



Bayesian integrated population modeling using JAGS

Multistate capture- recapture models

Multistate capture histories

State = individual, time-specific categorical covariate

ID	1992	1993	1994	1995	1996	1997	1998	1999
1	0	1	2	2	0	2	0	0
2	1	1	1	0	0	0	0	0
3	0	2	0	0	0	0	0	0
4	0	0	2	1	0	2	0	0
5	0	0	0	1	1	2	1	1
6	0	0	0	2	2	1	2	0

Multistate capture histories

State = individual, time-specific categorical covariate

Examples of states:

- Geographical locations
- Breeding status
- Disease status

ID	1992	1993	1994	1995	1996	1997	1998	1999
1	0	1	2	2	0	2	0	0
2	1	1	1	0	0	0	0	0
3	0	2	0	0	0	0	0	0
4	0	0	2	1	0	2	0	0
5	0	0	0	1	1	2	1	1
6	0	0	0	2	2	1	2	0

A bit of history

Res. Popul. Ecol. (1973) 15, 1-8.

THE ESTIMATION OF POPULATION SIZE, MIGRATION RATES AND SURVIVAL IN A STRATIFIED POPULATION

A. Neil ARNASON

Computer Science Department, University of Manitoba,
Winnipeg, Canada

INTRODUCTION

CHAPMAN and JUNGE (1956, hereafter referred to as C & J) developed estimates of stratum size and migration rates for a population divided into $n \geq 2$ areas (strata) when animals were free to migrate from area to area. The method was based on data from sampling and marking observations on two occasions. The method was extended by DARROCH (1961) to allow sampling in different numbers of strata at the two sampling times, and to show how to treat some special problems that arise when using the method. These problems arise when a particular data matrix (which must be inverted) is singular or ill-conditioned. The same problems could occur with the estimates which will be given in this paper.

In order to account for deaths or losses from the areas due to permanent emigration out of the areas being sampled, it is necessary to sample on at least three occasions. I developed estimates for the three sample experiment on two areas (ARNASON 1972a) and later (ARNASON 1972b) gave asymptotic variance formulae for the estimates and suggested methods of predicting population sizes or time to extinction, using data from this experiment. The purpose of the present paper is to give the estimates for the general situation of sampling on three occasions in $n \geq 2$ areas. Modified estimates to account for losses on capture (as occur, for instance, in bird-banding studies) are also given.

A bit of history

BIOMETRICS 49, 177–193
March 1993

Estimating Migration Rates Using Tag-Recovery Data

Carl J. Schwarz

Department of Statistics, University of Manitoba,
Winnipeg, Manitoba R3T 2N2, Canada

Jake F. Schweigert

Biological Sciences Branch, Pacific Biological Station,
Department of Fisheries and Oceans, Nanaimo, British Columbia V9R 5K6, Canada

and

A. Neil Arnason

Department of Computer Science, University of Manitoba,
Winnipeg, Manitoba R3T 2N2, Canada

SUMMARY

Tag-recovery data are used to estimate migration rates among a set of strata. The model formulation is a simple matrix extension of the formulation of a tag-recovery experiment discussed by Brownie et al. (1985, *Statistical Inference from Band-Recovery Data—A Handbook*, 2nd edition, Washington, D.C.: U.S. Department of the Interior). Estimation is more difficult because of the convolution of parameters between release and recovery and this convolution may cause estimates of the survival/migration parameters to have low precision. Derived parameters of emigration, immigration, harvest derivation, and overall net survival are also estimated. The models are applied to estimate the migration of Pacific herring among spawning grounds off the west coast of Canada. If animals can be re-released after being recaptured, the model corresponds, in its migration/survival components, to that of Arnason (1972, *Researches in Population Ecology* 13, 97–113). This correspondence is developed, leading to more efficient estimators of these parameters.

Arnason-Schwarz model

A generalisation of the CJS model to multiple sites

Res. Popul. Ecol. (1973) 15, 1–8.

THE ESTIMATION OF POPULATION SIZE, MIGRATION
RATES AND SURVIVAL IN A STRATIFIED
POPULATION

A. Neil ARNASON

Computer Science Department, University of Manitoba,
Winnipeg, Canada

BIOMETRICS 49, 177–193
March 1993

Estimating Migration Rates Using Tag-Recovery Data

Carl J. Schwarz

Department of Statistics, University of Manitoba,
Winnipeg, Manitoba R3T 2N2, Canada

Arnason-Schwarz model

A generalisation of the CJS model to multiple sites

Res. Popul. Ecol. (1973) 15, 1–8.

THE ESTIMATION OF POPULATION SIZE, MIGRATION
RATES AND SURVIVAL IN A STRATIFIED
POPULATION

A. Neil ARNASON

Computer Science Department, University of Manitoba,
Winnipeg, Canada

BIOMETRICS 49, 177–193
March 1993

Estimating Migration Rates Using Tag-Recovery Data

Carl J. Schwarz

Department of Statistics, University of Manitoba,
Winnipeg, Manitoba R3T 2N2, Canada





**BIGGER AND BETTER
AND STRONGER**

LIVE
RNC
• 2016

Sites may be states !

Ecology, 73(1), 1992, pp. 306–312
© 1992 by the Ecological Society of America

ESTIMATING TRANSITION PROBABILITIES FOR STAGE-BASED POPULATION PROJECTION MATRICES USING CAPTURE–RECAPTURE DATA¹

JAMES D. NICHOLS AND JOHN R. SAUER

United States Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA

KENNETH H. POLLOCK

Institute of Statistics, North Carolina State University, Box 8203, Raleigh, North Carolina 27695-8203 USA

JAY B. HESTBECK²

United States Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA

Abstract. In stage-based demography, animals are often categorized into size (or mass) classes, and size-based probabilities of surviving and changing mass classes must be estimated before demographic analyses can be conducted. In this paper, we develop two procedures for the estimation of mass transition probabilities from capture–recapture data. The first approach uses a multistate capture–recapture model that is parameterized directly with the transition probabilities of interest. Maximum likelihood estimates are then obtained numerically using program SURVIV. The second approach involves a modification of Pollock's robust design. Estimation proceeds by conditioning on animals caught in a particular class at time i , and then using closed models to estimate the number of these that are alive in other classes at $i + 1$. Both methods are illustrated by application to meadow vole, *Microtus pennsylvanicus*, capture–recapture data. The two methods produced reasonable estimates that were similar. Advantages of these two approaches include the directness of estimation, the absence of need for restrictive assumptions about the independence of survival and growth, the testability of assumptions, and the testability of related hypotheses of ecological interest (e.g., the hypothesis of temporal variation in transition probabilities).

Key words: capture–recapture models; *Microtus pennsylvanicus*; multistate models; parameter estimation; Pollock's robust design; stage-based population projection matrices; stage transition probabilities.

Ecology, 75(7), 1994, pp. 2052–2065
© 1994 by the Ecological Society of America

ESTIMATING BREEDING PROPORTIONS AND TESTING HYPOTHESES ABOUT COSTS OF REPRODUCTION WITH CAPTURE–RECAPTURE DATA¹

JAMES D. NICHOLS AND JAMES E. HINES

National Biological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA

KENNETH H. POLLOCK

Institute of Statistics, North Carolina State University, Box 8203, Raleigh, North Carolina 27695-8203 USA

ROBERT L. HINZ AND WILLIAM A. LINK

National Biological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA

Abstract. The proportion of animals in a population that breeds is an important determinant of population growth rate. Usual estimates of this quantity from field sampling data assume that the probability of appearing in the capture or count statistic is the same for animals that do and do not breed. A similar assumption is required by most existing methods used to test ecologically interesting hypotheses about reproductive costs using field sampling data. However, in many field sampling situations breeding and nonbreeding animals are likely to exhibit different probabilities of being seen or caught. In this paper, we propose the use of multistate capture–recapture models for these estimation and testing problems. This methodology permits a formal test of the hypothesis of equal capture/sighting probabilities for breeding and nonbreeding individuals. Two estimators of breeding proportion (and associated standard errors) are presented, one for the case of equal capture probabilities and one for the case of unequal capture probabilities. The multistate modeling framework also yields formal tests of hypotheses about reproductive costs to future reproduction or survival or both fitness components. The general methodology is illustrated using capture–recapture data on female meadow voles, *Microtus pennsylvanicus*. Resulting estimates of the proportion of reproductively active females showed strong seasonal variation, as expected, with low breeding proportions in midwinter. We found no evidence of reproductive costs extracted in subsequent survival or reproduction. We believe that this methodological framework has wide application to problems in animal ecology concerning breeding proportions and phenotypic reproductive costs.

Key words: capture/sighting probability; *Microtus pennsylvanicus*; multistate capture–recapture models; proportion of animals breeding; reproductive costs; survival rate.

