



Bayesian population analysis using WinBUGS

Chapter 5: State-space models

Introduction



- So far:
 - Took raw counts as true population size
 - But: not accounting for observation error reduces power to detect effects / spurious detection of density-dependence
- State-space model:
 - A model that runs two time series in parallel, one captures the dynamics of the true (latent) state, the other the observations
 - Is a hierarchical model
- Composed of 2 sets of equations:
 - *State equation*: describes the true state of a system
 - *Observation equation*: relates the true state to the observation
- Very general framework
 - Time-series of counts
 - Capture-recapture data (broad sense)
 - Occupancy data



Time-series of counts

State process

True population size

$$N_{t+1} | N_t = \lambda_t N_t$$

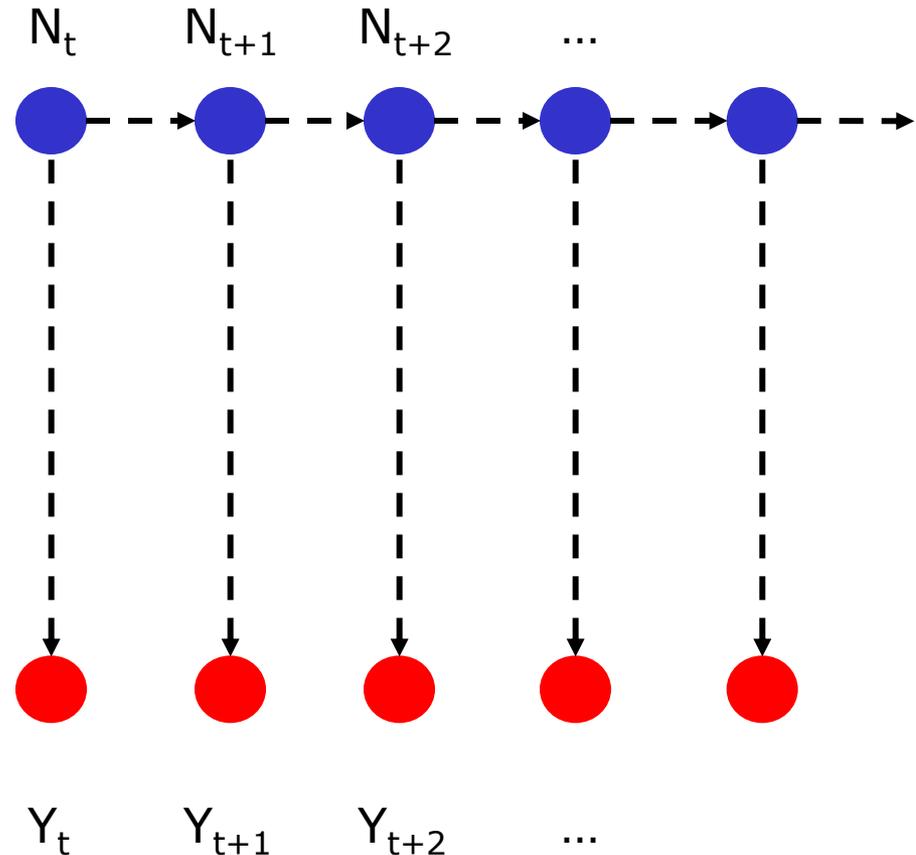
$$\lambda_t \sim N(\bar{\lambda}, \sigma_\lambda^2)$$

Observation process

Observed count

$$Y_t | N_t = N_t + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma_y^2)$$





Bayesian population analysis using WinBUGS

Chapter 7: Estimation of survival probabilities using capture- recapture data



Introduction

- The principle to estimate survival is fairly easy:
 - Follow individuals across time
 - Count individuals at time t (C_t) and assess how many of them are still alive after time Δt ($L_{t+\Delta t}$)
 - Survival probability is then

$$S_{\Delta t} = \frac{L_{t+\Delta t}}{C_t}$$

- However, there is a major problem: all individuals that are still alive, but not seen, are classified as dead
- Typically, we do not know $L_{t+\Delta t}$, but only $p * L_{t+\Delta t}$, where p is the detection probability
- Detection can be estimated, if we extend the experiment to at least one further occasion

Individual capture history: result of 2 processes

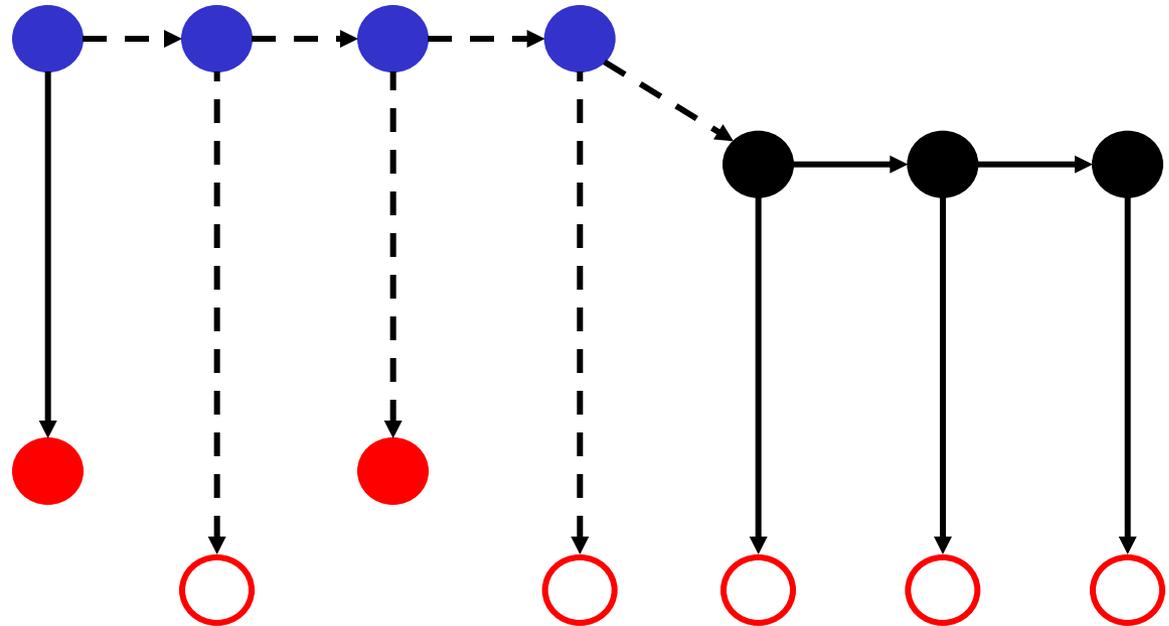
State process

Alive

Dead

Seen

Not seen



Observation process

--> Stochastic process

—> Deterministic process

State-space likelihood to analyse CR data

1. Survival process

$$z_{i,first} = 1$$

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli}(z_{i,t-1} \phi_{i,t-1})$$

where,

$z_{i,t}$: matrix, indicating whether individual i is alive at time t ($z = 1$), or dead ($z = 0$)

$\phi_{i,t}$: apparent survival probability for individual i from time t to $t+1$

