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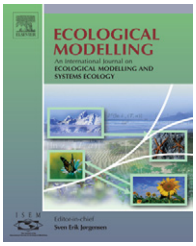

Short communication

State-space modelling of data on marked individuals

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ABSTRACT

State-space models have recently been proposed as a convenient and flexible framework for specifying stochastic models for the dynamics of wild animal populations. Here we focus on the modelling of data on marked individuals which is frequently used in order to estimate demographic parameters while accounting for imperfect detectability. We show how usual models to deal with capture–recapture and ring-recovery data can be fruitfully written as state-space models. An illustration is given using real data and a Bayesian approach using MCMC methods is implemented to estimate the parameters. Eventually, we discuss future developments that may be facilitated by the SSM formulation.

1. Introduction

The estimation of animal survival is essential in population biology to investigate population dynamics, with important applications in the understanding of ecological, evolutionary, conservation and management issues for wild populations (Pollock, 1991; Williams et al., 2002). While the time to event is known in medical, social or engineering sciences (death, marriage and failure respectively), models for estimating wild animal survival must incorporate nuisance parameters to account for incomplete detectability in monitoring individuals (Schwarz and Seber, 1999). Typically, individuals are captured,

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marked and can be resighted or recaptured (encountered thereafter) to construct encounter histories which consist of sequences of 1's and 0's according to whether a detection occurs or not. The likelihood for such data arises from products of multinomial distributions whose cell probabilities are complex functions of survival probabilities – parameters of primary interest – and encounter probabilities – nuisance parameters (Cormack, 1964; Jolly, 1965; Seber, 1965– CJS thereafter).

In this note, we show how the population process can be fruitfully disentangled, by distinguishing the underlying demographic process, i.e., the survival (as well as transitions between sites/states if needed), from its observation, i.e., the detectability. This leads us to consider a natural formulation for capture–recapture models using state-space models (SSMs). Our contribution is in line with a recent paper by Buckland et al. (2004) who have proposed to adopt SSMs as a convenient and flexible framework for specifying stochastic models for the dynamics of wild animal populations.

Thus far, SSMs have been mainly used for time series of animal counts (De Valpine, 2004; Millar and Meyer, 2000) or animal locations (Anderson-Sprecher and Ledolter, 1991) to allow true but unobservable states (the population size or trajectory) to be inferred from observed but noisy data (see Clark et al., 2005; Wang, 2007 for reviews). The novelty of our approach lies in the use of SSMs to fit capture–recapture models to encounter histories.

In Section 2, we discuss how to express the CJS model under the form of a SSM. The implementation details are provided, and real data are presented to compare parameter estimates as obtained using the standard product-multinomial and the SSM approaches. In Section 3, the flexibility of the state-space modeling approach is demonstrated by considering two widely used alternative schemes for collecting data on marked animals. Finally, Section 4 discusses important developments of capture–recapture models facilitated by the SSM formulation. We emphasize that this general framework has a great potential in population ecology modelling.

2. State-space modelling of capture–recapture data

We focus here on the CJS model for estimating animal survival based on capture–recapture data, as this model is widely used in the ecological and evolutionary literature (e.g., Lebreton et al., 1992).

2.1. Likelihood

We first define the observations and then the states of the system. We assume that n individuals are involved in the study with T encounter occasions. Let $X_{i,t}$ be the binary random variable taking values 1 if individual i is alive at time t and 0 if it is dead at time t. Let $Y_{i,t}$ be the binary random variable taking values 1 if individual i is encountered at time t and 0 otherwise. Note that we consider the encounter event as being physically captured or barely observed. The parameters involved in the likelihood are $\phi_{i,t}$, the probability that an animal i survives to time $t+1$ given that it is alive at time t ($t = 1, \ldots, T-1$), and $p_{i,t}$ the probability of detecting individual i at time t ($t = 2, \ldots, T$). Let finally e_i be the occasion where individual i is encountered for the first time. A general state-space formulation of the CJS model is therefore given by