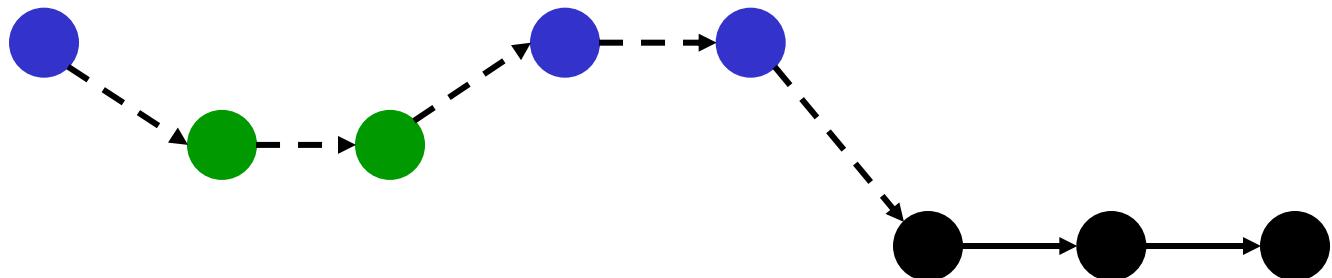
Conditional nature of the 2 processes

State process

Site A

Site B

Dead



→ Stochastic process
→ Deterministic process

Conditional nature of the 2 processes

State process

Site A

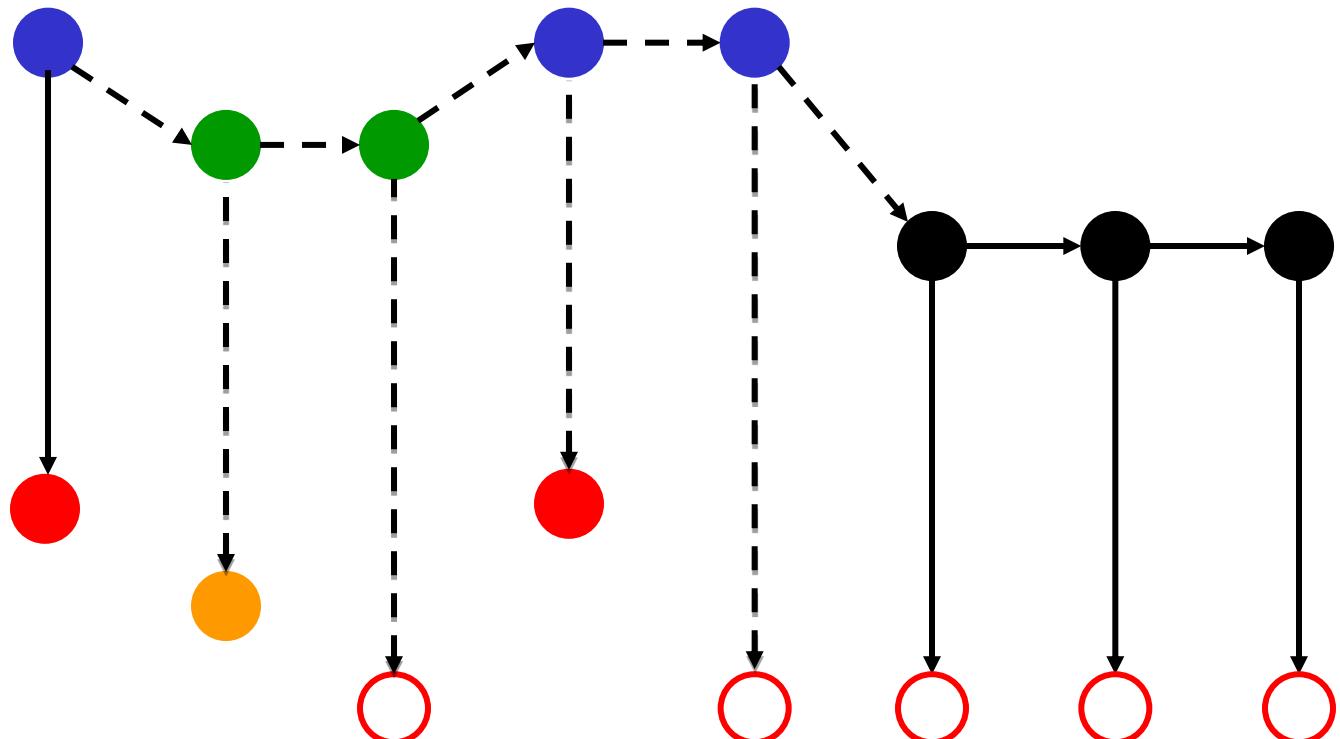
Site B

Dead

Seen at A

Seen at B

Not seen



Observation process

---> Stochastic process
—> Deterministic process

State process

States at time t

States at time t+1

<i>site A</i>	<i>site B</i>	<i>dead</i>
<i>site A</i>	Φ_{AA}	Φ_{AB}
<i>site B</i>	Φ_{BA}	Φ_{BB}
<i>dead</i>	0	1

$\Phi_{xy,t}$ is probability to be in state y at time $t+1$, given presence in state x at time t

State process

States at time t

States at time t+1

	<i>site A</i>	<i>site B</i>	<i>dead</i>
<i>site A</i>	Φ_{AA}	Φ_{AB}	$1 - \Phi_{AA} - \Phi_{AB}$
<i>site B</i>	Φ_{BA}	Φ_{BB}	$1 - \Phi_{BA} - \Phi_{BB}$
<i>dead</i>	0	0	1

Observation process

States at time t

Observations at time t

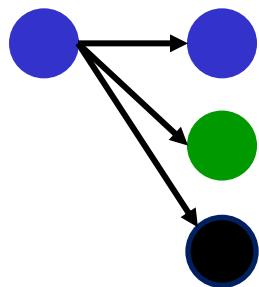
	<i>Seen at A</i>	<i>Seen at B</i>	<i>Not seen</i>
<i>site A</i>	p_A	0	$1 - p_A$
<i>site B</i>	0	p_B	$1 - p_B$
<i>dead</i>	0	0	1

State process

Site A

Site B

Dead

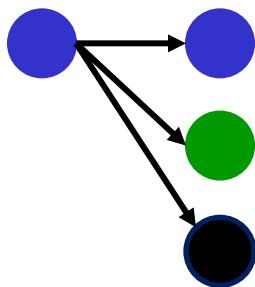


State process

Site A

Site B

Dead



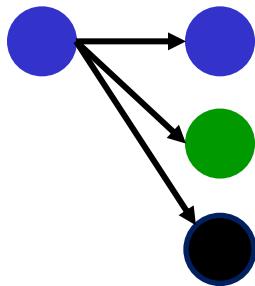
$z_{i,t}$ is state of individual i at time t ; either alive in site A, in site B or dead.

State process

Site A

Site B

Dead



$$\Omega =$$

States at time t

States at time $t+1$

site A	site B	dead	
site A	Φ_{AA}	Φ_{AB}	
site B	Φ_{BA}	Φ_{BB}	
dead	0	0	1

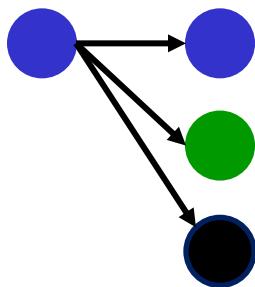
$z_{i,t}$ is state of individual i at time t ; either alive in site A, in site B or dead.

State process

Site A

Site B

Dead



$$\Omega =$$

States at time t

States at time $t+1$

site A	site B	dead
site A	Φ_{AA}	Φ_{AB}
site B	Φ_{BA}	Φ_{BB}
dead	0	1

BUGS language:

$$z_{i,t+1} : dcat(\Omega_{z_{i,t},})$$

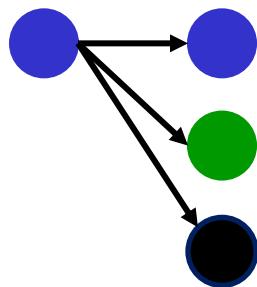
$z_{i,t}$ is state of individual i at time t ; either alive in site A, in site B or dead.

State process

Site A

Site B

Dead



$$\Omega =$$

States at time t

States at time $t+1$

site A	site B	dead	
site A	Φ_{AA}	Φ_{AB}	
site B	Φ_{BA}	Φ_{BB}	
dead	0	0	1

BUGS language:

$$z_{i,t+1} : dcat(\Omega_{z_{i,t},})$$

dcat() is categorical distribution = multinomial distribution with a single trial
Takes a vector of probabilities for each category as argument

Observation process

Site A

Site B



Dead

Observation process

Site A

Site B



Dead

$y_{i,t}$ is observation of individual i at time t ; either seen in site A, in site B or not seen.

Observation process

Site A

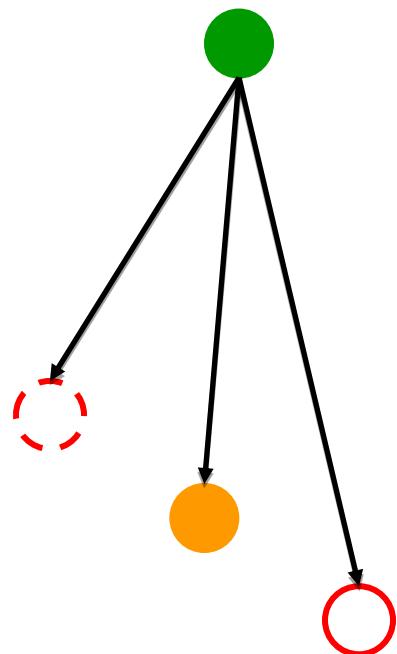
Site B

Dead

Seen at A

Seen at B

Not seen



$y_{i,t}$ is observation of individual i at time t ; either seen in site A, in site B or not seen.

Observation process

Site A

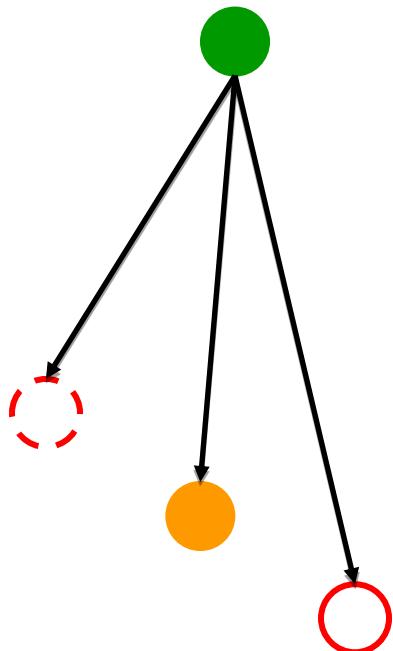
Site B

Dead

Seen at A

Seen at B

Not seen



$\Theta =$

States at time t

Observations at time t

	Seen at A	Seen at B	Not seen
site A	p_A	0	$1 - p_A$
site B	0	p_B	$1 - p_B$
dead	0	0	1

$y_{i,t}$ is observation of individual i at time t ; either seen in site A, in site B or not seen.

Observation process

Site A

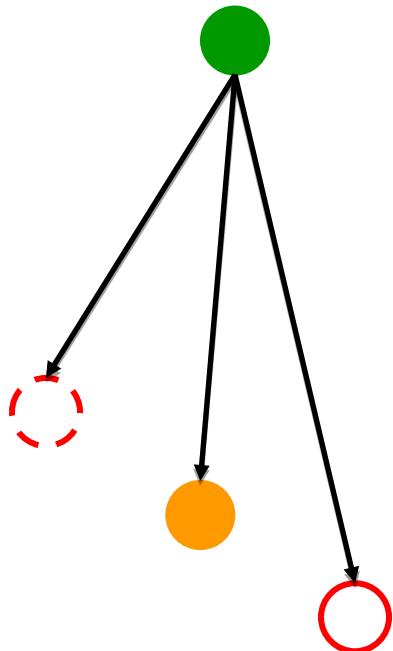
Site B

Dead

Seen at A

Seen at B

Not seen



$$\Theta =$$

States at time t

Observations at time t

	Seen at A	Seen at B	Not seen
site A	p_A	0	$1-p_A$
site B	0	p_B	$1-p_B$
dead	0	0	1

BUGS language:
 $y_{i,t} : dcat(\Theta_{z_{i,t},})$

$y_{i,t}$ is observation of individual i at time t ; either seen in site A, in site B or not seen.

