Bayesian integrated population modeling using JAGS

# Multistate capture-recapture models

# Multistate capture histories

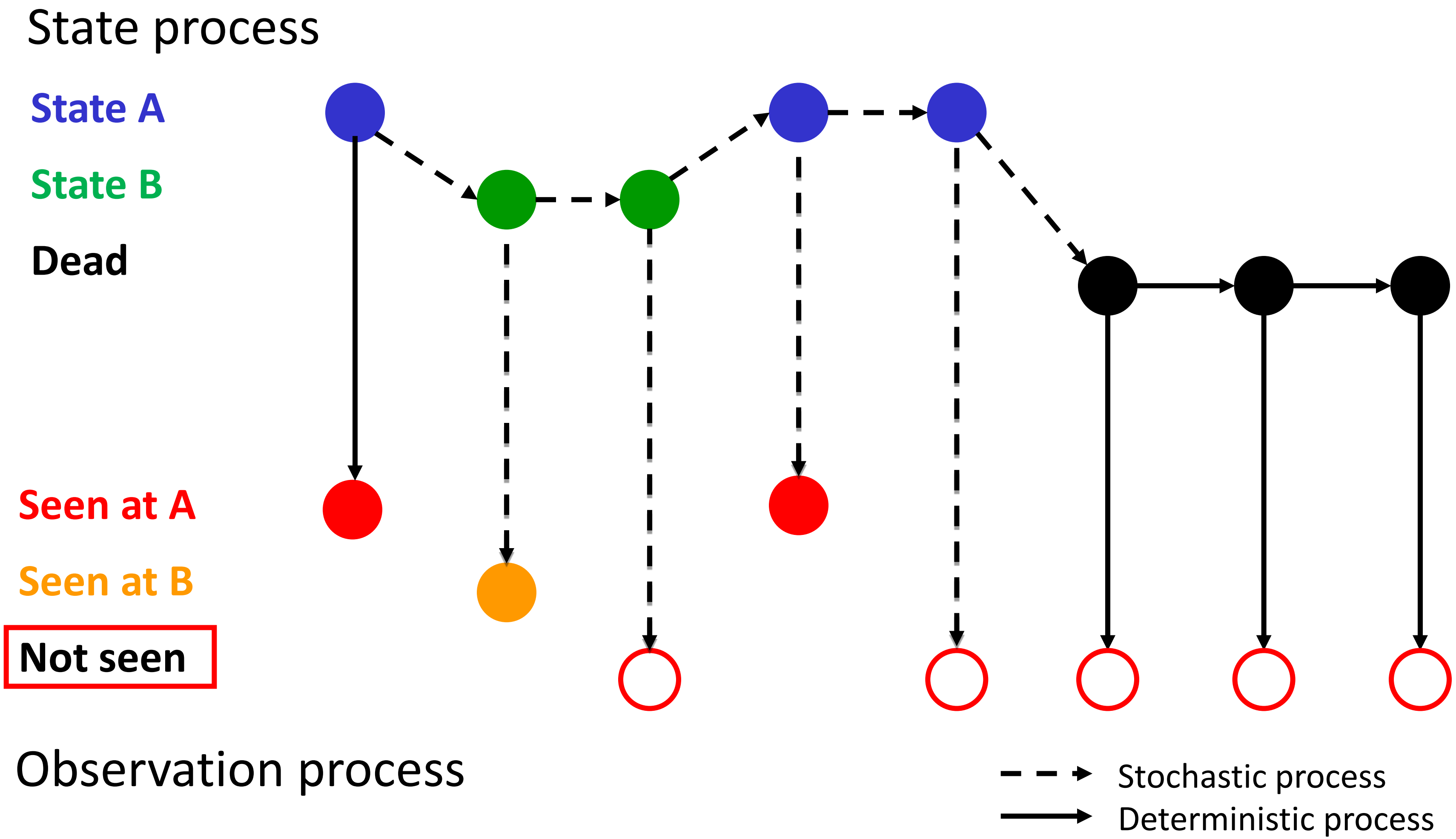
**State** = individual, categorical covariate that may change temporally

