.533248, 0.191116)$.

Analyses used models with the chosen input value of M and with $\boldsymbol{\phi}$ and $\boldsymbol{p}$ constant, so that any wrong model selection or biased estimates could be attributed to wrong modeling of $\boldsymbol{\tau}$. Three analysis models were fitted for each generated data set, one with homogeneous $\boldsymbol{\tau}$, one with heterogeneous $\boldsymbol{\tau}$, and one ignoring return times (the JSSA model with constant $\boldsymbol{\phi}$ and $\boldsymbol{p}$).

4.2. *Model Selection Results*

Model selection by AICc gave the following results, with similar results from using BIC.

For females, 100 data sets generated with homogeneous return times had the correct model selected every time. Data generated with heterogeneous return times had the homogeneous model selected 95 times, the heterogeneous model once, and the JSSA model four times. Failure to detect the heterogeneity was presumably caused by setting the amount of heterogeneity too low; this amount was an arbitrary choice since we had no actual heterogeneity from the true data to guide us.

For males, data sets generated from homogeneous return times had the correct model selected 95 times and JSSA five times. Generation from heterogeneous return times led to correct model selection 95 times and JSSA selection five times. The correct choice between homogeneous and heterogeneous return times was driven by the high level of heterogeneity found in the sturgeon data, which was used in the data generation. Since males have shorter return times than females, they are nearer to satisfying the JSSA model assumptions, which is reflected in the higher numbers where JSSA was chosen.

4.3. *Parameter Estimation Results*

Table 3 shows the input and estimated values of parameters under the different scenaria. Results from the JSSA model $\{\beta(t), \phi(c), p(c)\}$ are shown, but the other seven JSSA models with $\beta(c1c)$, $\phi(t)$ and/or $p(t)$ gave closely similar output. The percentage relative bias is $100 \times (\hat{\theta} - \theta)/\theta$ for each input parameter θ, where $\hat{\theta}$ is the mean estimate over 100 simulated populations. For the heterogeneous analysis models, the tau estimates quoted are the averages over the groups, $\widehat{\tau}_r = \sum_{g=1}^{2} \widehat{\pi}_g \widehat{\tau}_{rg}$.

Bias in $\hat{N}$ and the other parameters was very small when data were analyzed by the correct model (Table 3). For the males, analysis of heterogeneous $\boldsymbol{\tau}$ data by the homogeneous $\boldsymbol{\tau}$ model gave poor estimates of the return times averaged over the heterogeneity groups. However, in Section 4.2 it was seen that the homogeneous model was never chosen in the face of such extreme heterogeneity. There was no corresponding "wrong model" bias when a heterogeneous model was used on homogeneous data. The JSSA model overestimated N and underestimated $\boldsymbol{p}$ when applied to return-time data, to the extent that for both sexes and both types of data generation, all 100 $\hat{N}$ values were above the input value. The percentage relative bias was higher for females, who have longer return times than males. Shorter return times give a better approximation to the JSSA model assumptions, which presumably renders the bias in $\hat{N}$ less severe. In Section 4.2, JSSA was sometimes chosen in preference to return time models, suggesting that a useful strategy could be to use return time models anyway, regardless of the AIC or BIC criteria, if the two models give substantially different estimates of N.

The JSSA model's overestimation of abundance is of particular concern. If there is unmodeled Markovian nonbreeding, and return-time models are not included in the candidate set, fitting the JSSA-type models alone will overestimate abundance.

4.4. *Current Population Trends*

Since both female and male sturgeon analyses showed increasing current population size estimates (Figure 2), we investigated the possibility that some biases in N_j estimates might induce a trend when none occurred. We simulated 100 populations from the estimated parameters for each group, female and male, and found that the expected values of $\widehat{N}_j$ matched the inputs. This confirmed that the increases in the populations were real, and not artefacts of the model fitting process.