2. Observation process

$$y_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_{i,t})$$

where,

$y_{i,t}$: is the observed capture history for individual i at time t

$p_{i,t}$: recapture probability for individual i at time t

Data

Parameters

$$y_{i,t} = \begin{matrix} 0 & 1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Data

$$y_{i,t} = \begin{matrix} 0 & 1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Parameters

$$\phi_{i,t} = \begin{matrix} NA & \phi_{1,2} & \phi_{1,3} & \phi_{1,4} \\ \phi_{2,1} & \phi_{2,2} & \phi_{2,3} & \phi_{2,4} \\ NA & NA & \phi_{3,3} & \phi_{3,4} \\ NA & \phi_{4,2} & \phi_{4,3} & \phi_{4,4} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Data

$$y_{i,t} = \begin{matrix} 0 & 1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Parameters

$$\phi_{i,t} = \begin{matrix} NA & \phi_{1,2} & \phi_{1,3} & \phi_{1,4} \\ \phi_{2,1} & \phi_{2,2} & \phi_{2,3} & \phi_{2,4} \\ NA & NA & \phi_{3,3} & \phi_{3,4} \\ NA & \phi_{4,2} & \phi_{4,3} & \phi_{4,4} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Data

$$y_{i,t} = \begin{matrix} 0 & \mathbf{1} & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Parameters

$$\phi_{i,t} = \begin{matrix} NA & \phi_{1,2} & \phi_{1,3} & \phi_{1,4} \\ \phi_{2,1} & \phi_{2,2} & \phi_{2,3} & \phi_{2,4} \\ NA & NA & \phi_{3,3} & \phi_{3,4} \\ NA & \phi_{4,2} & \phi_{4,3} & \phi_{4,4} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$
$$p_{i,t} = \begin{matrix} NA & p_{1,2} & p_{1,3} & p_{1,4} \\ p_{2,1} & p_{2,2} & p_{2,3} & p_{2,4} \\ NA & NA & p_{3,3} & p_{3,4} \\ NA & p_{4,2} & p_{4,3} & p_{4,4} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Data

$$y_{i,t} = \begin{matrix} 0 & 1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Parameters

$$\phi_{i,t} = \begin{matrix} NA & \phi_{1,2} & \phi_{1,3} & \phi_{1,4} \\ \phi_{2,1} & \phi_{2,2} & \phi_{2,3} & \phi_{2,4} \\ NA & NA & \phi_{3,3} & \phi_{3,4} \\ NA & \phi_{4,2} & \phi_{4,3} & \phi_{4,4} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

$$p_{i,t} = \begin{matrix} NA & p_{1,2} & p_{1,3} & p_{1,4} \\ p_{2,1} & p_{2,2} & p_{2,3} & p_{2,4} \\ NA & NA & p_{3,3} & p_{3,4} \\ NA & p_{4,2} & p_{4,3} & p_{4,4} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

Modelling

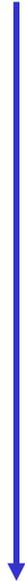
along time axis



$\phi_{i,t} =$

NA	$\phi_{1,2}$	$\phi_{1,3}$	$\phi_{1,4}$
$\phi_{2,1}$	$\phi_{2,2}$	$\phi_{2,3}$	$\phi_{2,4}$
NA	NA	$\phi_{3,3}$	$\phi_{3,4}$
NA	$\phi_{4,2}$	$\phi_{4,3}$	$\phi_{4,4}$
.	.	.	.
.	.	.	.

along individual axis



time axis:

- temporal variation (fixed, random)
- temporal covariates
- time-constant

individual axis:

- groups (fixed, random)
- individual covariates

interaction of time and individual axis:

- age effect (transients)
- additive effects (group + time)
- cohort effects
- trap-response



- Mortality and permanent emigration are confounded. Therefore we estimate «apparent», but not true survival.

Assumptions

- Design:
 - No mark lost
 - Identity of individuals recorded without error
 - Captured individuals are a random sample
- Model:
 - Homeogeneity of survival and recapture probabilities
 - Independence

Multinomial likelihood to analyse CR data

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

Capture histories

```
1 0 1 0
1 1 0 0
1 0 1 1
0 1 0 0
```

m-array

Release occ.	Recapture occ.			Never recaptured
	2	3	4	
1				
2	-			
3	-	-		

Multinomial likelihood to analyse CR data

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

Capture histories

1 0 1 0

1 1 0 0

1 0 1 1

0 1 0 0

m-array

Release occ.	Recapture occ.			Never recaptured
	2	3	4	
1		1		
2	-			
3	-	-		1

Multinomial likelihood to analyse CR data

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

Capture histories

1 0 1 0

1 1 0 0

1 0 1 1

0 1 0 0

m-array

Release occ.	Recapture occ.			Never recaptured
	2	3	4	
1	1	1		
2	-			1
3	-	-		1

Multinomial likelihood to analyse CR data

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

Capture histories

```
1 0 1 0
1 1 0 0
1 0 1 1
0 1 0 0
```

m-array

Release occ.	Recapture occ.			Never recaptured
	2	3	4	
1	1	1+1		
2	-			1
3	-	-	1	1

Multinomial likelihood to analyse CR data

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

Capture histories

1 0 1 0
1 1 0 0
1 0 1 1
0 1 0 0

m-array

Release occ.	Recapture occ.			Never recaptured
	2	3	4	
1	1	1+1		
2	-			1+1
3	-	-	1	1

Multinomial likelihood to analyse CR data

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

Capture histories

```
1 0 1 0
1 1 0 0
1 0 1 1
0 1 0 0
```

m-array

Release occ.	Recapture occ.			Never recaptured
1	2	3	4	0
2	-	0	0	2
3	-	-	1	1

Multinomial likelihood to analyse CR data

Cell probabilities of the m-array:

Rel.	Recapture occ.			Never
	2	3	4	
1	$\phi_1 p_1$	$\phi_1 (1-p_1) \phi_2 p_2$	$\phi_1 (1-p_1) \phi_2 (1-p_2) \phi_3 p_3$	$1-\Sigma_1$
2	-	$\phi_2 p_2$	$\phi_2 (1-p_2) \phi_3 p_3$	$1-\Sigma_2$
3	-	-	$\phi_3 p_3$	$1-\Sigma_3$

Likelihood of the m-array:

$$P(m\text{-array}_{t,}) \sim \text{Multinomial}(pr_{t,}, \text{released}_t)$$

where

$pr_{t,}$ are the cell probabilities of the m-array for release occasion t
 released_t are the number of released individuals at occasion t

Posterior predictive model checking

- we should check the fit of the model: goodness-of-fit test
- are the model assumptions fulfilled?
- posterior predictive model checking is a possibility to assess the model

How does it work? Key idea

- compare the data (Y) with expected values (E) derived from the model using an appropriate discrepancy measure
- in order to assess whether the size of the discrepancy measure is unusual, we simulate replicate data (Y_{rep}) under the model and compute the same discrepancy measure using E
- this second comparison shows us how far apart Y and E can be if the assumptions are met
- as possible discrepancy measure is e.g. $d = (Y^2 - E^2)^{0.5}$
- if the data are consistent with the model then d and d_{rep} are the same (on average)
- the proportion of $[d > d_{\text{rep}}]$ gives us a Bayesian P -value