Usual re-parameterisation

- $\Phi_{xy,t}$: probability to be in state y at time $t+1$, given presence in state x at time t

$$\begin{bmatrix} \Phi_{AA} & \Phi_{AB} & 1 - \Phi_{AA} - \Phi_{AB} \\ \Phi_{BA} & \Phi_{BB} & 1 - \Phi_{BA} - \Phi_{BB} \\ 0 & 0 & 1 \end{bmatrix}$$

Usual re-parameterisation

- $\Phi_{xy,t}$: probability to be in state y at time $t+1$, given presence in state x at time t

$$\begin{bmatrix} \Phi_{AA} & \Phi_{AB} & 1 - \Phi_{AA} - \Phi_{AB} \\ \Phi_{BA} & \Phi_{BB} & 1 - \Phi_{BA} - \Phi_{BB} \\ 0 & 0 & 1 \end{bmatrix}$$

- ϕ_x : probability to **survive** from time t to time $t+1$, given presence in state x at time t
- $\psi_{xy,t}$: probability to move from state x to state y shortly before time $t+1$,
given survival from time t to time $t+1$

Usual re-parameterisation

- $\Phi_{xy,t}$: probability to be in state y at time $t+1$, given presence in state x at time t

$$\begin{bmatrix} \Phi_{AA} & \Phi_{AB} & 1 - \Phi_{AA} - \Phi_{AB} \\ \Phi_{BA} & \Phi_{BB} & 1 - \Phi_{BA} - \Phi_{BB} \\ 0 & 0 & 1 \end{bmatrix}$$

- ϕ_x : probability to **survive** from time t to time $t+1$, given presence in state x at time t
- $\psi_{xy,t}$: probability to move from state x to state y shortly before time $t+1$, **given survival** from time t to time $t+1$

$$\begin{bmatrix} \phi_A(1 - \psi_{AB}) & \phi_A \psi_{AB} & 1 - \phi_A \\ \phi_B \psi_{BA} & \phi_B(1 - \psi_{BA}) & 1 - \phi_B \\ 0 & 0 & 1 \end{bmatrix}$$



Model implementation in JAGS

```
# Likelihood
for (i in 1:nind) {
    }
} #i
```

Model implementation in JAGS

```
# Likelihood
for (i in 1:nind) {
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
}

} #i
```

Model implementation in JAGS

```
# Likelihood
for (i in 1:nind) {
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
  for (t in (f[i]+1):n.occasions) {

    } #t
} #i
```

Model implementation in JAGS

```
# Likelihood
for (i in 1:nind) {
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
  for (t in (f[i]+1):n.occasions) {
    # State process: draw S(t) given S(t-1)
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
  } #t
} #i
```

ps is the big phi matrix

Model implementation in JAGS

```
# Likelihood
for (i in 1:nind) {
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
  for (t in (f[i]+1):n.occasions) {
    # State process: draw S(t) given S(t-1)
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
    # Observation process: draw O(t) given S(t)
    y[i,t] ~ dcat(po[z[i,t], i, t-1,])
  } #t
} #i
```

po is the big theta matrix

Model implementation in JAGS

```
# Likelihood
for (i in 1:nind) {
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
  for (t in (f[i]+1):n.occasions) {
    # State process: draw S(t) given S(t-1)
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
    # Observation process: draw O(t) given S(t)
    y[i,t] ~ dcat(po[z[i,t], i, t-1,])
  } #t
} #i
```

Written generally, no changes needed, regardless model fitted

Model implementation in JAGS

```
# Define state-transition and observation matrices
for (i in 1:nind) {
    } #i
} #t
```

Define the structure of the multistate model

Model implementation in JAGS

```
# Define state-transition and observation matrices
for (i in 1:nind) {
  # Define probabilities of state S(t+1) given S(t)
  for (t in f[i]:(n.occasions-1)){
    ps[1,i,t,1] <- phiA[t] * (1-psiAB[t])
    ps[1,i,t,2] <- phiA[t] * psiAB[t]
    ps[1,i,t,3] <- 1-phiA[t]
    ps[2,i,t,1] <- phiB[t] * psIBA[t]
    ps[2,i,t,2] <- phiB[t] * (1-psiBA[t])
    ps[2,i,t,3] <- 1-phiB[t]
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- 1
  } #t
} #i
```

$$\begin{bmatrix} \phi_A(1-\psi_{AB}) & \phi_A\psi_{AB} & 1-\phi_A \\ \phi_B\psi_{BA} & \phi_B(1-\psi_{BA}) & 1-\phi_B \\ 0 & 0 & 1 \end{bmatrix}$$

Define the structure of the multistate model

Model implementation in JAGS

```
# Define state-transition and observation matrices
for (i in 1:nind) {
  # Define probabilities of state S(t+1) given S(t)
  for (t in f[i]:(n.occasions-1)){
    ps[1,i,t,1] <- phiA[t] * (1-psiAB[t])
    ps[1,i,t,2] <- phiA[t] * psiAB[t]
    ps[1,i,t,3] <- 1-phiA[t]
    ps[2,i,t,1] <- phiB[t] * psiba[t]
    ps[2,i,t,2] <- phiB[t] * (1-psiBA[t])
    ps[2,i,t,3] <- 1-phiB[t]
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- 1

    # Define probabilities of O(t) given S(t)
    po[1,i,t,1] <- pA[t]
    po[1,i,t,2] <- 0
    po[1,i,t,3] <- 1-pA[t]
    po[2,i,t,1] <- 0
    po[2,i,t,2] <- pB[t]
    po[2,i,t,3] <- 1-pB[t]
    po[3,i,t,1] <- 0
    po[3,i,t,2] <- 0
    po[3,i,t,3] <- 1
  } #t
} #i
```

$$\begin{bmatrix} \phi_A(1-\Psi_{AB}) & \phi_A\Psi_{AB} & 1-\phi_A \\ \phi_B\Psi_{BA} & \phi_B(1-\Psi_{BA}) & 1-\phi_B \\ 0 & 0 & 1 \end{bmatrix}$$

$$\begin{bmatrix} p_A & 0 & 1-p_A \\ 0 & p_B & 1-p_B \\ 0 & 0 & 1 \end{bmatrix}$$

Define the structure of the multistate model

Model implementation in JAGS

$$\phi(s), \psi(\cdot), p(s)$$

Define linear constraints on parameters & specify the needed priors

Model implementation in JAGS

```
#           constraints
for (t in 1:(n.occasions-1)){
  phiA[t] <- mean.phi[1]
  phiB[t] <- mean.phi[2]
  psiAB[t] <- mean.psi[1]
  psiBA[t] <- mean.psi[2]
  pA[t] <- mean.p[1]
  pB[t] <- mean.p[2]
}
```

$$\phi(s), \psi(.), p(s)$$

Define linear constraints on parameters & specify the needed priors

Model implementation in JAGS

```
# Priors and constraints
for (t in 1:(n.occasions-1)) {
  phiA[t] <- mean.phi[1]
  phiB[t] <- mean.phi[2]
  psiAB[t] <- mean.psi[1]
  psiBA[t] <- mean.psi[2]
  pA[t] <- mean.p[1]
  pB[t] <- mean.p[2]
}
for (u in 1:2) {
  mean.phi[u] ~ dunif(0, 1)
  mean.psi[u] ~ dunif(0, 1)
  mean.p[u] ~ dunif(0, 1)
}
```

$$\phi(s), \psi(\cdot), p(s)$$

Define linear constraints on parameters & specify the needed priors

Model implementation in JAGS

```
# Likelihood
for (i in 1:nind){
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
  for (t in (f[i]+1):n.occasions){
    # State process: draw S(t) given S(t-1)
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
    # Observation process: draw O(t) given S(t)
    y[i,t] ~ dcat(po[z[i,t], i, t-1,])
  } #t
} #i

# Priors and constraints
for (t in 1:(n.occasions-1)){
  phiA[t] <- mean.phi[1]
  phiB[t] <- mean.phi[2]
  psiAB[t] <- mean.psi[1]
  psiBA[t] <- mean.psi[2]
  pA[t] <- mean.p[1]
  pB[t] <- mean.p[2]
}
for (u in 1:2){
  mean.phi[u] ~ dunif(0, 1)      # Priors for mean state-spec. survival
  mean.psi[u] ~ dunif(0, 1)      # Priors for mean transitions
  mean.p[u] ~ dunif(0, 1)        # Priors for mean state-spec. recapture
}

# Define state-transition and observation matrices
for (i in 1:nind){
  # Define probabilities of state S(t+1) given S(t)
  for (t in f[i]:n.occasions-1)){
    ps[1,i,t,1] <- phiA[t] * (1-psiAB[t])
    ps[1,i,t,2] <- phiA[t] * psiAB[t]
    ps[1,i,t,3] <- 1-phiA[t]
    ps[2,i,t,1] <- phiB[t] * psiBA[t]
    ps[2,i,t,2] <- phiB[t] * (1-psiBA[t])
    ps[2,i,t,3] <- 1-phiB[t]
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- 1

    # Define probabilities of O(t) given S(t)
    po[1,i,t,1] <- pA[t]
    po[1,i,t,2] <- 0
    po[1,i,t,3] <- 1-pA[t]
    po[2,i,t,1] <- 0
    po[2,i,t,2] <- pB[t]
    po[2,i,t,3] <- 1-pB[t]
    po[3,i,t,1] <- 0
    po[3,i,t,2] <- 0
    po[3,i,t,3] <- 1
  } #t
} #i
```

Live demo



Exercise 3

Multistate models are very flexible (Lebreton et al. 2009)

Multistate models are very flexible: some examples

0. CJS models are multistate models w/ 2 states: alive and dead

Multistate models are very flexible: some examples

0. CJS models are multistate models w/ 2 states: alive and dead

$$\begin{array}{c} States \text{ at time } t+1 \\ \begin{matrix} & alive & dead. \\ alive & \phi & 1 - \phi \\ dead & 0 & 1 \end{matrix} \end{array}$$

Multistate models are very flexible: some examples

0. CJS models are multistate models w/ 2 states: alive and dead

States at time t+1

alive *dead.*

alive $\begin{bmatrix} \phi & 1 - \phi \\ 0 & 1 \end{bmatrix}$

Observations at time t

seen *not seen*

alive $\begin{bmatrix} p & 1 - p \\ 0 & 1 \end{bmatrix}$

States at time t

Multistate models are very flexible: some examples

0. CJS models are multistate models w/ 2 states: alive and dead

```
# Define state-transition and observation
matrices
for (i in 1:nind) {
  # Define probabilities of state S(t+1) given
  S(t)
  for (t in f[i]:(n.occasions-1)) {
    ps[1,i,t,1] <- phi[t]
    ps[1,i,t,2] <- 1 - phi[t]
    ps[2,i,t,1] <- 0
    ps[2,i,t,2] <- 1
    # Define probabilities of O(t) given S(t)
    po[1,i,t,1] <- p[t]
    po[1,i,t,2] <- 1 - p[t]
    po[2,i,t,1] <- 0
    po[2,i,t,2] <- 1
  } #t
} #i
```

$$\begin{bmatrix} \phi & 1 - \phi \\ 0 & 1 \end{bmatrix}$$
$$\begin{bmatrix} p & 1 - p \\ 0 & 1 \end{bmatrix}$$

Multistate models are very flexible: some examples

0. CJS models are multistate models w/ 2 states: alive and dead

```
# Define state-transition and observation
matrices
for (i in 1:nind) {
  # Define probabilities of state S(t+1) given
  S(t)
  for (t in f[i]:(n.occasions-1)) {
    ps[1,i,t,1] <- phi[t]
    ps[1,i,t,2] <- 1 - phi[t]
    ps[2,i,t,1] <- 0
    ps[2,i,t,2] <- 1
    # Define probabilities of O(t) given S(t)
    po[1,i,t,1] <- p[t]
    po[1,i,t,2] <- 1 - p[t]
    po[2,i,t,1] <- 0
    po[2,i,t,2] <- 1
  } #t
} #i
```

$$\begin{bmatrix} \phi & 1 - \phi \\ 0 & 1 \end{bmatrix}$$
$$\begin{bmatrix} p & 1 - p \\ 0 & 1 \end{bmatrix}$$