$$Y_{i,t}|X_{i,t} \sim \text{Bernoulli}\,(X_{i,t}p_{i,t}), \tag{1}$$

$$X_{i,t+1}|X_{i,t} \sim \text{Bernoulli}\,(X_{i,t}\phi_{i,t}), \tag{2}$$

for $t \geq e_i$, with $p_{i,e_i} = 1$ and where Eqs. (1) and (2) are the observation and the state equations respectively. This formulation naturally separates the nuisance parameters (the encounter probabilities) from the parameters of actual interest, i.e., the survival probabilities, the latter being involved exclusively in the state Eq. (2). Such a clear distinction between a demographic process and its observation makes the description of a biological dynamic system much simpler and allows complex models to be fitted (Pradel, 2005; Clark et al., 2005). We will refer to this formulation as the individual state-space CJS model (individual SSM CJS hereafter). The rationale behind the above formulation is as follows. We give the full details for the observation Eq. (1) only, as a similar reasoning easily leads to Eq. (2). If individual i is alive at time t, then it has probability $p_{i,t}$ of being encountered and probability $1 - p_{i,t}$ otherwise, which translates into $Y_{i,t}$ is distributed as Bernoulli ($p_{i,t}$) given $X_{i,t} = 1$. Now if individual i is dead at time t, then it cannot be encountered, which translates into $Y_{i,t}$ is distributed as Bernoulli (0) given $X_{i,t} = 0$. Putting together those two pieces of reasoning, the distribution of the observation $Y_{i,t}$ conditional on the state $X_{i,t}$ is given by Eq. (1).

Statistical inference then requires the likelihood of the state-space model specified above. Assuming independence of individuals, the likelihood is given by the product of all individual likelihood components. The likelihood component for individual i is the probability of the vector of observations $\mathbf{Y}_i^T = (Y_{i,e_i}, \ldots, Y_{i,T})$ which gathers the information set up to time T for this particular individual. Conditional on the first detection, the likelihood component corresponding to individual i is therefore given by (e.g., Harvey, 1989)

$$\int_{X_{i,e_i}} \cdots \int_{X_{i,T}} [X_{i,e_i}] \left\{ \prod_{t=e_i+1}^{T} [Y_{i,t}|X_{i,t}][X_{i,t}|X_{i,t-1}] \right\} dX_{i,e_i} \ldots dX_{i,T} \tag{3}$$

where $[X]$ denotes the distribution of X and X_{i,e_i} the initial state of individual i which is assumed to be alive. Because we deal with binary random vectors, we used the counting measure instead of the Lebesgue measure.

In its original formulation, the CJS makes important assumptions regarding individuals. First, all individuals share the same parameters, which means that the survival and detection probabilities depend on the time index only. In mathematical notation, we have $\phi_{i,t} = \phi_t$ and $p_{i,t} = p_t$ for all $i = 1, \ldots, n$, so Eqs. (1) and (2) become $X_{i,t+1}|X_{i,t} \sim \text{Bernoulli}(X_{i,t}\phi_t)$ and $Y_{i,t}|X_{i,t} \sim \text{Bernoulli}(X_{i,t}p_t)$ respectively. Second, the CJS model also assumes independence between individuals. By using simple relationships between Bernoulli and Binomial distributions, one can finally fruitfully formulates the original

CJS model under the following state-space model:

$$Y_t|X_t \sim \text{Bin}(X_t - u_t, p_t) \tag{4}$$

$$X_{t+1}|X_t \sim \text{Bin}(X_t, \phi_t) + u_{t+1} \tag{5}$$

where X_t is the number of survivors from time t plus the number of newly marked individuals at time t, u_t, and Y_t is the total number of previously marked individuals encountered at time t. We will refer to this formulation as the population state-space CJS model (population SSM CJS hereafter). Interestingly, specifying the system under a state-space formulation now requires much less equations than the individual SSM CJS model, which may avoid the computational burden. Nevertheless, while the individual SSM CJS involves parameters for every single individual and sampling occasion, the population SSM CJS model makes the strong assumptions that all individuals behave the same as well as independently, which may be of little relevance from the biological point of view. To cope with this issue, in-between modeling can be achieved by considering age effects or groups classes in the population SSM model (Lebreton et al., 1992). Finally, covariates can be incorporated in order to assess the effect of environment such as climate change, most conveniently by writing the relationship between the target probabilities and the predictors on the logit scale (Pollock, 2002).

2.2. *Implementation*

Fitting SSMs is complicated due to the high-dimensional integral involved in the individual likelihood Eq. (3). To circumvent this issue, several techniques have been proposed including Kalman filtering, Monte-Carlo particle filtering (such as sequential importance sampling) and MCMC (see Clark et al., 2005; Wang, 2007 for reviews). Our objective here is not to discuss these different methods. For our purpose, we adopt the MCMC technique which is now widely used in biology (Ellison, 2004; Clark, 2005), in particular for estimating animal survival (Schwarz and Seber, 1999; Brooks et al., 2000). Besides, this is to our knowledge the only methodology which comes with an efficient and flexible program to implement it, which, in our case, will allow biologists to easily and rapidly adopt our approach.