Bayesian population analysis using WinBUGS

Chapter 8: Estimation of survival probabilities using mark- recovery data

Conditional nature of the 2 processes

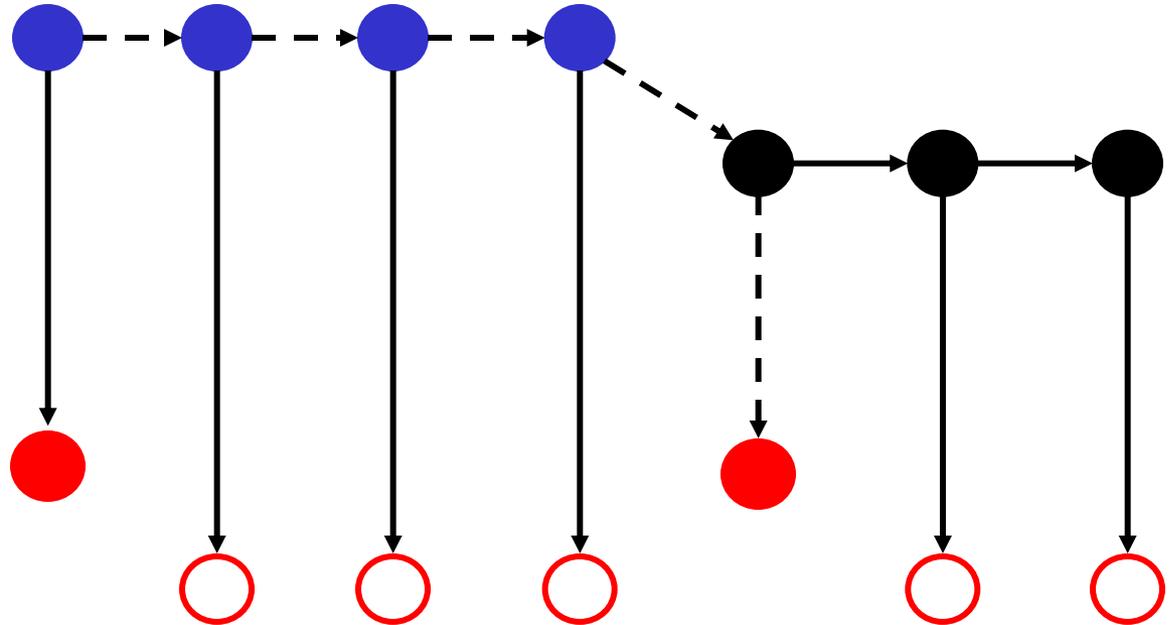
State process

Alive

Dead

Recovered

Not recovered



Observation process

- - -> Stochastic process

—> Deterministic process

State-space likelihood to analyse MR data

1. Survival process

$$z_{i,first} = 1$$

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli}(z_{i,t-1} s_{i,t-1})$$

where,

$z_{i,t}$: matrix, indicating whether individual i is alive at time t ($z = 1$), or dead ($z = 0$)

$s_{i,t}$: survival probability for individual i from time t to $t+1$

2. Observation process

$$y_{i,t} | z_{i,t-1} - z_{i,t} = 1 \sim \text{Bernoulli}([z_{i,t-1} - z_{i,t}] r_{i,t})$$

where,

$y_{i,t}$: is the observed capture history for individual i at time t

$r_{i,t}$: recovery probability for individual i at time t

Multinomial likelihood to analyse MR data

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

Recovery histories

```
1 0 1 0
1 1 0 0
1 0 0 0
0 1 0 0
```

m-array

Release occ.	Recovery occ.			Never recovered
	2	3	4	
1				
2	-			
3	-	-		

Multinomial likelihood to analyse MR data

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

Recovery histories

1 0 1 0

1 1 0 0

1 0 0 0

0 1 0 0

m-array

Release occ.	Recovery occ.			Never recovered
	2	3	4	
1		1		
2	-			
3	-	-		

Multinomial likelihood to analyse MR data

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

Recovery histories

1 0 1 0

1 1 0 0

1 0 0 0

0 1 0 0

m-array

Release occ.	Recovery occ.			Never recovered
	2	3	4	
1	1	1		
2	-			
3	-	-		

Multinomial likelihood to analyse MR data

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

Recovery histories

1 0 1 0

1 1 0 0

1 0 0 0

0 1 0 0

m-array

Release occ.	Recovery occ.			Never recovered
	2	3	4	
1	1	1		1
2	-			
3	-	-		

Multinomial likelihood to analyse MR data

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

Recovery histories

1 0 1 0
1 1 0 0
1 0 0 0
0 1 0 0

m-array

Release occ.	Recovery occ.			Never recovered
	2	3	4	
1	1	1		1
2	-			1
3	-	-		

Multinomial likelihood to analyse MR data

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

Recovery histories

```
1 0 1 0
1 1 0 0
1 0 0 0
0 1 0 0
```

m-array

Release occ.	Recovery occ.			Never recovered
	2	3	4	
1	1	1	0	1
2	-	0	0	1
3	-	-	0	0

Multinomial likelihood to analyse MR data

Cell probabilities of the m-array:

Rel.	Recovery occ.			Never
	2	3	4	
1	$(1-S_1) r_1$	$S_1 (1-S_2) r_2$	$S_1 S_2 (1-S_3) r_3$	$1-\Sigma_1$
2	-	$(1-S_2) r_2$	$S_2 (1-S_3) r_3$	$1-\Sigma_2$
3	-	-	$(1-S_3) r_3$	$1-\Sigma_3$

Likelihood of the m-array:

$$P(m - array_{t,}) \sim Multinomial(pr_{t,}, released_t)$$

where

$pr_{t,}$ are the cell probabilities of the m-array for release occasion t

$released_t$ are the number of released individuals at occasion t

S_t is the survival probability from t to $t+1$

r_t is the recovery probability at occasion t



Bayesian population analysis using WinBUGS

Chapter 9: Multistate capture-recapture models

Conditional nature of the 2 processes

State process

State 1

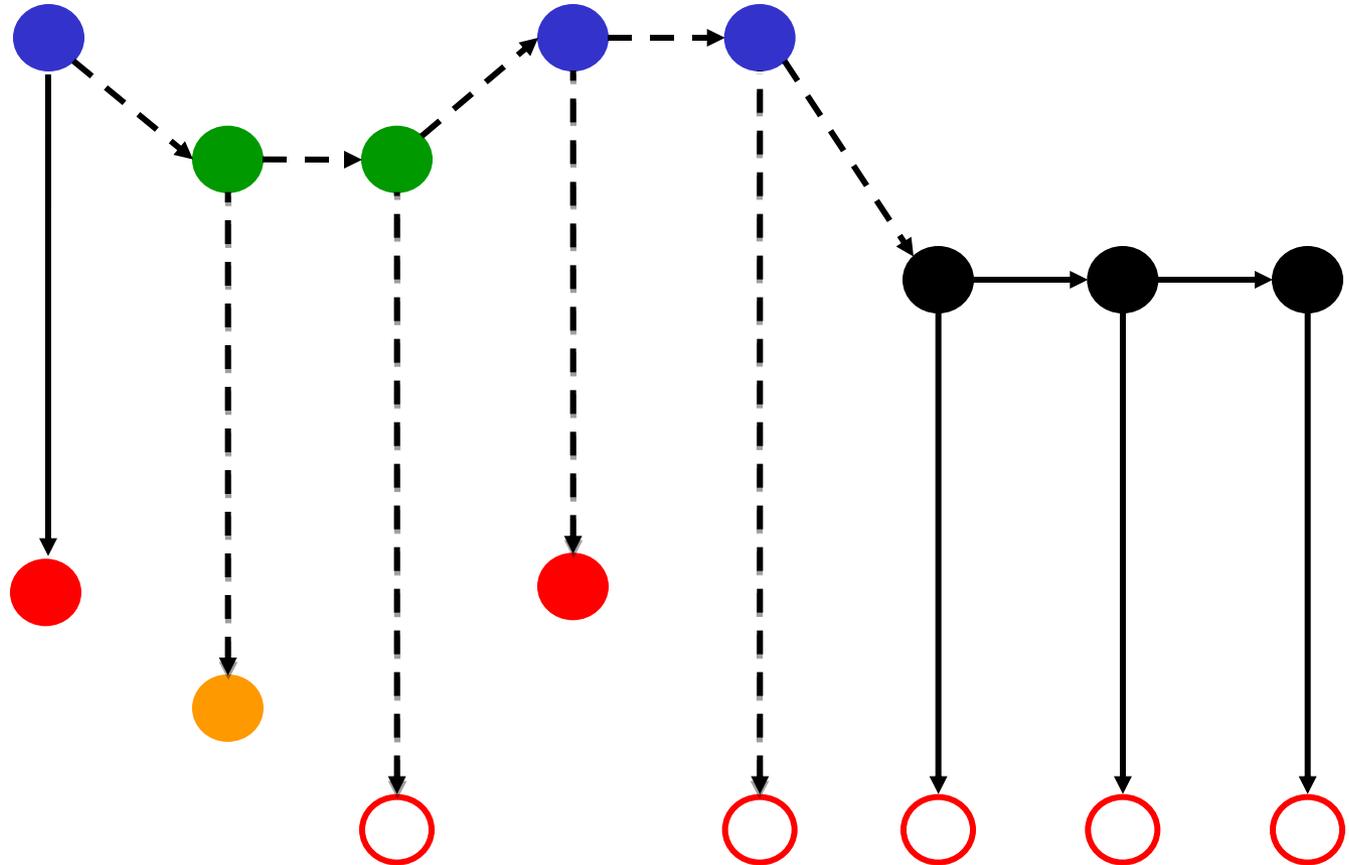
State 2

Dead

Seen 1

Seen 2

Not seen



Observation process

--> Stochastic process
-> Deterministic process

State process

		States at time $t+1$		
		state 1	state 2	dead
States at time t	state 1	Φ_{11}	Φ_{12}	$1 - \Phi_{11} - \Phi_{12}$
	state 2	Φ_{21}	Φ_{22}	$1 - \Phi_{21} - \Phi_{22}$
	dead	0	0	1

Observation process

		Observations at time t		
		Seen at 1	Seen at 2	Not seen
States at time t	state 1	p_1	0	$1 - p_1$
	state 2	0	p_2	$1 - p_2$
	dead	0	0	1

State process

State 1



State 2



Dead



$\Omega =$
States at time t

state 1
state 2
dead

States at time $t+1$

state 1	state 2	dead
Φ_{11}	Φ_{12}	$1 - \Phi_{11} - \Phi_{12}$
Φ_{21}	Φ_{22}	$1 - \Phi_{21} - \Phi_{22}$
0	0	1

BUGS language:

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

Observation process

State 1

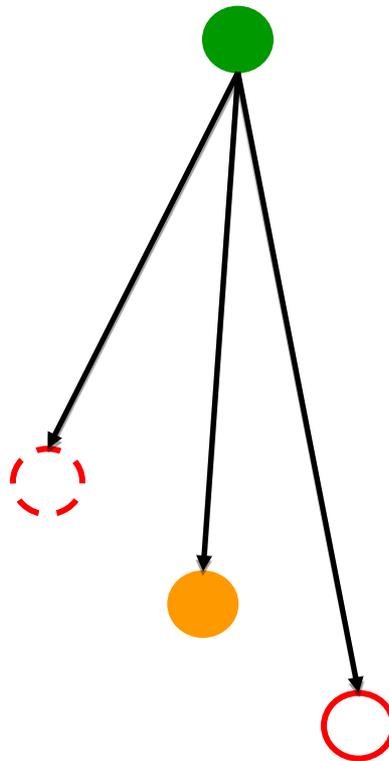
State 2

Dead

Seen 1

Seen 2

Not seen



Observations at time t

	Seen at 1	Seen at 2	Not seen
state 1	p_1	0	$1 - p_1$
state 2	0	p_2	$1 - p_2$
dead	0	0	1

$\Theta =$

States at time t

BUGS language:

$$y_{i,t} | z_{i,t} \sim \text{dcat}(\Theta_{z_{i,t}})$$

Possible re-parameterisation

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

$$\begin{bmatrix} \Phi_{11} & \Phi_{12} & 1 - \Phi_{11} - \Phi_{12} \\ \Phi_{21} & \Phi_{22} & 1 - \Phi_{21} - \Phi_{22} \\ 0 & 0 & 1 \end{bmatrix}$$

- 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 $t+1$

$$\begin{bmatrix} \phi_1 (1 - \psi_{12}) & \phi_1 \psi_{12} & 1 - \phi_1 \\ \phi_2 \psi_{21} & \phi_2 (1 - \psi_{21}) & 1 - \phi_2 \\ 0 & 0 & 1 \end{bmatrix}$$

Multistate models are very flexible: some examples

1. Age-dependent survival

State process

States at time t

States at time $t+1$

	juvenile	adult	dead
juvenile	0	ϕ_{juv}	$1 - \phi_{juv}$
adult	0	ϕ_{ad}	$1 - \phi_{ad}$
dead	0	0	1

Observation process

States at time t

Observations at time t

	Seen as juv	Seen as ad	Not seen
juvenile	0	0	1
adult	0	p	$1 - p$
dead	0	0	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
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

Observations at time t

Observation process

States at time t

	seen at A	seen at B	seen at C	not seen
site A	p_A	0	0	$1 - p_A$
site B	0	p_B	0	$1 - p_B$
site C	0	0	p_C	$1 - p_C$
dead	0	0	0	1

Multistate models are very flexible: some examples

2. Movement among 3 sites

States at time t+1

State process

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

States at time t

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 possible options:

- Multinomial link function
- Dirichlet prior

Multistate models are very flexible: some examples

3. Combination of life and dead encounters

States at time $t+1$

State process

		<i>alive</i>	<i>rec. dead</i>	<i>dead</i>
<i>States at time t</i>	<i>alive</i>	s	$1 - s$	0
	<i>recently dead</i>	0	0	1
	<i>dead</i>	0	0	1

Observations at time t

Observation process

		<i>seen</i>	<i>recovered</i>	<i>not seen</i>
<i>States at time t</i>	<i>alive</i>	p	0	$1 - p$
	<i>rec. dead</i>	0	r	$1 - r$
	<i>dead</i>	0	0	1

Multistate models are very flexible: some examples

4. Temporary emigration

States at time t+1

State process

		<i>inside</i>	<i>outside</i>	<i>dead</i>	
<i>States at time t</i>	<i>inside</i>	[$\phi(1 - \psi_{IO})$	$\phi\psi_{IO}$	$1 - \phi$
	<i>outside</i>		$\phi\psi_{OI}$	$\phi(1 - \psi_{OI})$	$1 - \phi$
	<i>dead</i>		0	0	1
]			

Observations at time t

Observation process

		<i>Seen</i>	<i>Not seen</i>	
<i>States at time t</i>	<i>inside</i>	[p	$1 - p$
	<i>outside</i>		0	1
	<i>dead</i>		0	1
]		

Multistate models are very flexible: some examples

5. Immediate trap response

State process

		<i>States at time t+1</i>		
		<i>a, seen</i>	<i>a, not s</i>	<i>dead</i>
<i>States at time t</i>	<i>alive, seen</i>	ϕp_S	$\phi(1 - p_S)$	$1 - \phi$
	<i>alive, not seen</i>	ϕp_N	$\phi(1 - p_N)$	$1 - \phi$
	<i>dead</i>	0	0	1