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 |

# Conditional nature of the 2 processes



State process

**State A**

**State B**

**Dead**

**Seen at A**

**Seen at B**

**Not seen**

Observation process

Stochastic process

Deterministic process

# State process

States at time t+1

States at time t

$$\begin{array}{cc} & \begin{array}{ccc} \text{state } A & \text{state } B & \text{dead} \end{array} \\ \begin{array}{c} \text{state } A \\ \text{state } B \\ \text{dead} \end{array} & \begin{bmatrix} \Phi_{AA} & \Phi_{AB} & 1-\Phi_{AA}-\Phi_{AB} \\ \Phi_{BA} & \Phi_{BB} & 1-\Phi_{BA}-\Phi_{BB} \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

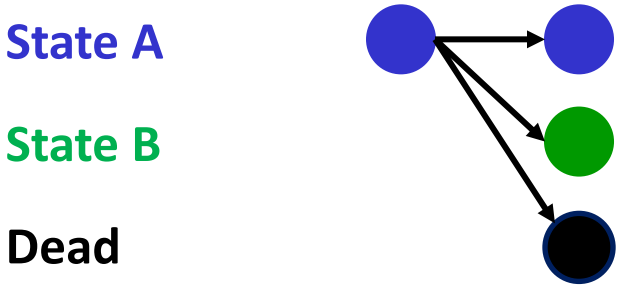
# Observation process

Observations at time t

States at time t

$$\begin{array}{cc} & \begin{array}{ccc} \text{Seen at A} & \text{Seen at B} & \text{Not seen} \end{array} \\ \begin{array}{c} \text{state } A \\ \text{state } B \\ \text{dead} \end{array} & \begin{bmatrix} p_A & 0 & 1-p_A \\ 0 & p_B & 1-p_B \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

# State process



**State A**

**State B**

**Dead**

*States at time t+1*

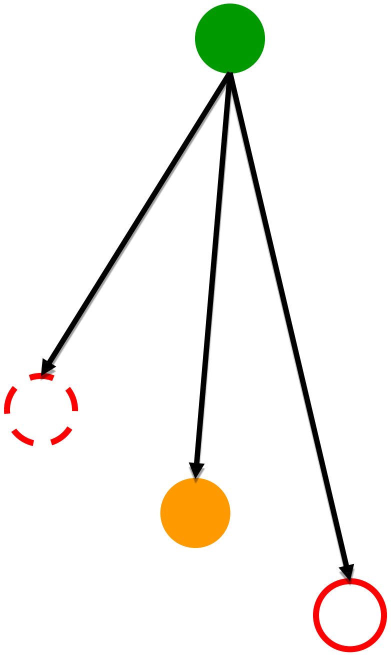
*States at time t*

$$\Omega = \begin{array}{c|ccc} & \textit{state A} & \textit{state B} & \textit{dead} \\ \hline \textit{state A} & \Phi_{AA} & \Phi_{AB} & 1-\Phi_{AA}-\Phi_{AB} \\ \textit{state B} & \Phi_{BA} & \Phi_{BB} & 1-\Phi_{BA}-\Phi_{BB} \\ \textit{dead} & 0 & 0 & 1 \end{array}$$

## *BUGS language:*

$$z_{i,t+1} \middle| z_{i,t} \sim dcat\left(\Omega_{z_{i,t},}\right)$$

# Observation process



**State A**

**State B**

**Dead**

**Seen at A**

**Seen at B**

**Not seen**

*Observations at time t*

*States at time t*

$$\Theta = \begin{array}{c|ccc} & \text{Seen at A} & \text{Seen at B} & \text{Not seen} \\ \hline \text{state A} & p_A & 0 & 1-p_A \\ \text{state B} & 0 & p_B & 1-p_B \\ \text{dead} & 0 & 0 & 1 \end{array}$$

*BUGS language:*

$$y_{i,t} \mid z_{i,t} \sim dcat\left(\Theta_{z_{i,t},}\right)$$

# *Usual re-parameterisation*

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

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

- $\phi_x$: 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

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

# 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
```

# 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 of which model is fitted

# 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