In addition to the difficulty of estimating model parameters, the use of SSMs raises several important issues regarding identifiability, model selection and goodness-of-fit (Buckland et al., 2004) that will not be discussed here. Noteworthy, Bayesian modelling using MCMC methods offer possible solutions reviewed in Gimenez et al. (submitted).

2.3. *Illustration*

We consider capture–recapture data on the European dipper (*Cinclus cinclus*) that were collected between 1981 and 1987 (Lebreton et al., 1992). The data consist of marking and recaptures of 294 birds ringed as adults in eastern France. We applied standard maximum-likelihood estimation (Lebreton et al., 1992) and MCMC techniques (Brooks et al., 2000) using the product-multinomial likelihood and the state-space likelihood of Eq. (3) in combination with Eqs. (1) and (2). We ran two overdispersed parallel MCMC chains to check whether convergence was reached (Gelman, 1996). We used 10,000 iterations with 5000 burned iterations for posterior summarization. We used uniform flat priors for both survival and detection probabilities. The simulations were performed using WinBUGS (Spiegelhalter et al., 2003). The R (Ihaka and Gentleman, 1996) package R2WinBUGS (Sturtz et al., 2005) was used to call WinBUGS and export results in R. This was especially helpful when converting the raw encounter histories into the appropriate format, generating initial values and calculate posterior modes. The programs are available in Appendix A. Posterior summaries for encounter and survival probabilities are given in Table 1, along with their posterior probability distributions that are displayed in Fig. 1.

Survival estimates were uniformally similar whatever the method used (Table 1). In particular, there is a clear decrease

Table 1 – Estimated survival and detection probabilities for the Dipper data using the CJS model and three different methods, the state-space model (SSM) using a Monte Carlo Markov Chain (MCMC) method, the product-multinomial model (PMM) using a MCMC method and the PMM using a maximum-likelihood (ML) method

Parameter	SSM using MCMC posterior median/mode (S.D.)	PMM using MCMC posterior median/mode (S.D.)	PMM using ML MLE (S.E.)
ϕ_1	0.721/0.722 (0.132)	0.723/0.693 (0.132)	0.718 (0.156)
ϕ_2	0.448/0.456 (0.071)	0.448/0.460 (0.071)	0.435 (0.069)
ϕ_3	0.480/0.493 (0.060)	0.480/0.476 (0.061)	0.478 (0.060)
ϕ_4	0.628/0.624 (0.061)	0.627/0.616 (0.060)	0.626 (0.059)
ϕ_5	0.602/0.601 (0.057)	0.602/0.607 (0.057)	0.599 (0.056)
ϕ_6	0.713/0.640 (0.142)	0.720/0.628 (0.143)	– (–)[a]
p_2	0.671/0.658 (0.134)	0.670/0.691 (0.134)	0.696 (0.166)
p_3	0.883/0.918 (0.083)	0.883/0.904 (0.083)	0.923 (0.073)
p_4	0.888/0.914 (0.063)	0.889/0.912 (0.063)	0.913 (0.058)
p_5	0.882/0.885 (0.057)	0.883/0.904 (0.057)	0.901 (0.054)
p_6	0.913/0.920 (0.052)	0.912/0.935 (0.051)	0.932 (0.046)
p_7	0.735/0.724 (0.142)	0.727/0.648 (0.143)	– (–)[a]

The two first methods were implemented using program WinBUGS (Spiegelhalter et al., 2003), while program M-SURGE (Choquet et al., 2004) was used to implement the last one.

[a] Non-identifiability detected.