Observation process

		<i>Observations at time t</i>	
		<i>Seen</i>	<i>Not seen</i>
<i>States at time t</i>	<i>alive, seen</i>	1	0
	<i>alive, not seen</i>	0	1
	<i>dead</i>	0	1



Bayesian population analysis using WinBUGS

Chapter XY:
Multistate capture-recapture
models with state
uncertainty: multievent
models

Multievent models

- Most general capture-recapture models
- All capture-recapture models introduced so far can be seen as a special case of a multievent model
- Is a multistate model that allows for state assignment errors
- Seminal paper: Pradel (2005), *Biometrics*
- In contrast to multistate models, 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

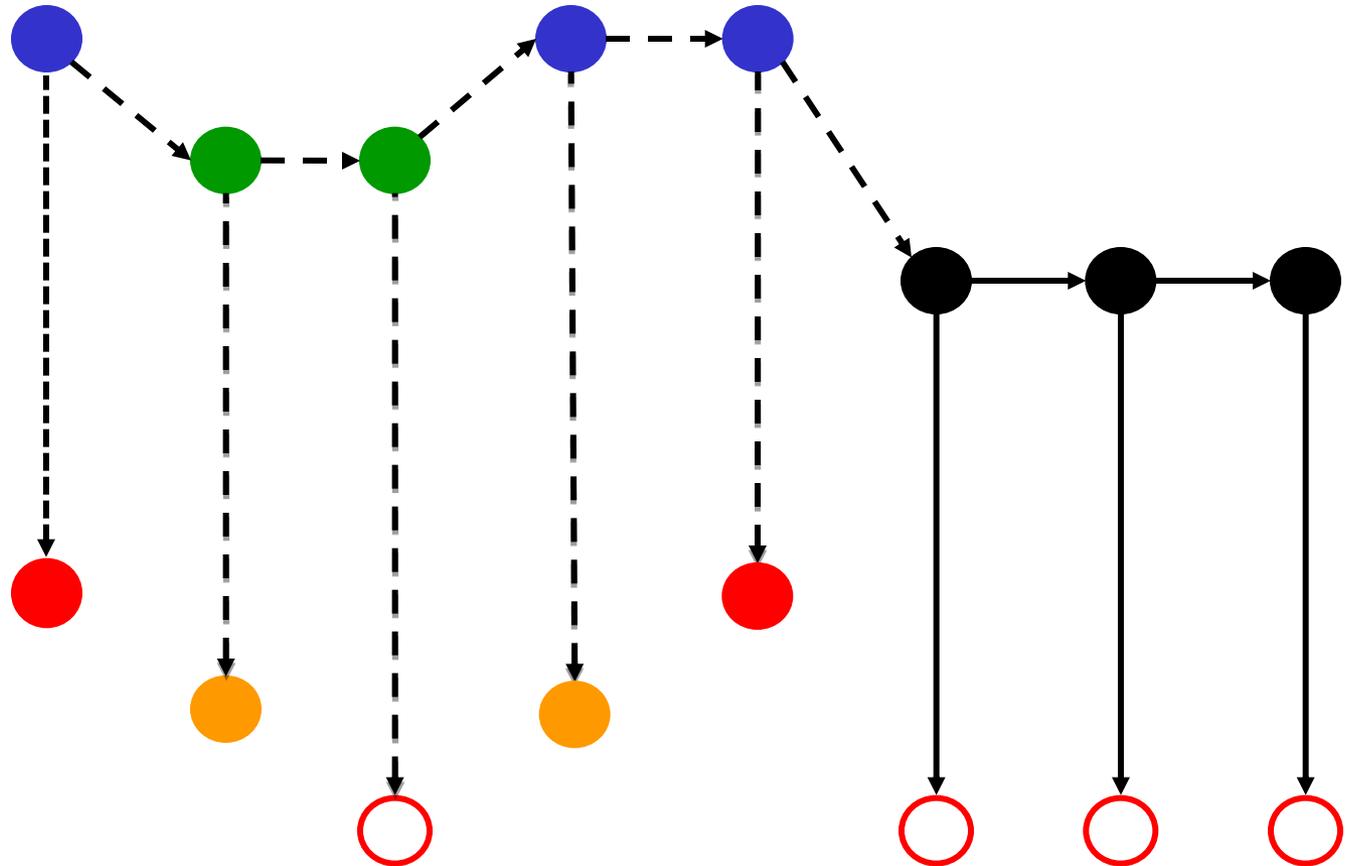
Dead

Seen 1

Seen 2

Not seen

Observation process



--> Stochastic process
-> Deterministic process

At first encounter

Initial state probability

$$\text{States at first encounter} \begin{matrix} \text{state 1} \\ \text{state 2} \\ \text{dead} \end{matrix} \begin{bmatrix} 1 - \pi & \pi & 0 \end{bmatrix}$$

State assignment

Observations at first encounter

$$\text{States at first encounter} \begin{matrix} \text{state 1} \\ \text{state 2} \\ \text{dead} \end{matrix} \begin{matrix} \text{seen at 1} & \text{seen at 2} & \text{not seen} \end{matrix} \begin{bmatrix} \beta_1 & 1 - \beta_1 & 0 \\ 1 - \beta_2 & \beta_2 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

After first encounter

State process

		<i>States at time t+1</i>		
		<i>state 1</i>	<i>state 2</i>	<i>dead</i>
<i>States at time t</i>	<i>state 1</i>	Φ_{11}	Φ_{12}	$1 - \Phi_{11} - \Phi_{12}$
	<i>state 2</i>	Φ_{21}	Φ_{22}	$1 - \Phi_{21} - \Phi_{22}$
	<i>dead</i>	0	0	1

Observation process

		<i>Observations at time t</i>		
		<i>seen at 1</i>	<i>seen at 2</i>	<i>not seen</i>
<i>States at time t</i>	<i>state 1</i>	$\beta_1 p_1$	$(1 - \beta_1) p_1$	$1 - p_1$
	<i>state 2</i>	$(1 - \beta_2) p_2$	$\beta_2 p_2$	$1 - p_2$
	<i>dead</i>	0	0	1

An example: uncertain disease status

- An individual that does not have the disease is seen, 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 without disease (Seen -)
- Seen with disease (Seen +)
- Not seen

At first encounter

Initial state probability

$$\text{Disease state: } \begin{array}{c} \text{Alive -} \\ \text{Alive +} \\ \text{Dead} \end{array} \begin{bmatrix} \mathbf{1} & -\pi & \pi & \mathbf{0} \end{bmatrix}$$

π : Probability of being infected at first encounter

BUGS language:

$$\Pi = \begin{bmatrix} \mathbf{1} & -\pi & \pi & \mathbf{0} \end{bmatrix}$$

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

At first encounter

State assignment

Observations at first encounter

States at first encounter

	Seen -	Seen +	Not seen
Alive -	1	0	0
Alive +	β	$1 - \beta$	0
Dead	0	0	1

β : Probability of not diagnosing the disease

BUGS language:

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

$$y_{i,f[i]} \mid z_{i,f[i]} \sim \text{dcat} \left(O_{z_{i,f[i]}} \right)$$

After first encounter

State process

$$\begin{array}{l} \text{States at time } t \\ \text{Alive -} \\ \text{Alive +} \\ \text{Dead} \end{array} \begin{array}{c} \text{States at time } t+1 \\ \text{Alive -} \\ \text{Alive +} \\ \text{Dead} \end{array} \begin{bmatrix} \phi_H (1 - \psi_{HD}) & \phi_H \psi_{HD} & 1 - \phi_H \\ \phi_D \psi_{DH} & \phi_D (1 - \psi_{DH}) & 1 - \phi_D \\ 0 & 0 & 1 \end{bmatrix}$$

ϕ_H : survival probability of healthy individuals

ϕ_D : survival probability of individuals infected with the disease

ψ_{HD} : infection probability

ψ_{DH} : probability to become healthy

BUGS language:

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

$$z_{i,t+1} \mid z_{i,t} \sim \text{dcat}(\Omega_{z_{i,t}})$$

After first encounter

Observation process

Observations at time t

	Seen -	Seen +	Not seen
States at time t			
Alive -	p_H	0	$1 - p_H$
Alive +	βp_D	$(1 - \beta) p_D$	$1 - p_D$
Dead	0	0	1

p_H : probability to encounter a healthy individual

p_D : probability to encounter an individual infected with the disease

β : Probability of not diagnosing the disease

BUGS language:

$$\Theta = \begin{bmatrix} p_H & 0 & 1 - p_H \\ \beta p_D & (1 - \beta) p_D & 1 - p_D \\ 0 & 0 & 1 \end{bmatrix} \quad y_{i,t} | z_{i,t} \sim \text{dcat}(\Theta_{z_{i,t}})$$



Bayesian population analysis using WinBUGS

Chapter 10: Estimation of survival, recruitment and population size using capture-recapture data



Introduction

- The open capture-recapture models seen so far conditioned on first capture
- Leading zeros contain information about the arrival time of individuals in the population
- Jolly-Seber model:
 - Unconditional
 - Information about recruitment related parameters and survival
 - Estimation of population size

True capture history (z)

0	1	1	1	0
1	1	1	1	0
0	0	1	0	0
0	0	1	1	1

Summary statistics

N_s (Superpopulation size): 4

N (Annual population size): {1, 2, 4, 3, 1}

B (Annual number of new recruits): {1, 1, 2, 0, 0}

b (proportion of new recruits [relative to N_s]): {0.25, 0.25, 0.5, 0, 0}

$$B \sim \text{Multinomial}(N_s, \mathbf{b})$$

Φ (Survival probability): {1.0, 1.0, 0.75, 0.33}

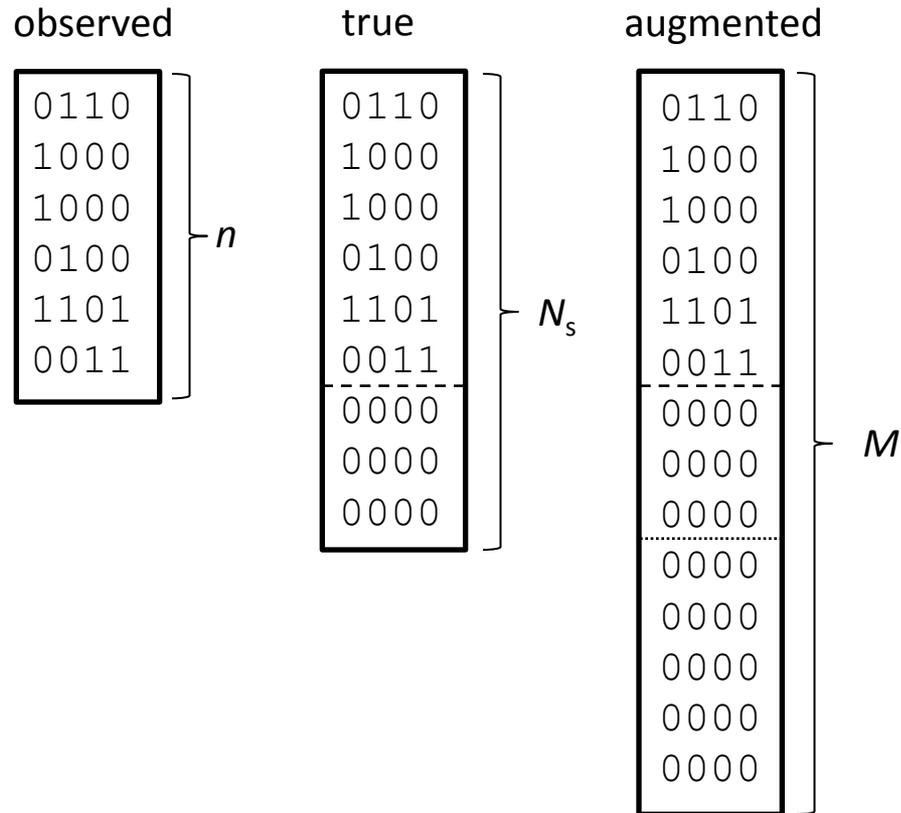
Observed capture history (y)

0	1	1	1	0	0	0	1	1	0
1	1	1	1	0	1	0	0	1	0
0	0	1	0	0	0	0	1	1	0
0	0	1	1	1					

Problem:

The multinomial distribution does not work with MCMC, as the total (N_s) is unknown.

Data augmentation



- The data set has now a fixed dimension (length M)
- B can now be modelled as a removal process from M

Conditional nature of the 2 processes

State process

Not yet entered

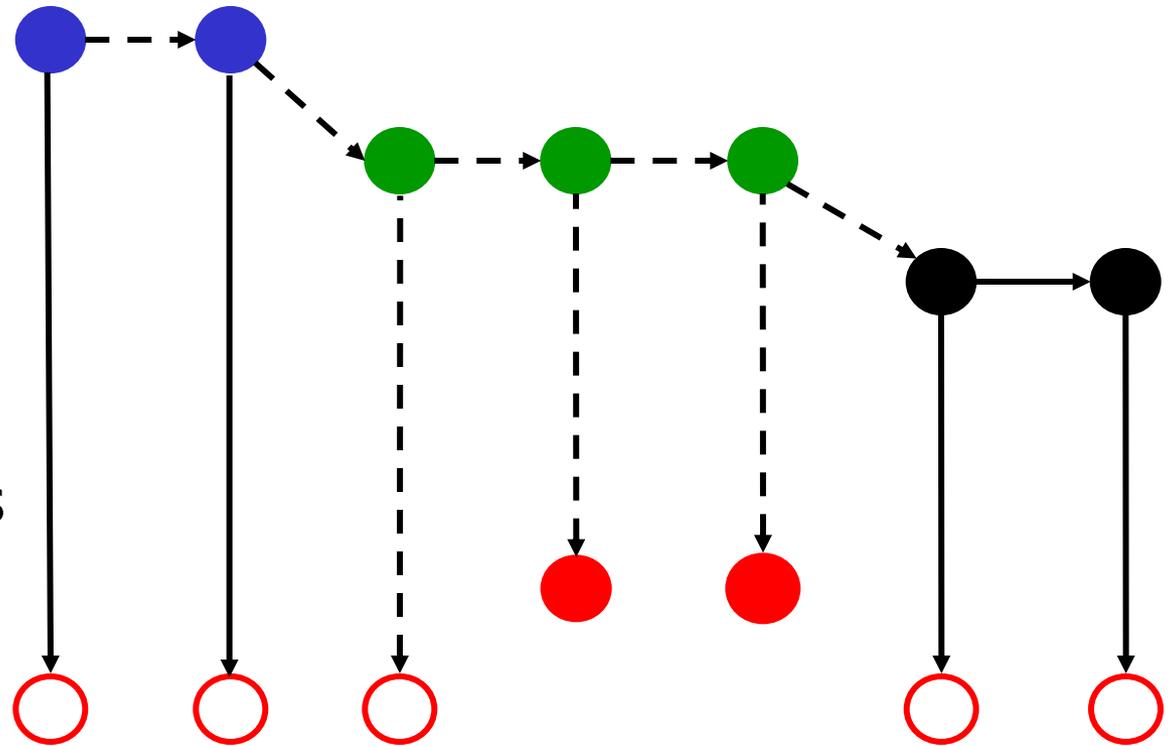
Alive

Dead

Observation process

Seen

Not seen



- - - -> Stochastic process (transition and recapture)