Some code here: https://github.com/oliviergimenez/multievent_jags_R

Multistate models are very flexible: some examples

1. Breeder vs. non-breeders

State-space likelihood

$$\begin{array}{c} & & \text{States at time } t+1 \\ & \text{breeding} & \text{non-br.} & \text{dead} \\ \text{States at time } t & \text{breeding} & \left[\begin{array}{ccc} \phi_B(1-\psi_{BN}) & \phi_B\psi_{BN} & 1-\phi_B \\ \phi_N\psi_{NB} & \phi_N(1-\psi_{NB}) & 1-\phi_N \\ 0 & 0 & 1 \end{array} \right] \\ \text{non-breeding} & & & \\ \text{dead} & & & \end{array}$$

Multistate models are very flexible: some examples

1. Breeder vs. non-breeders

State-space likelihood

States at time t+1

		breeding	non-br.	dead
States at time t	breeding	$\phi_B(1 - \psi_{BN})$	$\phi_B \psi_{BN}$	$1 - \phi_B$
	non-breeding	$\phi_N \psi_{NB}$	$\phi_N(1 - \psi_{NB})$	$1 - \phi_N$
	dead	0	0	1

Observations at time t

States at time t	seen, br.	seen, non-br.	not seen	
	breeding	p_B	0	$1 - p_B$
	non-breeding	0	p_N	$1 - p_N$
	dead	0	0	1

Multistate models are very flexible: some examples

2. Movement among 3 sites

		States at time $t+1$			
State process		site A	site B	site C	dead
States at time t	site A	$\phi_A(1 - \psi_{AB} - \psi_{AC})$	$\phi_A\psi_{AB}$	$\phi_A\psi_{AC}$	$1 - \phi_A$
	site B	$\phi_B\psi_{BA}$	$\phi_B(1 - \psi_{BA} - \psi_{BC})$	$\phi_B\psi_{BC}$	$1 - \phi_B$
	site C	$\phi_C\psi_{CA}$	$\phi_C\psi_{CB}$	$\phi_C(1 - \psi_{CA} - \psi_{CB})$	$1 - \phi_C$
	dead	0	0	0	1

Multistate models are very flexible: some examples

2. Movement among 3 sites

		States at time $t+1$			
State process	<i>States at time t</i>	site A	site B	site C	dead
		$\phi_A(1 - \psi_{AB} - \psi_{AC})$	$\phi_A \psi_{AB}$	$\phi_A \psi_{AC}$	$1 - \phi_A$
		$\phi_B \psi_{BA}$	$\phi_B(1 - \psi_{BA} - \psi_{BC})$	$\phi_B \psi_{BC}$	$1 - \phi_B$
		$\phi_C \psi_{CA}$	$\phi_C \psi_{CB}$	$\phi_C(1 - \psi_{CA} - \psi_{CB})$	$1 - \phi_C$
		0	0	0	1

		Observations at time t			
Observation process	<i>States at time t</i>	seen at A	seen at B	seen at C	not seen
		p_A	0	0	$1 - p_A$
		0	p_B	0	$1 - p_B$
		0	0	p_C	$1 - p_C$
		0	0	0	1

Multistate models are very flexible: some examples

2. Movement among 3 sites

		States at time $t+1$			
State process	<i>States at time t</i>	site A	site B	site C	dead
		$\phi_A(1 - \psi_{AB} - \psi_{AC})$	$\phi_A \psi_{AB}$	$\phi_A \psi_{AC}$	$1 - \phi_A$
site A	site B	$\phi_B \psi_{BA}$	$\phi_B(1 - \psi_{BA} - \psi_{BC})$	$\phi_B \psi_{BC}$	$1 - \phi_B$
site B	site C	$\phi_C \psi_{CA}$	$\phi_C \psi_{CB}$	$\phi_C(1 - \psi_{CA} - \psi_{CB})$	$1 - \phi_C$
site C	dead	0	0	0	1
dead					

The parameters ψ_{AB} and ψ_{AC} (as well as ψ_{BA} & ψ_{BC} and ψ_{CA} & ψ_{CB}) must be in the interval $[0, 1]$ and their sum must be ≤ 1 .

Multistate models are very flexible: some examples

2. Movement among 3 sites

		States at time $t+1$			
State process	States at time t	site A	site B	site C	dead
		$\phi_A(1 - \psi_{AB} - \psi_{AC})$	$\phi_A \psi_{AB}$	$\phi_A \psi_{AC}$	$1 - \phi_A$
site A	site B	$\phi_B \psi_{BA}$	$\phi_B(1 - \psi_{BA} - \psi_{BC})$	$\phi_B \psi_{BC}$	$1 - \phi_B$
site B	site C	$\phi_C \psi_{CA}$	$\phi_C \psi_{CB}$	$\phi_C(1 - \psi_{CA} - \psi_{CB})$	$1 - \phi_C$
site C	dead	0	0	0	1
dead					

The parameters ψ_{AB} and ψ_{AC} (as well as ψ_{BA} & ψ_{BC} and ψ_{CA} & ψ_{CB}) must be in the interval [0, 1] and their sum must be ≤ 1 .

Two options:

- Multinomial logit link function (ch 10 Kéry & Schaub 2012, Guéry et al. 2018)
- Dirichlet prior (ch 10 Kéry & Schaub 2012)

Multistate models are very flexible: some examples

3. Access to reproduction

State process

States at time t

		States at time $t+1$			
	<i>juvenile</i>	<i>1y NB</i>	<i>2y NB</i>	<i>breeder</i>	<i>dead</i>
<i>juvenile</i>	0	$\phi_1(1 - \alpha_1)$	0	$\phi_1\alpha_1$	$1 - \phi_1$
<i>1y NB</i>	0	0	$\phi_2(1 - \alpha_2)$	$\phi_2\alpha_2$	$1 - \phi_2$
<i>2y NB</i>	0	0	0	ϕ_3	$1 - \phi_3$
<i>breeder</i>	0	0	0	ϕ_B	$1 - \phi_B$
<i>dead</i>	0	0	0	0	1

Multistate models are very flexible: some examples

3. Access to reproduction

State process

States at time t

$$\begin{array}{c}
 \text{juvenile} \\
 1y NB \\
 2y NB \\
 \text{breeder} \\
 \text{dead}
 \end{array}
 \left[\begin{array}{ccccc}
 & & & & \text{States at time } t+1 \\
 \text{juvenile} & 0 & \phi_1(1-\alpha_1) & 0 & \phi_1\alpha_1 \\
 1y NB & 0 & 0 & \phi_2(1-\alpha_2) & \phi_2\alpha_2 \\
 2y NB & 0 & 0 & 0 & \phi_3 \\
 \text{breeder} & 0 & 0 & 0 & \phi_B \\
 \text{dead} & 0 & 0 & 0 & 1
 \end{array} \right]$$

Observations at time t

$$\begin{array}{c}
 \text{seen, breeder} \\
 \text{seen, 2y NB} \\
 \text{seen, 1y NB}
 \end{array}
 \left[\begin{array}{cccc}
 \text{not seen} & & & \\
 \text{seen, breeder} & 0 & 0 & 1 \\
 \text{seen, 2y NB} & 0 & 0 & 1-p_1 \\
 \text{seen, 1y NB} & p_1 & 0 & 1-p_1
 \end{array} \right]$$

Observation process

States at time t

$$\begin{array}{c}
 \text{juvenile} \\
 1y NB \\
 2y NB \\
 \text{breeder} \\
 \text{dead}
 \end{array}
 \left[\begin{array}{cccc}
 & & & \\
 \text{juvenile} & 0 & 0 & 1 \\
 1y NB & p_1 & 0 & 1-p_1 \\
 2y NB & 0 & p_2 & 1-p_2 \\
 \text{breeder} & 0 & 0 & p_3 \\
 \text{dead} & 0 & 0 & 1-p_3
 \end{array} \right]$$

Multistate models are very flexible: some examples

4. Temporary emigration

Multistate models are very flexible: some examples

4. Temporary emigration

State process

States at time t

		States at time $t+1$		
		inside	outside	dead
States at time t	inside	$\phi(1 - \psi_{IO})$	$\phi\psi_{IO}$	$1 - \phi$
	outside	$\phi\psi_{OI}$	$\phi(1 - \psi_{OI})$	$1 - \phi$
	dead	0	0	1

Multistate models are very flexible: some examples

4. Temporary emigration

State process

States at time t

States at time $t+1$		
	inside	outside
inside	$\phi(1 - \psi_{IO})$	$\phi\psi_{IO}$
outside	$\phi\psi_{OI}$	$\phi(1 - \psi_{OI})$
dead	0	0
		1

Observation process

States at time t

Observations at time t

	Seen	Not seen
inside	p	$1-p$
outside	0	1
dead	0	1

Multistate models are very flexible: some examples

5. Immediate trap response

Multistate models are very flexible: some examples

5. Immediate trap response

State process

States at time t

alive, seen

alive, not seen

dead

States at time $t+1$

$$\begin{matrix} & \begin{matrix} a, \text{seen} \\ a, \text{not seen} \\ \text{dead} \end{matrix} \\ \begin{matrix} \text{alive, seen} \\ \text{alive, not seen} \\ \text{dead} \end{matrix} & \begin{bmatrix} \phi p_s & \phi(1-p_s) & 1-\phi \\ \phi p_N & \phi(1-p_N) & 1-\phi \\ 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

Multistate models are very flexible: some examples

5. Immediate trap response

State process

States at time t

alive, seen

alive, not seen

dead

States at time $t+1$

$$\begin{matrix} & & a, \text{not } s & \text{dead} \\ a, \text{seen} & \left[\begin{array}{ccc} \phi p_s & \phi(1-p_s) & 1-\phi \\ \phi p_N & \phi(1-p_N) & 1-\phi \\ 0 & 0 & 1 \end{array} \right] \end{matrix}$$

Observation process

Observations at time t

States at time t

alive, seen

alive, not seen

dead

Not seen
Seen

$$\begin{bmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix}$$

Multistate models are very flexible: some examples

6. Combination of life and dead encounters

Multistate models are very flexible: some examples

6. Combination of life and dead encounters

State process

		States at time $t+1$		
		alive	rec. dead	dead
States at time t	alive	s	$1-s$	0
	recently dead	0	0	1
	dead	0	0	1

Multistate models are very flexible: some examples

6. Combination of life and dead encounters

State process

			States at time $t+1$			
			alive	rec. dead	dead	
			alive	s	$1-s$	0
States at time t			recently dead	0	0	1
			dead	0	0	1

Observation process

			Observations at time t			
			seen	recovered	not seen	
			alive	p	0	$1-p$
States at time t			rec. dead	0	r	$1-r$
			dead	0	0	1

What if you could achieve even more flexibility?



Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
- Breeding status in female roe deer is ascertained based on fawn detection

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
 - Breeding status in female roe deer is ascertained based on fawn detection
 - Sex status is ascertained based on morphological criteria in Audouin's gulls

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
 - Breeding status in female roe deer is ascertained based on fawn detection
 - Sex status is ascertained based on morphological criteria in Audouin's gulls
 - Disease status in house finches is ascertained based on birds' eyes examination

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
 - Breeding status in female roe deer is ascertained based on fawn detection
 - Sex status is ascertained based on morphological criteria in Audouin's gulls
 - Disease status in house finches is ascertained based on birds' eyes examination
 - Hybrid status in wolves is ascertained based on genetics

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
 - Breeding status in female roe deer is ascertained based on fawn detection
 - Sex status is ascertained based on morphological criteria in Audouin's gulls
 - Disease status in house finches is ascertained based on birds' eyes examination
 - Hybrid status in wolves is ascertained based on genetics
 - Dominance status in wolves is ascertained based on heterogeneity in detection

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
 - Breeding status in female roe deer is ascertained based on fawn detection
 - Sex status is ascertained based on morphological criteria in Audouin's gulls
 - Disease status in house finches is ascertained based on birds' eyes examination
 - Hybrid status in wolves is ascertained based on genetics
 - Dominance status in wolves is ascertained based on heterogeneity in detection
- We will need to explicitly consider state assignment in a model

Multievent capture-recapture models

- Multievent models extend multistate models with uncertainty in state assignment
 - Breeding status in female roe deer is ascertained based on fawn detection
 - Sex status is ascertained based on morphological criteria in Audouin's gulls
 - Disease status in house finches is ascertained based on birds' eyes examination
 - Hybrid status in wolves is ascertained based on genetics
 - Dominance status in wolves is ascertained based on heterogeneity in detection
- We will need to explicitly consider state assignment in a model
- All capture-recapture models can be seen as special cases of multievent models
- Seminal paper by Pradel (2005); see also Gimenez et al. (2012) for a review
- Dupuis (1995) had a similar idea, for the Arnason-Schwarz model

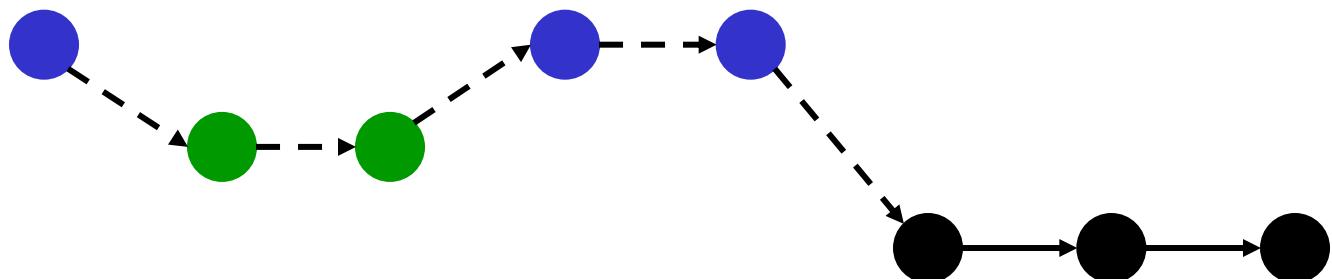
Conditional nature of the 2 processes

State process

State 1

State 2

Dead



--> Stochastic process
--> Deterministic process

Conditional nature of the 2 processes

State process

State 1

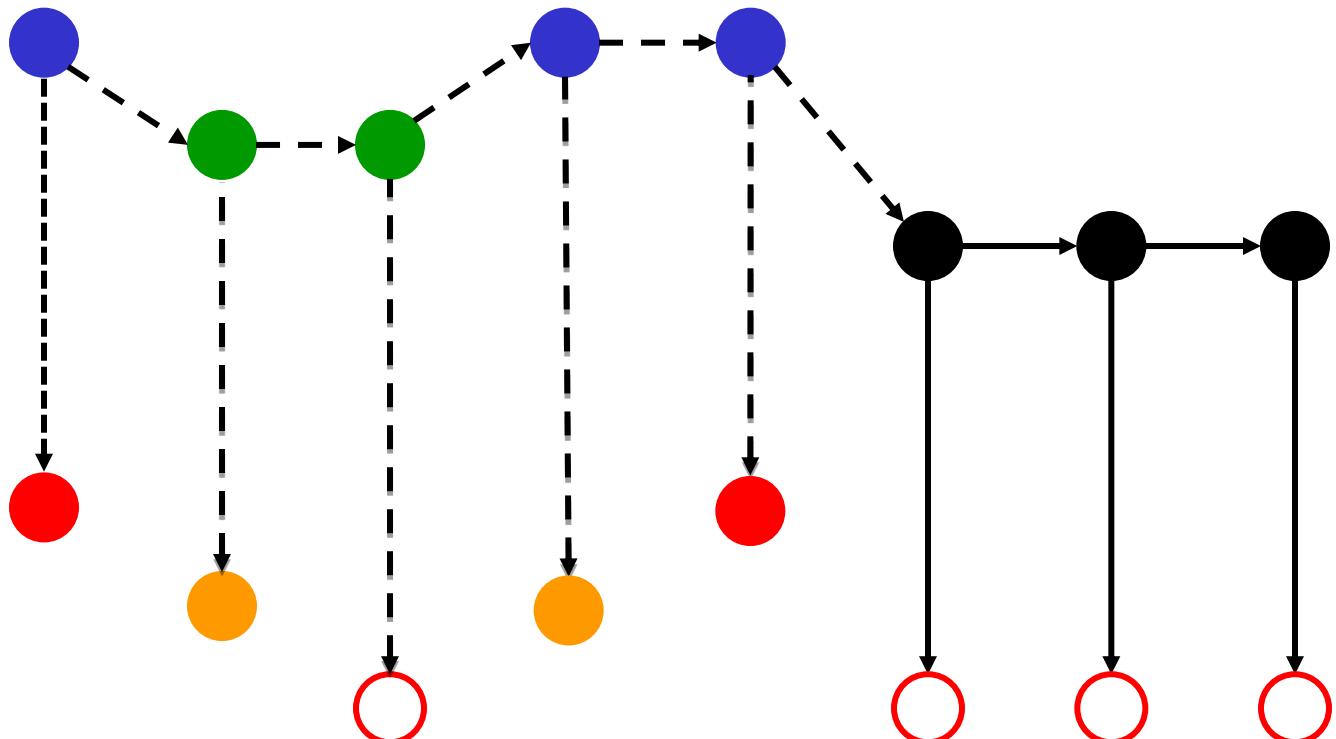
State 2

Dead

Seen 1

Seen 2

Not seen



Observation process

--> Stochastic process
—> Deterministic process

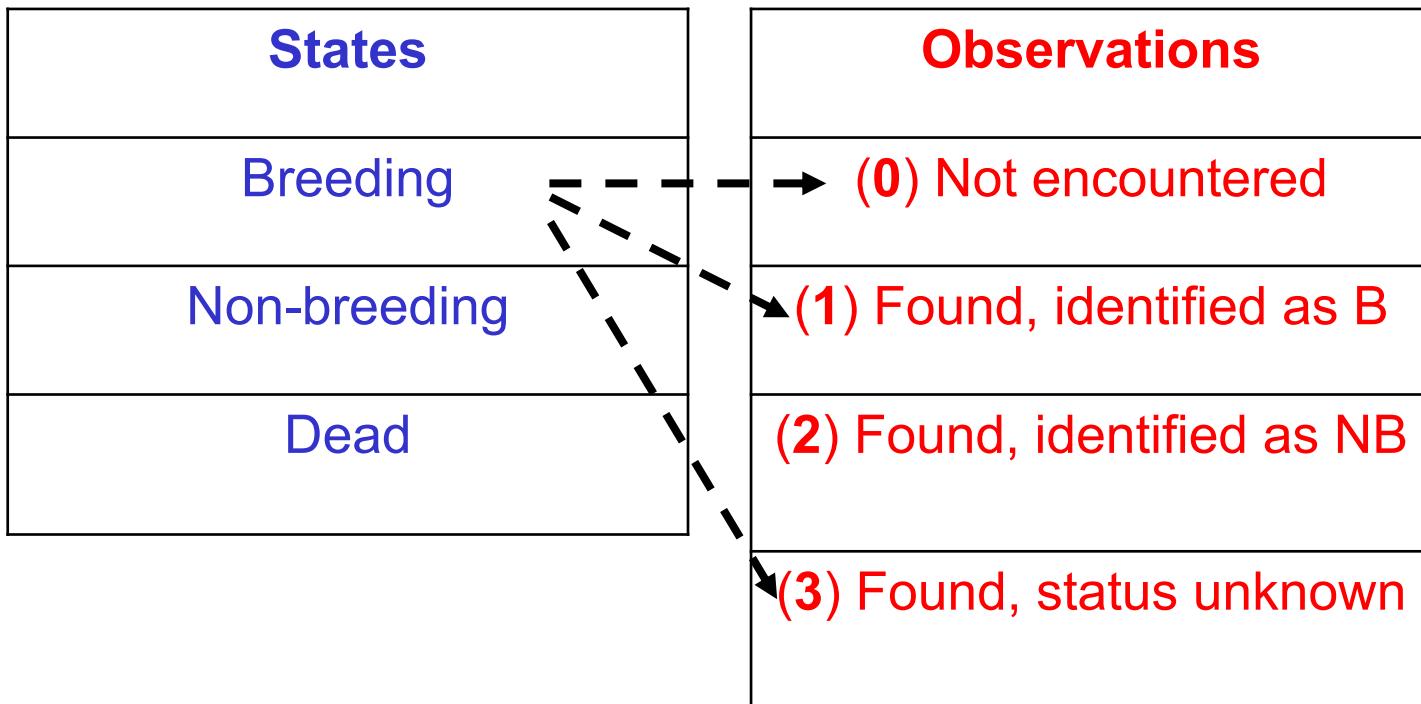
Uncertainty in breeding status

- **3 states**
 - breeding (B)
 - non-breeding (NB)
 - Dead (†)
- **4 observations**
 - Not encountered (0)
 - Found, ascertained as breeder (1)
 - Found, ascertained as non-breeder (2)
 - Found, status unknown (3)