Table 3

Estimated parameters from simulations, where "hom" and "het" represent models with homogeneous and heterogeneous return times respectively. Mean, standard deviation and percent relative bias of estimates are taken over 100 simulated populations. Heterogeneous models show each τ_r averaged over the groups (with the estimated relative weightings). For females, $\tau_1 = 0$

	Input	Analysis	Hom. generating model			Het. generating model		
Sex	parameter	model	Mean	SD	Bias	Mean	SD	Bias
Female	$N = 500$	Hom	496.7	26.9	−0.7	500.6	23.7	0.1
		Het	497.4	27.2	−0.5	501.8	24.3	0.4
		JSSA	651.0	67.8	30.2	707.1	75.5	41.4
	$\phi = 0.980$	Hom	0.992	0.012	1.2	0.990	0.015	1.0
		Het	0.991	0.012	1.1	0.990	0.015	1.0
		JSSA	1.000	0.000	2.0	1.000	0.000	2.0
	$p = 0.399$	Hom	0.418	0.041	4.8	0.417	0.042	4.5
		Het	0.418	0.041	4.8	0.415	0.042	4.0
		JSSA	0.110	0.003	−72.4	0.106	0.003	−73.4
	$\tau_2 = 0.119$	Hom	0.122	0.021	2.5	0.122	0.023	2.5
		Het	0.120	0.021	0.8	0.118	0.024	0.8
	$\tau_3 = 0.568$	Hom	0.562	0.039	−1.1	0.564	0.040	−0.7
		Het	0.561	0.040	−1.2	0.566	0.042	−0.4
	$\tau_4 = 0.313$	Hom	0.316	0.035	1.0	0.314	0.038	0.3
		Het	0.318	0.036	1.6	0.316	0.041	1.0
Male	$N = 600$	Hom	600.5	10.6	0.1	595.7	9.9	0.7
		Het	600.7	10.9	0.1	598.7	9.6	0.2
		JSSA	634.9	12.2	5.8	643.0	11.3	7.2
	$\phi = 0.977$	Hom	0.998	0.002	2.1	0.996	0.003	1.9
		Het	0.999	0.001	2.3	0.998	0.002	2.1
		JSSA	1.000	0.000	2.4	1.000	0.000	2.4
	$p = 0.553$	Hom	0.556	0.023	0.5	0.549	0.030	−0.7
		Het	0.544	0.023	−1.6	0.560	0.020	1.3
		JSSA	0.281	0.001	−49.2	0.292	0.001	−28.9
	$\tau_1 = 0.276$	Hom	0.275	0.022	−0.4	0.373	0.042	35.1
		Het	0.276	0.023	0.0	0.277	0.025	0.4
	$\tau_2 = 0.533$	Hom	0.532	0.024	−0.2	0.529	0.028	−0.8
		Het	0.533	0.024	0.0	0.535	0.023	0.4
	$\tau_3 = 0.191$	Hom	0.193	0.029	1.0	0.097	0.042	−49.2
		Het	0.197	0.031	3.1	0.189	0.023	−1.0

5. Discussion

We have proposed TE models which extend the JSSA models to allow for Markovian return times. This type of TE is detectable purely from the capture matrix, although there will often be biological knowledge to suggest such a mechanism is occurring. Our models may be used for studies where the robust design cannot be implemented, or for historical data sets where only the simple JS design was chosen.

In our example, without using any biological information about the species, we have a clear message that the return-time models are better. The group with the longer return times (females) had the strongest evidence for selecting a return-time model rather than a JSSA model.

We found that using a JSSA model in the presence of long-term Markovian TE gave overestimation of the population size. This bias is more marked with females, with their longer return times. Overestimation of abundance could have serious consequences when setting management policy for endangered populations or harvesting quotas for exploited populations.

In retrospect, it is understandable that the JSSA models overestimate abundance in the presence of breeding absences. On each occasion j, p_j is underestimated, as JSSA assumes all animals are present when in fact some are absent and unavailable for capture. An average capture probability for those present and absent is estimated. Underestimation of p_j leads to overestimation of N_j. A feature of these return-time capture matrices is that interior 1's (between the first and last capture of each animal) are not randomly spaced—for example, with the sturgeon females, there are never two captures in adjacent years (Forsythe et al., 2012). A randomization test could be constructed to test for the presence of this pattern.