————> Deterministic process

The CJS model for comparison

State process

Not yet entered

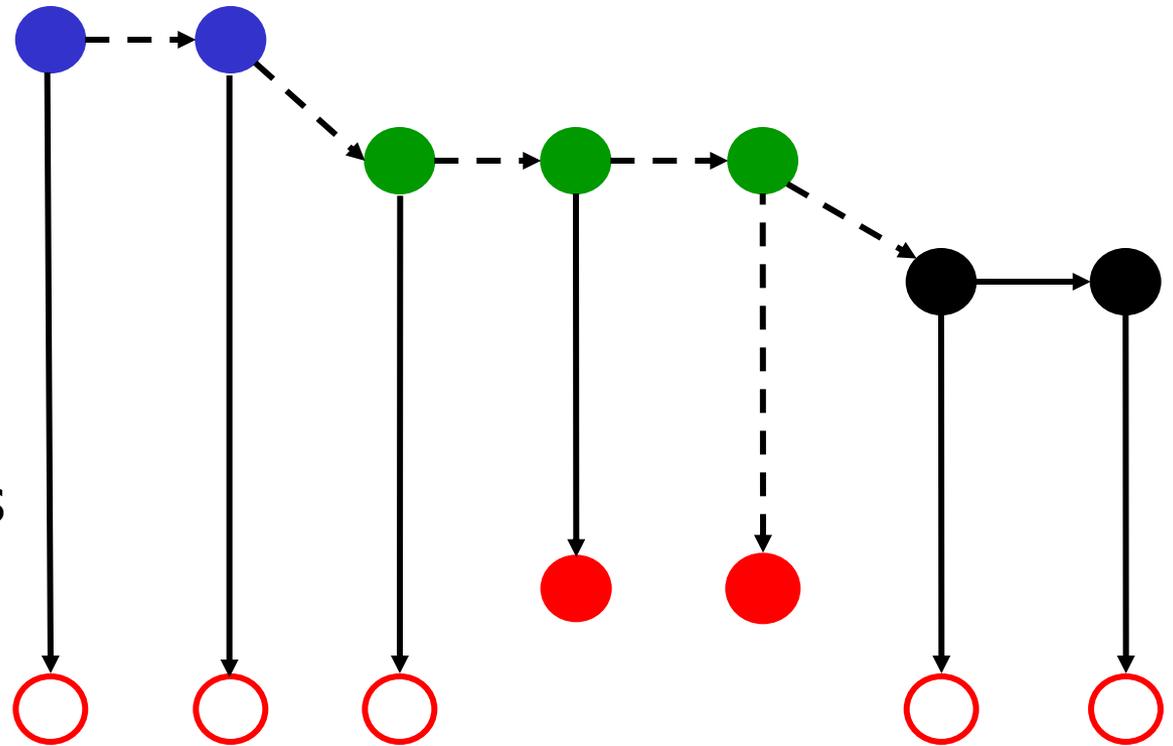
Alive

Dead

Observation process

Seen

Not seen



- - - -> Stochastic process (transition and recapture)

————> Deterministic process

The entry process

→ Different types of JS models, based on how the entry to the population is defined.

1. Restricted occupancy formulation

Imagine there is a pool of M individuals from which animals are recruited to enter the population

γ_t is the probability that an *available* individual is recruited at occasion t

$$B_1 = M\gamma_1$$

$$B_2 = M(1-\gamma_1)\gamma_2$$

Removal process

...

1. Restricted occupancy formulation

1. State process (entry and survival)

$$z_{i,1} \sim \text{Bernoulli}(\gamma_1)$$
$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli} \left(z_{i,t-1} \phi_{i,t} + \gamma_t \prod_{k=1}^{t-1} (1 - z_{i,k}) \right)$$

where,

$z_{i,t}$: matrix, indicating whether individual i is alive at time t ($z = 1$), or dead ($z = 0$) or has not yet entered ($z = 0$)

$\phi_{i,t}$: apparent survival probability for individual i from time t to $t+1$

γ_t : «removal» entry probability at time t

2. Observation process

$$y_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_{i,t})$$

where,

$y_{i,t}$: is the observed capture history for individual i at time t

$p_{i,t}$: recapture probability for individual i at time t

Derived parameters

$$N_t = \sum_{i=1}^M z_{i,t}$$

Population size at occasion t

$$B_t = \sum_{i=1}^M (1 - z_{i,t-1}) z_{i,t}$$

Number of new individuals at t

$$N_s = \sum \mathbf{B}$$

Size of the superpopulation

$$b_t = \frac{B_t}{N_s}$$

Entry probability

2. Formulation as multistate model

State process

$$\begin{array}{l} \text{Not yet recruited} \\ \text{alive} \\ \text{dead} \end{array} \begin{bmatrix} 1 - \gamma & \gamma & 0 \\ 0 & \phi & 1 - \phi \\ 0 & 0 & 1 \end{bmatrix}$$

Observation process

$$\begin{array}{l} \text{Not yet recruited} \\ \text{alive} \\ \text{dead} \end{array} \begin{bmatrix} 0 & 1 \\ p & 1 - p \\ 0 & 1 \end{bmatrix}$$

2. Formulation as multistate model

0	1	0	0	1
0	0	1	0	1
0	1	0	0	0
•	•	•	•	
0	0	0	0	0
0	0	0	0	0

Problem:

Multistate model is conditional
on initial capture

Practical solution:

Add a dummy occasion

Another solution:

Do not add a dummy occasion, but model the first occasion

$$z_{i,1} \sim \text{cat} \left(\begin{bmatrix} 1 - \gamma_1 & \gamma_1 & 0 \end{bmatrix} \right)$$

3. Superpopulation approach (Schwarz & Arnason 1996)

N_s : Number of individual that are alive during the study
(superpopulation)

b_t : Probability that a member of N_s enters the population at
occasion t (entry probability)

B_t : Number of entered individuals at occasion t

$\mathbf{B} \sim \text{multinomial}(N_s, \mathbf{b})$

3. Superpopulation approach (Schwarz & Arnason 1996)

To still use the augmented data set, we define:

$$\begin{aligned} \eta_1 &= b_1 & z_{i,1} &\sim \text{Bernoulli}(\eta_1) \\ \eta_2 &= \frac{b_2}{1-b_1} & P(z_{i,t} | z_{i,t-1}) &\sim \text{Bernoulli}\left(z_{i,t-1}\phi_{i,t} + \eta_t \prod_{k=1}^{t-1} (1 - z_{i,k})\right) \\ &\dots & w_i &\sim \text{Bernoulli}(\psi) \\ \eta_t &= \frac{b_t}{1 - \sum_{i=1}^{t-1} b_i} & y_{i,t} | z_{i,t} &\sim \text{Bernoulli}(z_{i,t} p_{i,t} w_i) \end{aligned}$$