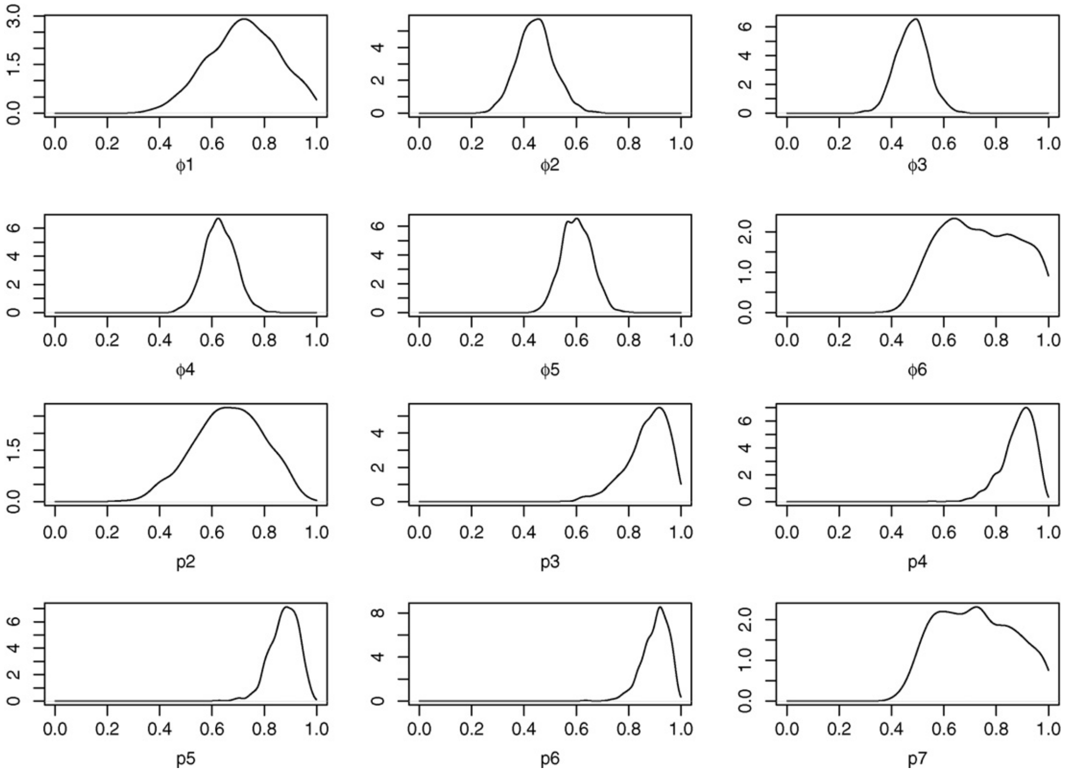

Fig. 1 – Posterior distributions for the survival and detection probabilities using the CJS model applied to the Dipper data set as estimated by the state-space model and MCMC methods.

in survival 1982–1983 and 1983–1984, corresponding to a major flood during the breeding season in 1983 (Lebreton et al., 1992).

In contrast, posterior medians of detection probabilities using the CJS SSM approach are quite different from the classical maximum-likelihood estimates, but more similar to the posterior medians obtained with the product-multinomial likelihood approach (Table 1). These discrepancies are no longer present when posterior modes are examined, as expected (recall that we use non-informative uniform distributions as priors for all parameters).

The last survival probability as well as the last detection probability are estimated with high variability (Table 1 and Fig. 1). The fact that these two parameters cannot be separately estimated is not surprising since the CJS model is known to be parameter-redundant (Catchpole and Morgan, 1997). Also, the first survival probability and the first detection probability are poorly estimated, due to the fact that very few individuals were marked at the first sampling occasion (approximately 7% of the full data set).

In terms of time computation, the MCMC approach using a product-multinomial likelihood took 30 s to run and a few second for the classical approach, while the MCMC approach using the SSM likelihood took 4 min (512Mo RAM, 2.6 GHz CPU).

3. Further state-space modelling

3.1. *Multistate capture–recapture models*

Multistate capture–recapture models (Arnason, 1973; Schwarz et al., 1993; AS hereafter) are a natural generalization of the CJS model in that individuals can move between states, according to probabilities of transition between those states. States can be either geographical sites or states of categorical variables like reproductive status or size class (Lebreton and Pradel, 2002). We provide here a state-space modelling formulation of the AS model (Dupuis, 1995; Newman, 1998; Clark et al., 2005). Without loss of generality, we consider two states. Let $X_{i,t}$ be the random state vector taking values (1, 0, 0), (0, 1, 0) and (0, 0, 1) if, at time t, individual i is alive in state 1, 2 or dead respectively. Let $Y_{i,t}$ be the random observation vector taking values (1, 0, 0), (0, 1, 0) and (0, 0, 1) if, at time t, individual i is encountered in state 1, 2 or not encountered. Parameters involved in the modelling include $\phi^{rs}_{i,t}$, the probability that an animal i survives to time $t+1$ given that it is alive at time t ($t = 1, \ldots, T-1$) and makes the transition between state r and state s over the same interval ($r, s = 1, 2$), as well as $p^{r}_{i,t}$ the probability of detecting individual i at time t in state r ($t = 2, \ldots, T, r = 1, 2$). A state-space formulation for the multistate AS model is given by:

$$Y_{i,t}|X_{i,t} \sim \text{multinomial}\left(1, X_{i,t}\begin{bmatrix} p^{1}_{i,t} & 0 & 1-p^{1}_{i,t} \\ 0 & p^{2}_{i,t} & 1-p^{2}_{i,t} \\ 0 & 0 & 1 \end{bmatrix}\right) \tag{6}$$

$$X_{i,t+1}|X_{i,t} \sim \text{multinomial}\left(1, X_{i,t}\begin{bmatrix} \phi^{11}_{i,t} & \phi^{12}_{i,t} & 1-\phi^{11}_{i,t}-\phi^{12}_{i,t} \\ \phi^{21}_{i,t} & \phi^{22}_{i,t} & 1-\phi^{21}_{i,t}-\phi^{22}_{i,t} \\ 0 & 0 & 1 \end{bmatrix}\right) \tag{7}$$

where Eqs. (6) and (7) are the observation and the state equations respectively. This formulation has similarities with that of Pradel (2005) who used hidden-Markov models to extend multistate models to cope with uncertainty in state assignment. Again, it should be noted that the state-space formulation allows the demographic parameters to be distinguished from the nuisance parameters. A similar reasoning to that adopted for the CJS model leads to Eqs. (6) and (7). As expected, Eqs. (6) and (7) reduce to Eqs. (1) and (2) if one considers a single state. Making similar assumptions as in the CJS model leads to the population AS SSM.

3.2. *Ring-recovery models*

The capture–recapture models presented above deals with apparent survival, which turns out to be true survival if emigration is negligeable. When marks of individuals (or individuals themselves) are actually recovered, true survival probabilities can be estimated using ring-recovery models (Brownie et al., 1985; RR models hereafter). Let $X_{i,t}$ be the binary random variable taking values 1 if individual *i* is alive at time *t* and 0 if it is dead at time *t*. Let $Y_{i,t}$ be the binary random variable taking values 1 if mark of individual *i* is recovered at time *t* and 0 otherwise. The parameters involved in the likelihood are $\phi_{i,t}$, the probability that an animal *i* survives to time $t+1$ given that it is alive at time *t* ($t = 1, \ldots, T-1$), and $\lambda_{i,t}$ the probability of recovering the mark of individual *i* at time *t* ($t = 2, \ldots, T$). A general state-space formulation of the RR model is therefore given by:

$$Y_{i,t}|X_{i,t}, X_{i,t-1} \sim \text{Bernoulli}\left((X_{i,t-1} - X_{i,t})\lambda_{i,t}\right) \tag{8}$$

$$X_{i,t+1}|X_{i,t} \sim \text{Bernoulli}\left(X_{i,t}\phi_{i,t}\right) \tag{9}$$

where Eqs. (8) and (9) are the observation and the state equations respectively. While the state Eq. (9) is the same as that in the individual SSM CJS, the observation Eq. (8) deserves further explanation. If individual *i*, alive at time $t-1$, does not survive to time *t*, then its mark has probability $\lambda_{i,t}$ of being recovered and probability $1-\lambda_{i,t}$ otherwise, which translates into $Y_{i,t}$ is distributed as Bernoulli ($\lambda_{i,t}$) given $X_{i,t-1} = 1$ and $X_{i,t} = 0$, i.e., $X_{i,t-1} - X_{i,t} = 1$. Now if individual *i* is in a given state (dead or alive) at time $t-1$ and remains in this state till time *t*, then its mark cannot be recovered, which translates into $Y_{i,t}$ is distributed as Bernoulli (0) given $X_{i,t-1} = 0$ and $X_{i,t} = 0$ or $X_{i,t-1} = 1$ and $X_{i,t} = 1$, i.e., $X_{i,t-1} - X_{i,t} = 0$. The distribution of the observation $Y_{i,t}$ conditional on the combination of states $X_{i,t-1} - X_{i,t}$ is thus given by Eq. (8). Similar comments to that of previous sections can be made here as well. Finally, we note that because the probability distribution of the current observation does not only depend on the current state variable, the model defined by Eqs. (8) and (9) does not exactly matches the definition of a state-space model but can be rewritten as such (see Appendix B).