```
# 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)
   }
```

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

Define linear models for parameters and specify the needed priors

# 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

*Multistate m-array*

| | | 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 | 2 | | | | | | | |
| 2 | 1 | - | - | | | | | |
| 2 | 2 | - | - | | | | | |
| 3 | 1 | - | - | - | - | | | |
| 3 | 2 | - | - | - | - | | | **1** |

# 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

*Multistate m-array*

| | | 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 | 2 | | **1** | | | | | |
| 2 | 1 | - | - | | | | | |
| 2 | 2 | - | - | | | | | **1** |
| 3 | 1 | - | - | - | - | | | |
| 3 | 2 | - | - | - | - | | | **1** |

# 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

*Multistate m-array*

| | | 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 |
| 3 | 1 | - | - | - | - | | | |
| 3 | 2 | - | - | - | - | 1 | | 1 |

# 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

*Multistate m-array*

| | | 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** |

# 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 | 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) |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  | 2 |  | 3 |  | 4 |  |  |  |
| Release occasion | State of release | (1 | 2) | (1 | 2) | (1 | 2) | Never recapt. | Released |
| 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) |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
|  |  | 2 |  | 3 |  | 4 |  |  |
| Release occasion | State of release | (1 | 2) | (1 | 2) | (1 | 2) | Never recapt. |
| 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 | - | - | - | - | ... | ... | ... |

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

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

$$\begin{bmatrix} 0 & 0 & 0 & 2 & 0 & 0 & 0 \end{bmatrix} \sim Multinomial\left(\boldsymbol{P}_{11}, 2\right)$$

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

| | Reencounter occasion | | | Never reencountered |
|---|---|---|---|---|
| Release occasion | 2 | 3 | 4 | |
| 1 | $\boldsymbol{\Psi}_1 D(\boldsymbol{p}_1)$ | $\boldsymbol{\Psi}_1 D(\boldsymbol{q}_1)\boldsymbol{\Psi}_2 D(\boldsymbol{p}_2)$ | $\boldsymbol{\Psi}_1 D(\boldsymbol{q}_1)\boldsymbol{\Psi}_2 D(\boldsymbol{q}_2)\boldsymbol{\Psi}_3 D(\boldsymbol{p}_3)$ | $1-\Sigma_1$ |
| 2 | | $\boldsymbol{\Psi}_2 D(\boldsymbol{p}_2)$ | $\boldsymbol{\Psi}_2 D(\boldsymbol{q}_2)\boldsymbol{\Psi}_3 D(\boldsymbol{p}_3)$ | $1-\Sigma_2$ |
| 3 | | | $\boldsymbol{\Psi}_3 D(\boldsymbol{p}_3)$ | $1-\Sigma_3$ |

$$\boldsymbol{\Psi}_t = \begin{bmatrix} \phi_t^1\left(1-\psi_t^{12}\right) & \phi_t^1\psi_t^{12} \\ \phi_t^2\psi_t^{21} & \phi_t^2\left(1-\psi_t^{21}\right) \end{bmatrix}, \; D(\boldsymbol{p}_t) = \begin{bmatrix} p_t^1 & 0 \\ 0 & p_t^2 \end{bmatrix} \text{ and } D(\boldsymbol{q}_t) = \begin{bmatrix} 1-p_t^1 & 0 \\ 0 & 1-p_t^2 \end{bmatrix}$$