We made the biologically plausible assumption that there is a maximum M to the number of years of non-breeding before either dying or returning to breed. As long as $M < K - 1$ we may compare models for varying M, using AIC or BIC to decide the value of M. However for precise parameter estimates the duration of the study should preferably be substantially longer than the maximum return time. If there is no immigration (as in the isolated population of our example), the current population estimates fall into two categories, the early samples (1 to $M+1$) in which substantial numbers are entering the superpopulation (as they reach their first breeding during the study, FBIS), followed by later samples with new entrants restricted to new breeders. An assumption of approximate stability of the population allows us to estimate numbers of retirees, giving adjustments to the negative bias in N_j over the first M samples. If there is immigration, or the population is unstable, no such adjustments are available.

Our models have the potential to include individual heterogeneity of survival as well as return time. Finding two groups, one with high survival and slow return time, and the other with low survival but faster return time, could indicate a payoff in total reproductive output over a lifetime, with two competing strategies. However, for long-lived animals, a long-term data set would be needed, covering at least the typical lifetime.

Another potential development would be to combine these models with the age-structured models of Pledger et al. (2009), to determine if the expected return time changes as the animal ages.

6. Supplementary Materials

Web Appendix A referenced in Sections 1, 2.3, 2.4 and 3.2 is available with this paper at the Biometrics Website on Wiley Online Library.

Also available is a zip file JSreturn.zip containing R code, examples and instructions for fitting these JSreturn models.

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References

Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory*, B. N. Petrov and F. Csaki (eds), 267–281. Budapest: Academiai Kiado. .

Arnason, A. N. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology*, **15**, 1–8.

Bailey, L. L., Converse, S. J., and Kendall, W. L. (2010). Bias, precision, and parameter redundancy in complex multistate models with unobservable states. *Ecology*, **91**, 1598–1604.

Bailey, L. L., Kendall, W. L., and Church, D. R. (2009). Exploring extensions to multi-state models with multiple unobservable states. In *Modeling Demographic Processes in Marked Populations*, Thomson, D. L., Cooch, E. G., and Conroy, M. J. (eds), 693–709. New York: Springer.

Bailey, L. L., Kendall, W. L., Church, D. R., and Wilbur, H. M. (2004). Estimating survival and breeding probabilities for pond-breeding amphibians: A modified robust design. *Ecology* **85**, 2456–2466.

Baker, E. A. and Borgeson, D. J. (1999). Lake sturgeon abundance and harvest in Black Lake, Michigan, 1975–1999. *North American Journal of Fisheries Management* **19**, 1080–1088.

Barbraud, C. and Weimerskirch H. (2012). Estimating survival and reproduction in a quasi biennially breeding seabird with uncertain and unobservable states. *Journal of Ornithology* **152**, 605–615.

Bruch, R. (1999). Management of lake sturgeon on the Winnebago system—Long term impacts of harvest and regulations on population structure. *Journal of Applied Ichthyology* **15**, 142–152.

Brownie, C., Hines J. E., Nichols, J. D., Pollock, K. H., and Hestbeck, J. B. (1993). Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* **49**, 1173–1187.

Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* 2nd edition. New York: Springer-Verlag.

Church, D. R., Bailey, L. L., Wilbur, H. M., Kendall, W. L., and Hines, J. E. (2007). Iteroparity in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology* **88**, 891–903.

Clobert, J., Lebreton, J.-D., Allainé, D., and Gaillard, J. M. (1994). The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. *Biometrics* **50**, 375–387.

Converse, S. J., Kendall, W. L., Doherty, P. F.Jr., Naughton, M. B., and Hines, J. E. (2009). A traditional and a less-invasive robust design: Choices in optimizing effort allocation for seabird population studies. In *Modeling Demographic Processes in Marked Populations*, Thomson, D. L., Cooch, E. G., and Conroy, M. J. (eds), 727–744. New York: Springer.