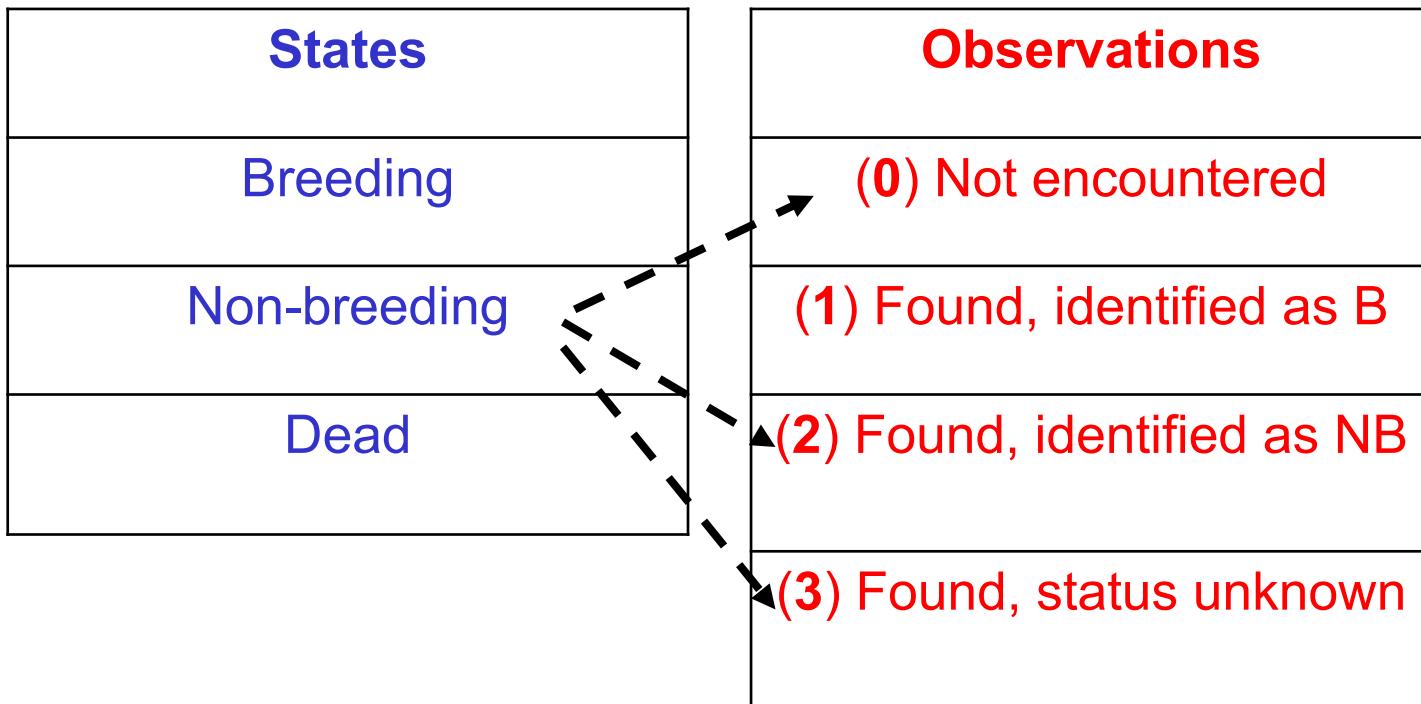
The model construction

States	Observations
Breeding	(0) Not encountered
Non-breeding	(1) Found, identified as B
Dead	(2) Found, identified as NB
	(3) Found, status unknown

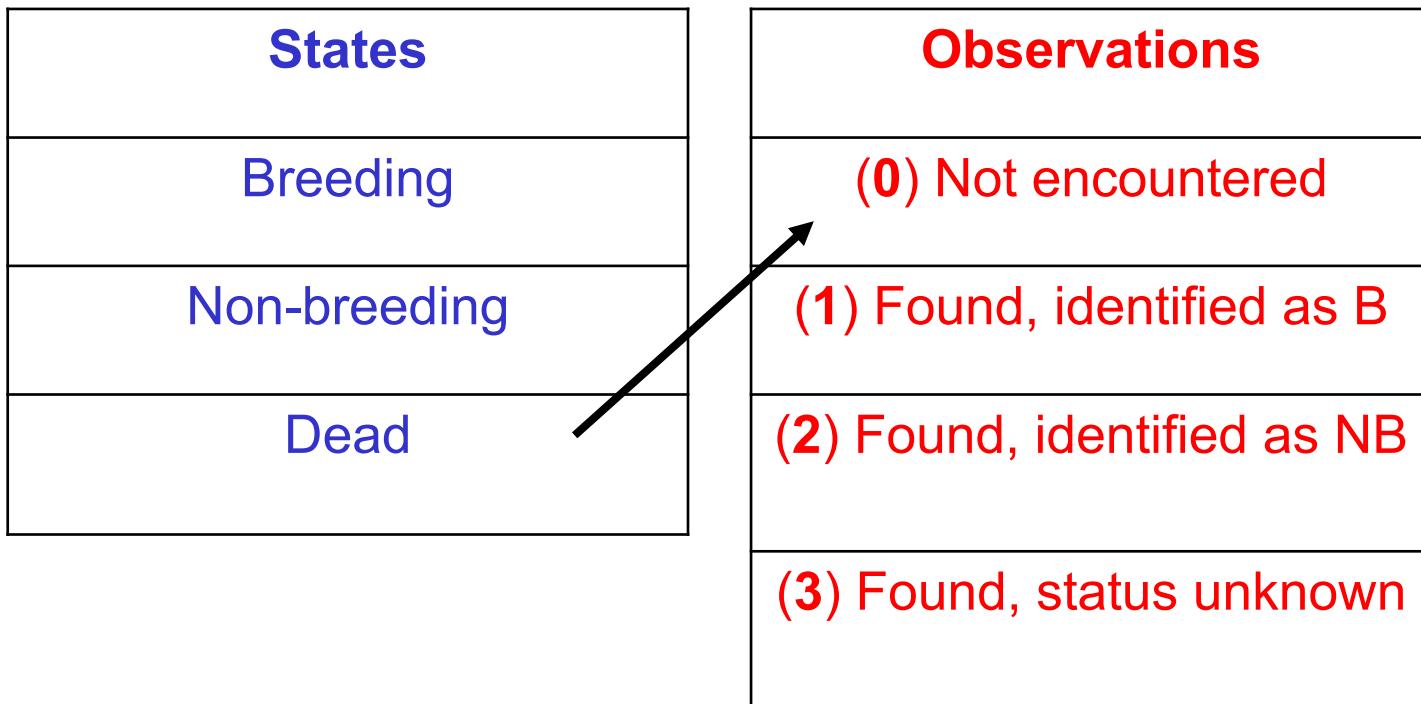
The model construction



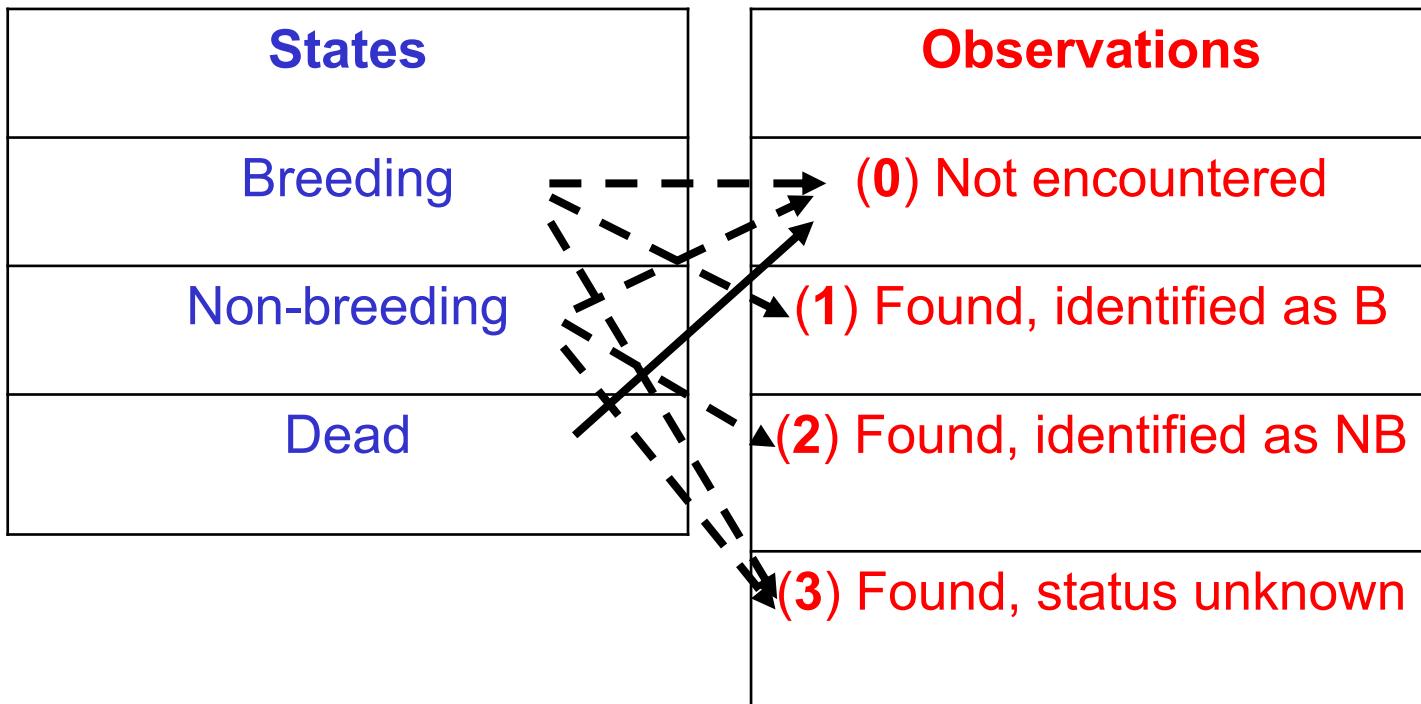
The model construction



The model construction



The model construction



Each live state can generate 3 different observations

Initial state probabilities

π_B probability that a newly encountered individual
is a breeder

$$\Pi_t = \begin{pmatrix} \text{B} & \text{NB} & \dagger \\ \pi_B & 1 - \pi_B & 0 \end{pmatrix}$$

Initial state probabilities

π_B probability that a newly encountered individual
is a breeder

$$\Pi_t = \begin{pmatrix} \text{B} & \text{NB} & \dagger \\ \pi_B & 1 - \pi_B & 0 \end{pmatrix}$$

BUGS language:

$$\Pi = [\pi \ 1 - \pi \ 0]$$

$$z_{i,f[i]} : dcat(\Pi)$$

transition parameters

$$\Phi_t = \begin{matrix} & \text{B} & \text{NB} & \dagger \\ \text{B} & \phi_B \psi_{B,B} & \phi_B (1 - \psi_{B,B}) & 1 - \phi_B \\ \text{NB} & \phi_{NB} \psi_{NB,B} & \phi_{NB} (1 - \psi_{NB,B}) & 1 - \phi_{NB} \\ \dagger & 0 & 0 & 1 \end{matrix}$$

transition parameters

$$\Phi_t = \begin{matrix} & \text{B} & \text{NB} & \dagger \\ \text{B} & \phi_B \psi_{B,B} & \phi_B (1 - \psi_{B,B}) & 1 - \phi_B \\ \text{NB} & \phi_{NB} \psi_{NB,B} & \phi_{NB} (1 - \psi_{NB,B}) & 1 - \phi_{NB} \\ \dagger & 0 & 0 & 1 \end{matrix}$$

BUGS language:

$$\Phi = \begin{bmatrix} \phi_B \psi_{B,B} & \phi_B (1 - \psi_{B,B}) & 1 - \phi_B \\ \phi_{NB} \psi_{NB,B} & \phi_{NB} (1 - \psi_{NB,B}) & 1 - \phi_{NB} \\ 0 & 0 & 1 \end{bmatrix} \quad z_{i,t+1} \sim \text{dcat}(\Phi_{z_{i,t}, 1:3})$$

observation parameters

δ_B = probability to assign an individual in state B to state B

δ_{NB} = probability to assign an individual in state NB to state NB

observation matrix

$$\mathbf{B}_t = \begin{matrix} & \begin{matrix} 1 & 2 & 3 & 4 \end{matrix} \\ \begin{matrix} B \\ NB \\ + \end{matrix} & \left[\begin{matrix} p_B\delta_B & 0 & p_B(1 - \delta_B) & 1 - p_B \\ 0 & p_{NB}\delta_{NB} & p_{NB}(1 - \delta_{NB}) & 1 - p_{NB} \\ 0 & 0 & 0 & 1 \end{matrix} \right] \end{matrix}$$