# 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)

# Multistate models are very flexible: some examples

## 1. Age-dependent survival

State-space likelihood

*States at time t+1*

State process

*States at time t*

$$\begin{array}{cc} & \begin{array}{ccc} \textit{juvenile} & \textit{adult} & \textit{dead} \end{array} \\ \begin{array}{c} \textit{juvenile} \\ \textit{adult} \\ \textit{dead} \end{array} & \begin{bmatrix} 0 & \phi_{juv} & 1-\phi_{juv} \\ 0 & \phi_{ad} & 1-\phi_{ad} \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

*Observations at time t*

Observation process

*States at time t*

$$\begin{array}{cc} & \begin{array}{ccc} \textit{Recap. as juv} & \textit{Recapt. as ad} & \textit{Not recapt.} \end{array} \\ \begin{array}{c} \textit{juvenile} \\ \textit{adult} \\ \textit{dead} \end{array} & \begin{bmatrix} 0 & 0 & 1 \\ 0 & p & 1-p \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

# Multistate models are very flexible: some examples

## 2. Breeder vs. non-breeders

State-space likelihood

*States at time t+1*

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

*Observations at time t*

$$\begin{array}{llccc}
 & & \text{seen, br.} & \text{seen, non-br.} & \text{not seen} \\
 & \text{breeding} & p_B & 0 & 1-p_B \\
\text{States at time } t & \text{non-breeding} & 0 & p_N & 1-p_N \\
 & \text{dead} & 0 & 0 & 1
\end{array}$$

# Multistate models are very flexible: some examples

## 3. Movement among 3 sites

,

State process

*States at time t+1*

*States at time t*

$$\begin{array}{c|cccc} & \text{site A} & \text{site B} & \text{site C} & \text{dead} \\ \hline \text{site A} & \phi_A(1-\psi_{AB}-\psi_{AC}) & \phi_A\psi_{AB} & \phi_A\psi_{AC} & 1-\phi_A \\ \text{site B} & \phi_B\psi_{BA} & \phi_B(1-\psi_{BA}-\psi_{BC}) & \phi_B\psi_{BC} & 1-\phi_B \\ \text{site C} & \phi_C\psi_{CA} & \phi_C\psi_{CB} & \phi_C(1-\psi_{CA}-\psi_{CB}) & 1-\phi_C \\ \text{dead} & 0 & 0 & 0 & 1 \end{array}$$

Observation process

*Observations at time t*

*States at time t*

$$\begin{array}{c|cccc} & \text{seen at A} & \text{seen at B} & \text{seen at C} & \text{not seen} \\ \hline \text{site A} & p_A & 0 & 0 & 1-p_A \\ \text{site B} & 0 & p_B & 0 & 1-p_B \\ \text{site C} & 0 & 0 & p_C & 1-p_C \\ \text{dead} & 0 & 0 & 0 & 1 \end{array}$$

# Multistate models are very flexible: some examples

## 3. Movement among 3 sites

,

*States at time t+1*

State process

*States at time t*

$$\begin{array}{cc}
 & \begin{array}{cccc} \text{site A} & \text{site B} & \text{site C} & \text{dead} \end{array} \\
\begin{array}{c} \text{site A} \\ \text{site B} \\ \text{site C} \\ \text{dead} \end{array} &
\begin{bmatrix}