4. Discussion

We have shown that, by separating the demographic process from its observation, CR models for estimating survival can be expressed as SSMs. In particular, the SSM formulation of the CJS model competes well with the standard method when applied to a real data set. Bearing this in mind, we see at least two further promising developments to our approach.

First, by scaling down from the population to the individual level while modelling the survival probabilities, individual random effects can readily be incorporated to cope with heterogeneity in the detection probability (Huggins, 2001) and deal with a frailty in the survival probability (Vaupel and Yashin, 1985). Second, the combination of various sources of information which has recently received a growing interest (e.g., recovery and recapture data, Catchpole et al., 1998; recovery and census data, Besbeas et al., 2002, 2003) can now be operated/conducted in a unique SSM framework and hence benefits from the corpus of related methods. Of particular importance, we are currently investigating the robust detection of density-dependence by accounting for error in the measurement of population size using the combination of census data and data on marked individuals.

Because most often, data collected in population dynamics studies give only a noisy output of the demographic process under investigation, the SSM framework provides a flexible and integrated framework for fitting a wide range of models which, with widespread adoption, has the potential to advance significantly ecological statistics (Buckland et al., 2004; Thomas et al., 2005).

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Appendix A. WinBUGS code for fitting the CJS model using the SSM formulation

```
#############################################################
# MODEL                                                     #
# State-space formulation of the Cormack-Jolly-Seber model  #
# observations = 0 (non-encountered) and 1 (encountered)    #
# states = 0 (dead) and 1 (alive)                           #
#############################################################
model
{
# Define the priors for survival phi and detectability p
p[1] <- 1
phi[1] <- 1
for (j in 2:K)
{
phi[j] ~ dbeta(1,1)
p[j] ~ dbeta(1,1)
}
# Define the SYSTEM PROCESS
for (i in 1:n)
  {
  # if first capture
  PrX[i,e[i]] <- 1 # Pr(alive | first capture) = 1
  X[i,e[i]+1] ~ dbern(PrX[i,e[i]]) # alive (a 1 is generated with certainty)
  PrO[i,e[i]] <- X[i,e[i]+1] # detection probability at initial detection is 100%
  # otherwise
      for (j in (e[i]+1):K)
      {
      PrX[i,j] <- phi[j] * X[i,j]
      X[i,j+1] ~ dbern(PrX[i,j])
      PrO[i,j] <- p[j] * X[i,j+1]
      }
  # fullfil the remaining cells with zeros
      for (j in 1:(e[i]-1))
      {
      PrX[i,j] <- 0
      X[i,j] <- 1
      PrO[i,j] <- 0
      }
  }
```

```
# Define the OBSERVATION PROCESS
for (h in 1:nx)
  {
  data[h,3] ~ dbern(PrO[data[h,1],data[h,2]])
  }
}
#######################################################################
# DATA
# 'K' is the number of encounter occasions

# 'n' is the number of individuals
# 'nx' is 'K' times 'n'
# 'e' is the vector of first encounters ('n' components)
# 'data' is a matrix with dimensions 'nx' times 3 where
#   the first column gives the current individual (1,...,'n'),
#   the second column gives the current encounter occasion (1,...,'K'),
#   the third column gives the observation (= 1 if detection, = 0 otherwise)
#   corresponding to the current individual and current encounter occasion
############################################################################
```

Appendix B

Let $Z_{i,t} = [X_{i,t-1}, X_{i,t}]$ be a bivariate random vector where its two components are denoted $Z^1_{i,t}$ and $Z^2_{i,t}$. Eq. (8) becomes

$$Y_{i,t}|Z_{i,t} \sim \text{Bernoulli}\left((Z^1_{i,t} - Z^2_{i,t})\lambda_{i,t}\right) \tag{10}$$

and Eq. (9) becomes

$$Z_{i,t+1}|Z_{i,t} = \begin{cases} (Z^1_{i,t+1}|Z_{i,t}) = Z^2_{i,t} \\ Z^2_{i,t+1}|Z_{i,t} \sim \text{Bernoulli}(Z^2_{i,t}\phi_{i,t}). \end{cases} \tag{11}$$

The system defined by Eqs. (10) and (11) is a state-space model and it is equivalent to the model defined by Eqs. (8) and (9).

Note that an alternative state-space formulation can be adopted using a multistate formulation of the RR model (Lebreton et al., 1999) and Section 3.1.

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