δ_B = probability to assign an individual in state B to state B

δ_{NB} = probability to assign an individual in state NB to state NB

observation matrix

$$\mathbf{B}_t = \begin{matrix} & \begin{matrix} 1 & 2 & 3 & 4 \end{matrix} \\ \begin{matrix} \mathbf{B} \\ \mathbf{NB} \\ \dagger \end{matrix} & \begin{bmatrix} p_B\delta_B & 0 & p_B(1 - \delta_B) & 1 - p_B \\ 0 & p_{NB}\delta_{NB} & p_{NB}(1 - \delta_{NB}) & 1 - p_{NB} \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

BUGS language:

$$B = \begin{bmatrix} p_B\delta_B & 0 & p_B(1 - \delta_B) & 1 - p_B \\ 0 & p_{NB}\delta_{NB} & p_{NB}(1 - \delta_{NB}) & 1 - p_{NB} \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad y_{i,t} \sim \text{dcat}(B_{z_{i,t}, 1:3})$$

observations parameters – 2 steps

Step 1: Encounter

$$\begin{matrix} & \color{green}E_B & \color{green}E_{NB} & \color{green}NE \\ \text{B} & \left[\begin{matrix} p_B & 0 & 1 - p_B \end{matrix} \right] \\ \text{NB} & \left[\begin{matrix} 0 & p_{NB} & 1 - p_{NB} \end{matrix} \right] \\ \dagger & \left[\begin{matrix} 0 & 0 & 1 \end{matrix} \right] \end{matrix}$$

Intermediate events: $\color{green}NE$ = ‘not encountered’; $\color{green}E$ = ‘encountered’

Step 2: Breeding
assessment

$$\begin{matrix} & 1 & 2 & 3 & 4 \\ \color{green}E_B & \left[\begin{matrix} \delta_B & 0 & 1 - \delta_B & 0 \end{matrix} \right] \\ \color{green}E_{NB} & \left[\begin{matrix} 0 & \delta_{NB} & 1 - \delta_{NB} & 0 \end{matrix} \right] \\ \color{green}NE & \left[\begin{matrix} 0 & 0 & 0 & 1 \end{matrix} \right] \end{matrix}$$

initial events

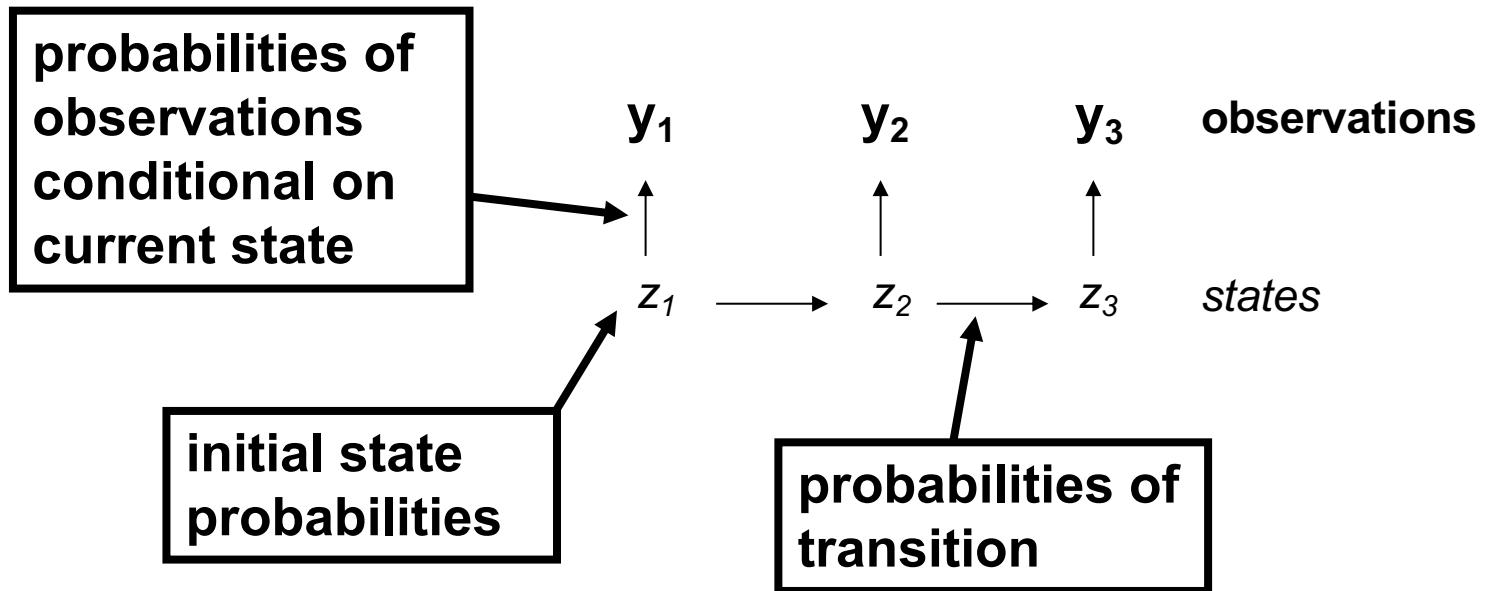
Step 1 (encounter) is degenerate because animals are all captured.

$$\begin{array}{c} E_B \quad E_{NB} \quad NE \\ \hline \text{B} \left[\begin{matrix} p_B & 0 & 1 - p_B \\ 0 & p_{NB} & 1 - p_{NB} \\ 0 & 0 & 1 \end{matrix} \right] & \xrightarrow{p = 1} & \text{B} \left[\begin{matrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{matrix} \right] \\ \text{NB} & & \text{NB} \\ \dagger & & \dagger \end{array}$$

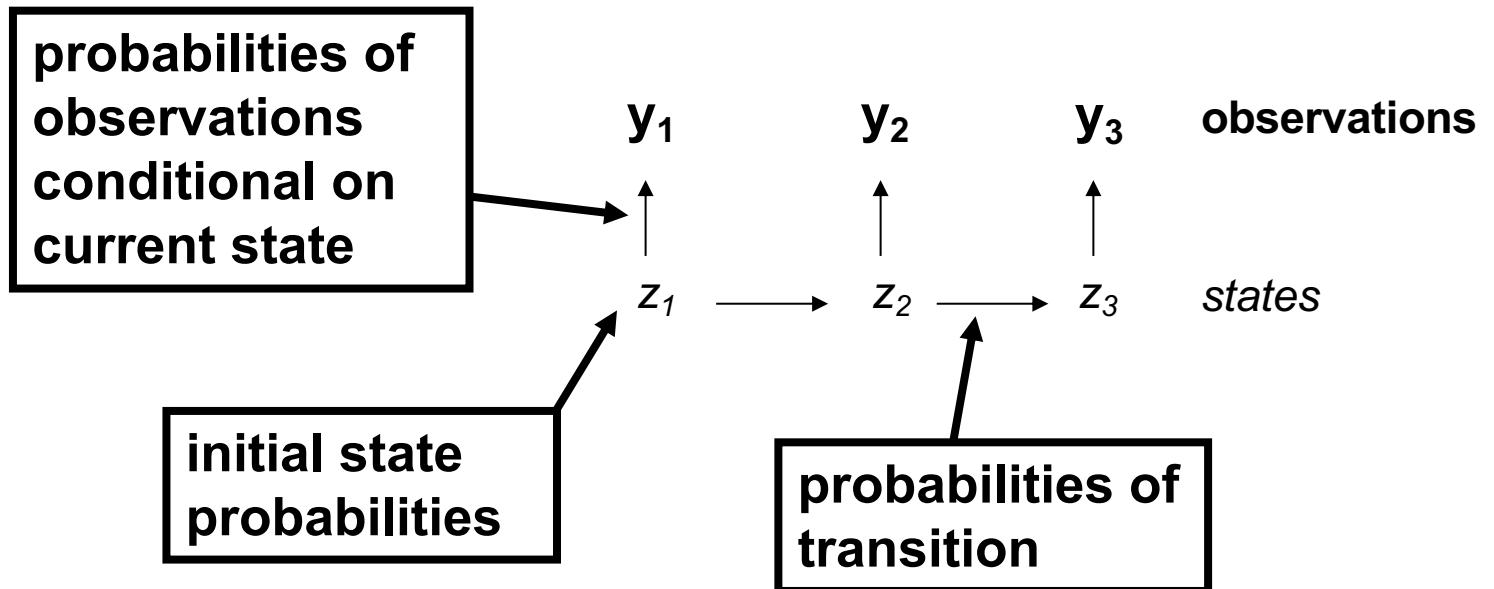
Step 2 (Breeding assessment) is unaffected

$$\begin{array}{cccc} 1 & 2 & 3 & 4 \\ \hline E_B & \left[\begin{matrix} \delta_B & 0 & 1 - \delta_B & 0 \end{matrix} \right] & & \\ E_{NB} & \left[\begin{matrix} 0 & \delta_{NB} & 1 - \delta_{NB} & 0 \end{matrix} \right] & & \\ NE & \left[\begin{matrix} 0 & 0 & 0 & 1 \end{matrix} \right] & & \end{array}$$

The multievent model



The multievent model



Multievent models are hidden Markov models (HMMs)

HMMs = SSMs with discrete states, and Markovian dynamics of states

ECOLOGY LETTERS

Ecology Letters, (2020) 23: 1878–1903

doi: 10.1111/ele.13610

REVIEW AND SYNTHESIS

Uncovering ecological state dynamics with hidden Markov models

Abstract

Brett T. McClintock,^{1*} 

Roland Langrock,²

Olivier Gimenez,³

Emmanuelle Cam,⁴

David L. Borchers,⁵

Richard Glennie⁵ and

Toby A. Patterson⁶ 

Ecological systems can often be characterised by changes among a finite set of underlying states pertaining to individuals, populations, communities or entire ecosystems through time. Owing to the inherent difficulty of empirical field studies, ecological state dynamics operating at any level of this hierarchy can often be unobservable or ‘hidden’. Ecologists must therefore often contend with incomplete or indirect observations that are somehow related to these underlying processes. By formally disentangling state and observation processes based on simple yet powerful mathematical properties that can be used to describe many ecological phenomena, hidden Markov models (HMMs) can facilitate inferences about complex system state dynamics that might otherwise be intractable. However, HMMs have only recently begun to gain traction within the broader ecological community. We provide a gentle introduction to HMMs, establish some common terminology, review the immense scope of HMMs for applied ecological research and provide a tutorial on implementation and interpretation. By illustrating how practitioners can use a simple conceptual template to customise HMMs for their specific systems of interest, revealing methodological links between existing applications, and highlighting some practical considerations and limitations of these approaches, our goal is to help establish HMMs as a fundamental inferential tool for ecologists.