\phi_A(1-\psi_{AB}-\psi_{AC}) & \phi_A\psi_{AB} & \phi_A\psi_{AC} & 1-\phi_A \\
\phi_B\psi_{BA} & \phi_B(1-\psi_{BA}-\psi_{BC}) & \phi_B\psi_{BC} & 1-\phi_B \\
\phi_C\psi_{CA} & \phi_C\psi_{CB} & \phi_C(1-\psi_{CA}-\psi_{CB}) & 1-\phi_C \\
0 & 0 & 0 & 1
\end{bmatrix}
\end{array}$$

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

- Multinomial logit link function
- Dirichlet prior

# Multistate models are very flexible: some examples

## 4. Access to reproduction

State process

*States at time t+1*

*States at time t*

$$\begin{array}{l|ccccc}
 & \textit{juvenile} & \textit{1y NB} & \textit{2y NB} & \textit{breeder} & \textit{dead} \\
\hline
\textit{juvenile} & 0 & \phi_1(1-\alpha_1) & 0 & \phi_1\alpha_1 & 1-\phi_1 \\
\textit{1y NB} & 0 & 0 & \phi_2(1-\alpha_2) & \phi_2\alpha_2 & 1-\phi_2 \\
\textit{2y NB} & 0 & 0 & 0 & \phi_3 & 1-\phi_3 \\
\textit{breeder} & 0 & 0 & 0 & \phi_B & 1-\phi_B \\
\textit{dead} & 0 & 0 & 0 & 0 & 1
\end{array}$$

Observation process

*Observations at time t*

*States at time t*

$$\begin{array}{l|cccc}
 & \textit{seen, 1y NB} & \textit{seen, 2y NB} & \textit{seen, breeder} & \textit{not seen} \\
\hline
\textit{juvenile} & 0 & 0 & 0 & 1 \\
\textit{1y NB} & p_1 & 0 & 0 & 1-p_1 \\
\textit{2y NB} & 0 & p_2 & 0 & 1-p_2 \\
\textit{breeder} & 0 & 0 & p_3 & 1-p_3 \\
\textit{dead} & 0 & 0 & 0 & 1
\end{array}$$

# Multistate models are very flexible: some examples

## 5. Temporary emigration

State process

$$\begin{array}{lcc}
 & & \textit{States at time } t+1 \\
 & & \begin{array}{ccc} \textit{inside} & \textit{outside} & \textit{dead} \end{array} \\
\textit{States at time } t & \begin{array}{l} \textit{inside} \\ \textit{outside} \\ \textit{dead} \end{array} & \begin{bmatrix} \phi(1-\psi_{IO}) & \phi\psi_{IO} & 1-\phi \\ \phi\psi_{OI} & \phi(1-\psi_{OI}) & 1-\phi \\ 0 & 0 & 1 \end{bmatrix}
\end{array}$$

Observation process

$$\begin{array}{lcc}
 & & \textit{Observations at time } t \\
 & & \begin{array}{cc} \textit{Seen} & \textit{Not seen} \end{array} \\
\textit{States at time } t & \begin{array}{l} \textit{inside} \\ \textit{outside} \\ \textit{dead} \end{array} & \begin{bmatrix} p & 1-p \\ 0 & 1 \\ 0 & 1 \end{bmatrix}
\end{array}$$

# Multistate models are very flexible: some examples

## 6. Immediate trap response

State process

*States at time t+1*

*States at time t*

$$\begin{array}{l|ccc} & \text{a, seen} & \text{a, not s} & \text{dead} \\ \hline \text{alive, seen} & \phi p_S & \phi(1-p_s) & 1-\phi \\ \text{alive, not seen} & \phi p_N & \phi(1-p_N) & 1-\phi \\ \text{dead} & 0 & 0 & 1 \end{array}$$

Observation process

*Observations at time t*

*States at time t*

$$\begin{array}{l|cc} & \text{Seen} & \text{Not seen} \\ \hline \text{alive, seen} & 1 & 0 \\ \text{alive, not seen} & 0 & 1 \\ \text{dead} & 0 & 1 \end{array}$$