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* **51**, 429–438.

de Lisle, S. P. and Grayson, K. L. (2011). Survival, breeding frequency and migratory orientation in the Jefferson salamander, *Ambystoma jeffersonianum. Herpetological Conservation and Biology* **6**, 215–227.

Forsythe, P. S., Crossman, J. A., Bello, N. M., Baker E. A., and Scribner, K. T. (2012). Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon *(Acipenser fulvescens). Canadian Journal of Fisheries and Aquatic Science* **69**, 60–72.

Frick, W. F., Reynolds, D. S., and Kunz, T. H. (2010). Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus. Journal of Animal Ecology* **79**, 128–136.

Fujiwara, M. and Caswell, H. (2002). A general approach to temporary emigration in mark-recapture analysis. *Ecology* **83**, 3266–3275.

Hunter, C. M. and Caswell, H. (2009). Rank and redundancy of multistate mark-recapture models for seabird populations with unobservable states. In *Modeling Demographic Processes in Marked Populations*, Thomson, D. L., Cooch, E. G., and Conroy, M. J. (eds), 797–825. New York: Springer.

Jolly, G. M. (1965). Explicit estimates from capture–recapture data with both death and immigration—Stochastic model. *Biometrika* **52**, 225–247.

Kendall, W. L. (2004). Coping with unobservable and mis-classified states in capture–recapture studies. *Animal Biodiversity and Conservation* **27**, 97–107.

Kendall, W. L. (2009). One size does not fit all: adapting mark-recapture and occupancy models for state uncertainty. In *Modeling Demographic Processes in Marked Populations*, Thomson, D. L., Cooch, E. G., and Conroy, M. J. (eds), 765–780. New York: Springer.

Kendall, W. L. and Bjorkland, R. (2001). Using open robust design models to estimate temporary emigration from capture–recapture data. *Biometrics* **57**, 1113–1122.

Kendall, W. L. and Nichols, J. D. (2002). Estimating state transition probabilities for unobservable states using capture–recapture/resighting data. *Ecology* **83**, 3276–3284.

Lebreton, J.-D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* **62**, 67–118.

Lebreton, J. D. and Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics* **29**, 353–369.

Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L., and Link, W. A. (1994). Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology* **75**, 2052–2065.

Pledger, S. (2000). Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* **56**, 434–442.

Pledger, S., Efford, M. G., Pollock, K. H., Collazo, J., and Lyons, J. (2009). Stopover duration analysis with departure probability dependent on unknown time since arrival. In *Modeling Demographic Processes in Marked Populations*, Thomson, D. L., Cooch, E. G., and Conroy, M. J. (eds), 349–363. New York: Springer.

Pledger, S., Pollock, K. H., and Norris, J. L. (2010). Open capture–recapture models with heterogeneity: II. Jolly-Seber model. *Biometrics* **66**, 883–890.

Pollock, K. H. (1982). A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* **46**, 757–760.

Pradel, R. (2005). Multievent: An extension of multistate capture–recapture models to uncertain states. *Biometrics* **61**, 442–447.

R Development Core Team (2010). R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.
ISBN 3-900051-07-0, http://www.R-project.org

Rivalan, P., Prévot-Julliard, A.-C., Choquet, R., Pradel, R., Jacquemin, B., and Girondot, M. (2005). Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia* DOI 10.1007/s00442-005-0159-4

Schaub, M., Giminez, O., Schmidt, B. R., and Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology* **85**, 2107–2113.

Schwarz C. J. and Arnason A. N. (1996). A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* **52**, 860–873.

Schwarz, G. E. (1978). Estimating the dimension of a model. *Annals of Statistics* **6**, 461–464.

Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika* **52**, 249–259.

Self, S. G. and Liang, K.-Y. (1987). Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. *Journal of the American Statistical Association* **82**, 605–610.

Smith, K. M. and Baker, E. A. (2005). Characteristics of spawning lake sturgeon in the upper Black River, Michigan. *North American Journal of Fisheries Management* **25**, 301–307.

Van Noordwijk, A. J. and de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. *American Naturalist* **128**, 137–142.

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