HMMs are a promising unifying modelling framework

ORIGINAL ARTICLE

WILEY  Biometrics
Since 1947 A JOURNAL OF THE INTERNATIONAL BIOMETRIC SOCIETY

Exact inference for integrated population modelling

P. Besbeas^{1,2} | B.J.T. Morgan² 

¹Department of Statistics, Athens University of Business and Economics, 10434 Athens, Greece

²National Centre for Statistical Ecology, School of Mathematics, Statistics and Actuarial Science, University of Kent, Canterbury, Kent CT2 7FS, England

Correspondence

P. Besbeas, Department of Statistics, Athens University of Business and Economics, 10434 Athens, Greece
Email: P.T.Besbeas@kent.ac.uk

Abstract

Integrated population modelling is widely used in statistical ecology. It allows data from population time series and independent surveys to be analysed simultaneously. In classical analysis the time-series likelihood component can be conveniently approximated using Kalman filter methodology. However, the natural way to model systems which have a discrete state space is to use hidden Markov models (HMMs). The proposed method avoids the Kalman filter approximations and Monte Carlo simulations. Subject to possible numerical sensitivity analysis, it is exact, flexible, and allows the use of standard techniques of classical inference. We apply the approach to data on Little owls, where the model is shown to require a one-dimensional state space, and Northern lapwings, with a two-dimensional state space. In the former example the method identifies a parameter redundancy which changes the perception of the data needed to estimate immigration in integrated population modelling. The latter example may be analysed using either first- or second-order HMMs, describing numbers of one-year olds and adults or adults only, respectively. The use of first-order chains is found to be more efficient, mainly due to the smaller number of one-year olds than adults in this application. For the lapwing modelling it is necessary to group the states in order to reduce the large dimension of the state space. Results check with Bayesian and Kalman filter analyses, and avenues for future research are identified.

**Fitting capture-recapture models in Jags may be slow -
A few tricks to speed up computations/improve convergence**



Fitting capture-recapture models in Jags may be slow - A few tricks to speed up computations/improve convergence

- If your parameters are not individual specific, or time-independent, then avoid unnecessary loops and memory usage.

Fitting capture-recapture models in Jags may be slow - A few tricks to speed up computations/improve convergence

- If your parameters are not individual specific, or time-independent, then avoid unnecessary loops and memory usage.
- Get rid of the latent states via marginalization (Yackulic et al. 2020).

Fitting capture-recapture models in Jags may be slow - A few tricks to speed up computations/improve convergence

- If your parameters are not individual specific, or time-independent, then avoid unnecessary loops and memory usage.
- Get rid of the latent states via marginalization (Yackulic et al. 2020).
- Use a condensed formulation of the likelihood with sufficient statistics called m-arrays. See bonus slides and King & McCrea (2014).

Fitting capture-recapture models in Jags may be slow - A few tricks to speed up computations/improve convergence

- If your parameters are not individual specific, or time-independent, then avoid unnecessary loops and memory usage.
- Get rid of the latent states via marginalization (Yackulic et al. 2020).
- Use a condensed formulation of the likelihood with sufficient statistics called m-arrays. See bonus slides and King & McCrea (2014).
- MCMC algorithms picked by Jags might be unadapted. Switch to Nimble to take full control of MCMC machinery, e.g. Maud's talk on Friday.

Fitting capture-recapture models in Jags may be slow - A few tricks to speed up computations/improve convergence

- If your parameters are not individual specific, or time-independent, then avoid unnecessary loops and memory usage.
- Get rid of the latent states via marginalization (Yackulic et al. 2020).
- Use a condensed formulation of the likelihood with sufficient statistics called m-arrays. See bonus slides and King & McCrea (2014).
- MCMC algorithms picked by Jags might be unadapted. Switch to Nimble to take full control of MCMC machinery, e.g. Maud's talk on Friday.
- Use more informative priors; pick better initial values (good guess).

Exercise 4

Bonus

Multistate models are very flexible: some examples

1. Age-dependent survival

State-space likelihood

State process States at time t

		<i>States at time $t+1$</i>
		juvenile adult dead
	juvenile	$\begin{bmatrix} 0 & \phi_{juv} & 1 - \phi_{juv} \\ 0 & \phi_{ad} & 1 - \phi_{ad} \\ 0 & 0 & 1 \end{bmatrix}$
	adult	
	dead	

Observation process States at time t

		<i>Observations at time t</i>
		Recapt. as juv Recapt. as ad Not recapt.
	juvenile	$\begin{bmatrix} 0 & 0 & 1 \\ 0 & p & 1-p \\ 0 & 0 & 1 \end{bmatrix}$
	adult	
	dead	

Multinomial model for multistate capture-recapture data

- As for single state capture-recapture, we can summarize multistate capture-recapture data in **multistate m-array** format
- Data analysed using the multinomial likelihood

Multinomial model for multistate capture-recapture data

From the capture-histories to the m-array data format

Multistate capture histories

1 0 2 0

2 2 0 0

1 0 2 1

0 1 0 0

Release occasion	State of release	First reencounter occasion (state of reencounter)				Never recapt.
		2		3		
(1	2)	(1	2)	(1	2)	
1	1				1	
1	2					
2	1	-	-			
2	2	-	-			
3	1	-	-	-	-	
3	2	-	-	-	-	1

Multistate m-array

Multinomial model for multistate capture-recapture data

From the capture-histories to the m-array data format

Multistate capture histories

1 0 2 0

2 2 0 0

1 0 2 1

0 1 0 0

		First reencounter occasion (state of reencounter)				
Release occasion	State of release	2		3		4
		(1	2)	(1	2)	(1
1	1					1
1	2		1			
2	1	-	-			
2	2	-	-			1
3	1	-	-	-	-	
3	2	-	-	-	-	1

Multistate m-array

Multinomial model for multistate capture-recapture data

From the capture-histories to the m-array data format

Multistate capture histories

1	0	2	0
2	2	0	0
1	0	2	1
0	1	0	0

		First reencounter occasion (state of reencounter)				Never recapt.
Release occasion	State of release	2		3		
		(1	2)	(1	2)	(1
1	1					1+1
1	2			1		
2	1	-	-			
2	2	-	-			1
3	1	-	-	-	-	
3	2	-	-	-	-	1

Multistate m-array

Multinomial model for multistate capture-recapture data

From the capture-histories to the m-array data format

Multistate capture histories

1	0	2	0
2	2	0	0
1	0	2	1
0	2	0	0

		First reencounter occasion (state of reencounter)							
		2		3		4			
Release occasion	State of release	(1 2)		(1 2)		(1 2)		Never recapt.	
1	1							1+1	
1	2		1						
2	1	-	-						
2	2	-	-					1+1	
3	1	-	-	-	-				
3	2	-	-	-	-	-	1	1	

Multistate m-array

Multinomial model for multistate capture-recapture data

From the capture-histories to the m-array data format

Multistate capture histories

1	0	2	0
2	2	0	0
1	0	2	1
0	2	0	0

		First reencounter occasion (state of reencounter)						
Release occasion	State of release	2		3		4		Never recapt.
		(1	2)	(1	2)	(1	2)	
1	1	0	0	0	2	0	0	0
1	2	0	1	0	0	0	0	0
2	1	-	-	0	0	0	0	0
2	2	-	-	0	0	0	0	2
3	1	-	-	-	-	0	0	0
3	2	-	-	-	-	1	0	1

Multistate m-array

		First reencounter occasion (state of reencounter)							
Release occasion	State of release	2		3		4		Never recapt.	Released
		(1)	(2)	(1)	(2)	(1)	(2)		
1	1	0	0	0	2	0	0	0	2
1	2	0	1	0	0	0	0	0	1
2	1	-	-	0	0	0	0	0	0
2	2	-	-	0	0	0	0	2	2
3	1	-	-	-	-	0	0	0	0
3	2	-	-	-	-	1	0	1	2

		First reencounter occasion (state of reencounter)							
Release occasion	State of release	2		3		4		Never recapt.	
		(1)	(2)	(1)	(2)	(1)	(2)		
1	1	$\phi^1 \psi^{11} p^1$	$\phi^1 \psi^{12} p^2$	-	$1 - \Sigma$
1	2	$\phi^2 \psi^{21} p^1$	$\phi^2 \psi^{22} p^2$
2	1	-	-
2	2	-	-
3	1	-	-	-	-
3	2	-	-	-	-

$$\phi^1 \psi^{11} (1-p^1) \phi^1 \psi^{11} p^1 + \phi^1 \psi^{12} (1-p^2) \phi^2 \psi^{21} p^1$$

		First reencounter occasion (state of reencounter)							
Release occasion	State of release	2		3		4		Never recapt.	Released
		(1	2)	(1	2)	(1	2)		
1	1	0	0	0	2	0	0	0	2
1	2	0	1	0	0	0	0	0	1
2	1	-	-	0	0	0	0	0	0
2	2	-	-	0	0	0	0	2	2
3	1	-	-	-	-	0	0	0	0
3	2	-	-	-	-	1	0	1	2

		First reencounter occasion (state of reencounter)							
Release occasion	State of release	2		3		4		Never recapt.	Released
		(1	2)	(1	2)	(1	2)		
1	1	$\phi^1 \psi^{11} p^1$	$\phi^1 \psi^{12} p^2$	1- Σ	
1	2	$\phi^2 \psi^{21} p^1$	$\phi^2 \psi^{22} p^2$	
2	1	-	-	
2	2	-	-	
3	1	-	-	-	-	
3	2	-	-	-	-	

$$\begin{bmatrix} 0 & 0 & 0 & 2 & 0 & 0 & 0 \end{bmatrix}: \text{Multinomial}(P_{11}, 2)$$

How to write the probabilities of the multistate m-array?

		Reencounter occasion			Never reencountered
		2	3	4	
Release occasion	1	$\Psi_1 D(\mathbf{p}_1)$	$\Psi_1 D(\mathbf{q}_1) \Psi_2 D(\mathbf{p}_2)$	$\Psi_1 D(\mathbf{q}_1) \Psi_2 D(\mathbf{q}_2) \Psi_3 D(\mathbf{p}_3)$	$1 - \Sigma_1$
	2		$\Psi_2 D(\mathbf{p}_2)$	$\Psi_2 D(\mathbf{q}_2) \Psi_3 D(\mathbf{p}_3)$	$1 - \Sigma_2$
	3			$\Psi_3 D(\mathbf{p}_3)$	$1 - \Sigma_3$
	4				

$$\Psi_t = \begin{bmatrix} \phi_t^1 (1 - \Psi_t^{12}) & \phi_t^1 \Psi_t^{12} \\ \phi_t^2 \Psi_t^{21} & \phi_t^2 (1 - \Psi_t^{21}) \end{bmatrix}, D(\mathbf{p}_t) = \begin{bmatrix} p_t^1 & 0 \\ 0 & p_t^2 \end{bmatrix} \text{ and } D(\mathbf{q}_t) = \begin{bmatrix} 1 - p_t^1 & 0 \\ 0 & 1 - p_t^2 \end{bmatrix}$$

Comparison of approaches

- **State-space likelihood**
 - Very intuitive, very flexible modelling
 - State transition matrix must include the *death* state
 - Observation matrix must include the observation *not seen*
 - Rows of transition and observation matrices must sum to 1
 - Computationally demanding
- **Multinomial likelihood**
 - Reduced flexibility in modelling (no individual random effects)
 - The definition of transition matrix and of recapture vector very similar to the corresponding definitions in MARK or E-SURGE
 - Computational advantages (shorter run-time, faster convergence)