# Multistate models are very flexible: some examples

## 7. Combination of life and dead encounters

State process

*States at time t+1*

*States at time t*

$$\begin{array}{lccc} & \textit{alive} & \textit{rec. dead} & \textit{dead} \\ \textit{alive} & s & 1-s & 0 \\ \textit{recently dead} & 0 & 0 & 1 \\ \textit{dead} & 0 & 0 & 1 \end{array}$$

Observation process

*Observations at time t*

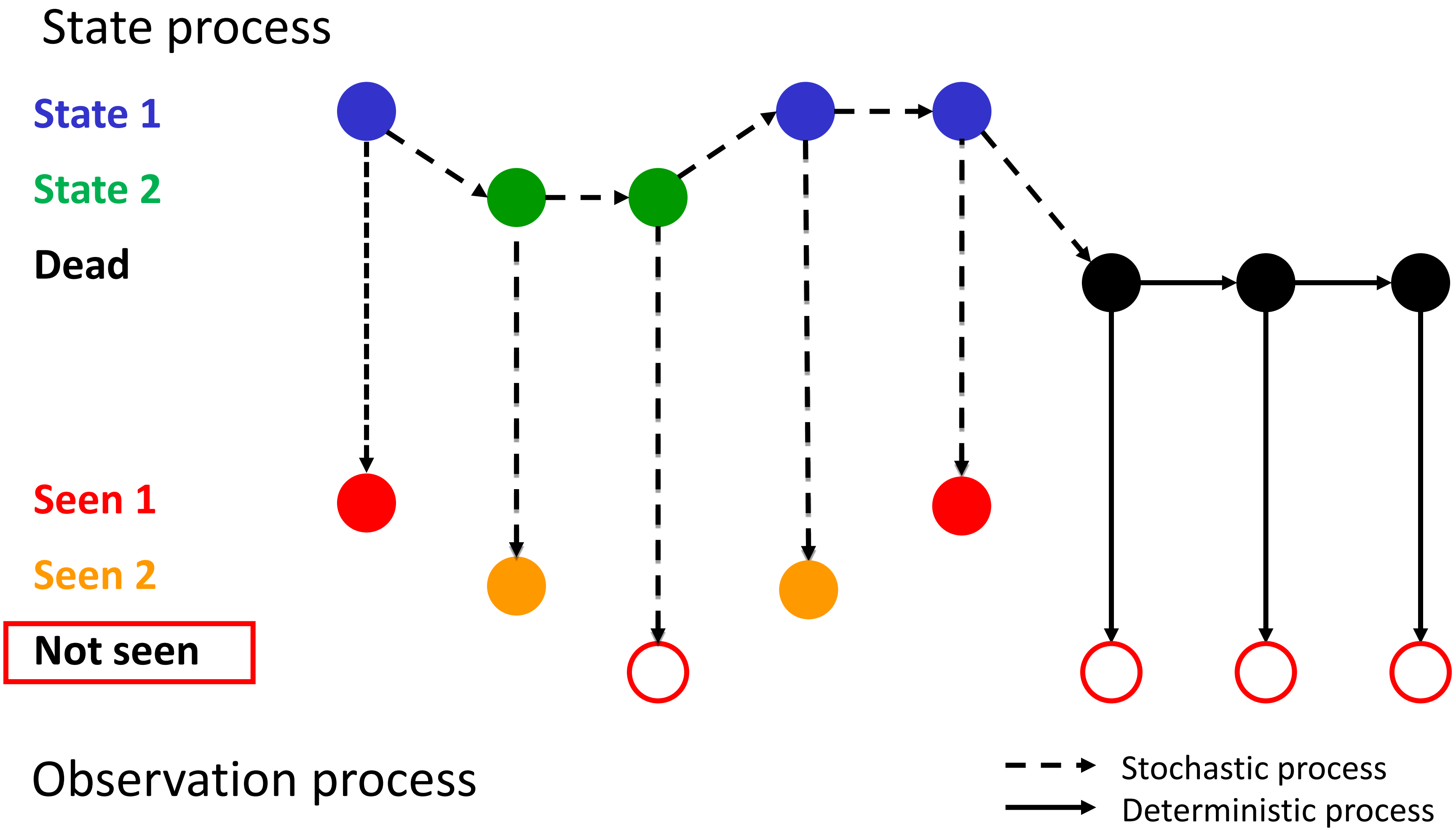
*States at time t*

$$\begin{array}{lccc} & \textit{seen} & \textit{recovered} & \textit{not seen} \\ \textit{alive} & p & 0 & 1-p \\ \textit{rec. dead} & 0 & r & 1-r \\ \textit{dead} & 0 & 0 & 1 \end{array}$$

# Multievent models

- Is a multistate model that allows for state assignment errors (state uncertainty)
- All capture-recapture models introduced so far can be seen as a special case of a multievent model
- Most general capture-recapture model
- Seminal paper: Pradel (2005), Biometrics
- We need a model of state assignment at the first encounter
- Additional parameters (state assignment probabilities)
- Ecological examples:
    - Sex assignment uncertainty (Pradel *et al.* 2008, Can. J. Stat.)
    - Disease status uncertainty (Cooch & Conn 2009, J. Appl. Ecol.)
    - Memory models (Rouan *et al.* 2009, JABES)
    - Heterogeneity / finite mixtures (Péron *et al.* 2010, Oikos)

# 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

# At first encounter

## *Initial state probability*

*States at first encounter*

$$\begin{array}{ccc} \textit{state 1} & \textit{state 2} & \textit{dead} \\ \left[1-\pi\right. & \pi & \left.0\right] \end{array}$$

## *State assignment*

*Observations at first encounter*

*States at first encounter*

$$\begin{array}{c|ccc|} & \textit{seen at 1} & \textit{seen at 2} & \textit{not seen} \\ \textit{state 1} & \beta_1 & 1-\beta_1 & 0 \\ \textit{state 2} & 1-\beta_2 & \beta_2 & 0 \\ \textit{dead} & 0 & 0 & 1 \end{array}$$

# After first encounter

## State process

States at time t+1

States at time t

$$\begin{array}{cc} & \begin{array}{ccc} \text{state 1} & \text{state 2} & \text{dead} \end{array} \\ \begin{array}{l} \text{state 1} \\ \text{state 2} \\ \text{dead} \end{array} & \begin{bmatrix} \Phi_{11} & \Phi_{12} & 1-\Phi_{11}-\Phi_{12} \\ \Phi_{21} & \Phi_{22} & 1-\Phi_{21}-\Phi_{22} \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

## Observation process

Observations at time t

States at time t

$$\begin{array}{cc} & \begin{array}{ccc} \text{seen at 1} & \text{seen at 2} & \text{not seen} \end{array} \\ \begin{array}{l} \text{state 1} \\ \text{state 2} \\ \text{dead} \end{array} & \begin{bmatrix} \beta_1 p_1 & \left(1-\beta_1\right) p_1 & 1-p_1 \\ \left(1-\beta_2\right) p_2 & \beta_2 p_2 & 1-p_2 \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

## An example: uncertain disease status

- If an individual is seen that does not have the disease, we will never diagnose that the individual is infected.
- Yet, we may fail to diagnose the disease in infected individuals.
- Interest: disease dependent survival
- Disease state dynamics

States:

- Alive, without disease (Alive -)
- Alive, with disease (Alive +)
- Dead

Observations:

- Seen, no disease recorded (Seen -)
- Seen, disease recorded (Seen +)
- Not seen

# At first encounter

*Initial state probability*

$$\begin{array}{lccc} & \text{Alive -} & \text{Alive +} & \text{Dead} \\ \text{Disease state:} & \left[1-\pi\right. & \pi & \left.0\right] \end{array}$$

$\pi$: Probability of being infected at first encounter

*BUGS language:*

$$\Pi = \left[1-\pi \quad \pi \quad 0\right]$$

$$z_{i,f[i]} \sim dcat\left(\Pi\right)$$

# At first encounter

*State assignment*

*Observations at first encounter*

*States at first encounter*

$$\begin{array}{l|ccc|} & \text{Seen -} & \text{Seen +} & \text{Not seen} \\ \text{Alive -} & 1 & 0 & 0 \\ \text{Alive +} & \beta & 1-\beta & 0 \\ \text{Dead} & 0 & 0 & 1 \end{array}$$

$\beta$: Probability of not diagnosing the disease

*BUGS language:*

$$\mathrm{O} = \begin{bmatrix} 1 & 0 & 0 \\ \beta & 1-\beta & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

$$y_{i,f[i]} \big| z_{i,f[i]} \sim dcat\left(\mathrm{O}_{z_{i,f[i]},}\right)$$

# After first encounter

## *State process*

*States at time t+1*

*States at time t*

$$\begin{array}{c|ccc} & \text{Alive -} & \text{Alive +} & \text{Dead} \\ \hline \text{Alive -} & \phi_H(1-\psi_{HD}) & \phi_H\psi_{HD} & 1-\phi_H \\ \text{Alive +} & \phi_D\psi_{DH} & \phi_D(1-\psi_{DH}) & 1-\phi_D \\ \text{Dead} & 0 & 0 & 1 \end{array}$$

$\phi_H$: survival probability of healthy individuals

$\phi_D$: survival probability of individuals infected with the disease

$\psi_{HD}$: infection probability

$\psi_{DH}$: recovery probability (probability to become healthy)

*BUGS language:*

$$\Omega = \begin{bmatrix} \phi_H(1-\psi_{HD}) & \phi_H\psi_{HD} & 1-\phi_H \\ \phi_D\psi_{DH} & \phi_D(1-\psi_{DH}) & 1-\phi_D \\ 0 & 0 & 1 \end{bmatrix}$$

$$z_{i,t+1} \,|\, z_{i,t} \sim dcat\left(\Omega_{z_{i,t},}\right)$$

# After first encounter

## *Observation process*

*Observations at time t*

*States at time t*

$$\begin{array}{l|ccc|} & \text{Seen -} & \text{Seen +} & \text{Not seen} \\ \text{Alive -} & p_H & 0 & 1-p_H \\ \text{Alive +} & \beta p_D & (1-\beta)p_D & 1-p_D \\ \text{Dead} & 0 & 0 & 1 \end{array}$$

$p_H$: probability to encounter a healthy individual
$p_D$: probability to encounter an individual infected with the disease
$\beta$: Probability of not diagnosing the disease

*BUGS language:*

$$\Theta = \begin{bmatrix} p_H & 0 & 1-p_H \\ \beta p_D & (1-\beta)p_D & 1-p_D \\ 0 & 0 & 1 \end{bmatrix}$$

$$y_{i,t} \mid z_{i,t} \sim dcat\left(\Theta_{z_{i,t},}\right)$$