Bayesian population analysis using WinBUGS

Chapter 11: Integrated population models

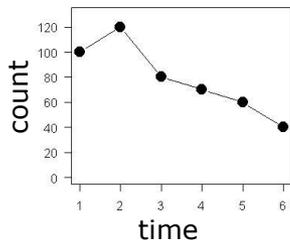
Population analyses

- **Focus on population growth rates**
 - Data: time series from a population
 - Relevant factors operating at the population level can be identified
 - Demographic mechanism remains unknown
- **Focus on demographic parameters**
 - Data: capture-recapture, brood success, ...
 - Link between environment and demography can be identified
 - Relevance at population scale remains unknown (mostly)
- **Integrated analysis: combination of the two**
 - Data: time series, capture-recapture, brood success, ...
 - Describe population dynamics as a result of varying demographic rates

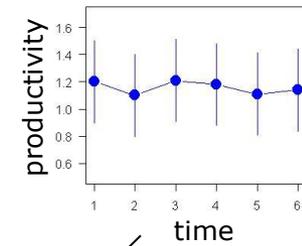
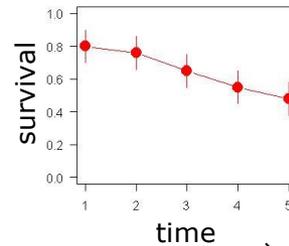
The traditional approach...

- Estimate demographic rates
- Use a population model to reconstruct population development
- Compare with observed population development

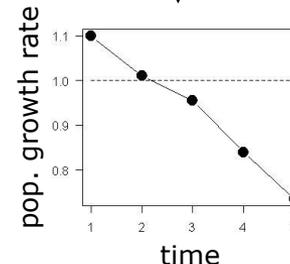
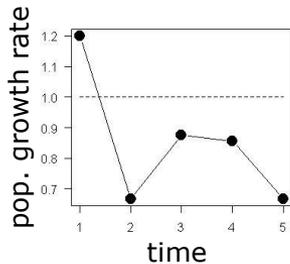
Observed population development



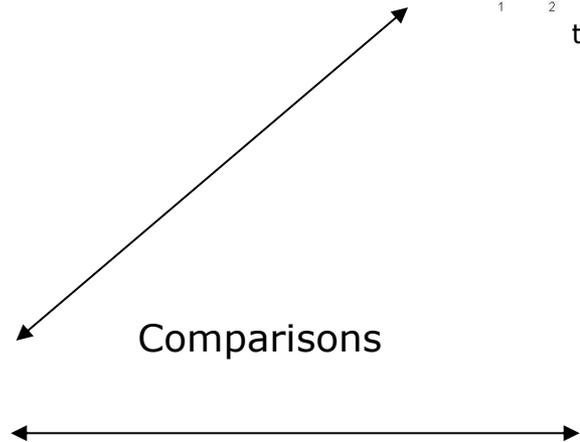
Estimated demographic parameters



Population model



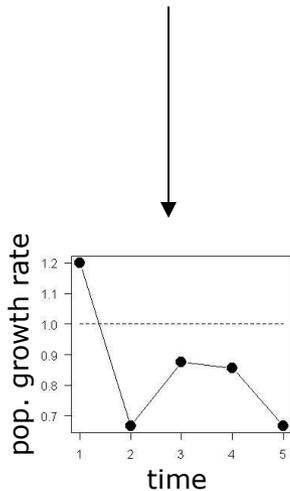
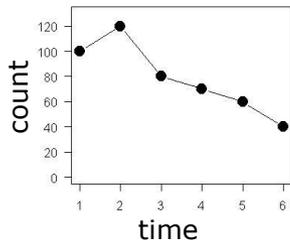
Comparisons



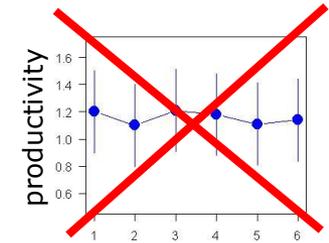
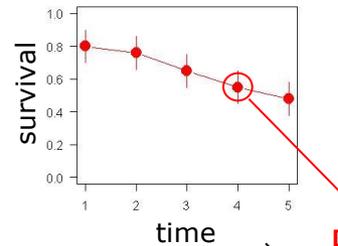
...and its disadvantages

- Difficult to account for uncertainty in the inputs, or for representing uncertainty about the conclusions
- Some demographic rates may not be estimable
- Inefficient

Observed population development

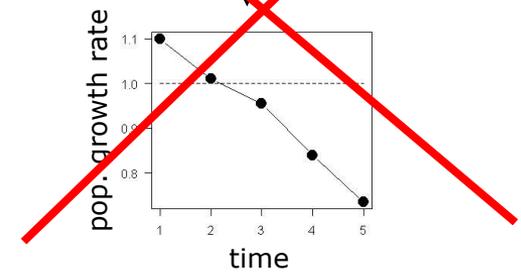


Estimated demographic parameters



Point estimates used as input

~~Population model~~



The new wave: fully integrated models

Basic idea

- Set up a population model with which count and demographic data are analysed *simultaneously*

Potential advantages

- More comprehensive use of available information
 - More demographic rates become estimable (e.g. fecundity)
 - Increased precision of estimates
- Formal representation of uncertainty

Potential disadvantages

- More complicated
 - Complex structure
 - Computer calculation power

An IPM for wrynecks:

Available data:

- Population counts
- Capture-recapture data of nestling and adults
- Data on reproductive output

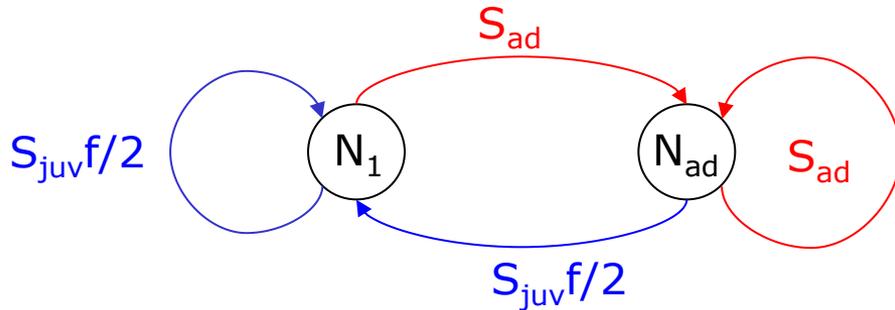
3 basic steps:

- Set up a population model
- Write the likelihood for the single data sets
- Write the joint likelihood



1. Set up a population model

Pre-breeding census
Female-based



Population sizes :

$$N_{1,t+1} = N_{1,t} S_{juv,t} \frac{f_t}{2} + N_{ad,t} S_{juv,t} \frac{f_t}{2}$$

$$N_{ad,t+1} = N_{1,t} S_{ad,t} + N_{ad,t} S_{ad,t}$$

To model demographic stochasticity, we write

$$N_{1,t+1} \sim \text{Po} \left((N_{1,t} + N_{ad,t}) S_{juv,t} \frac{f_t}{2} \right)$$

↑ generates an integer number between 0 and ∞

$$N_{ad,t+1} \sim \text{Bin} (N_{1,t} + N_{ad,t}, S_{ad,t})$$

↑ generates an integer number between 0 and $N_{1,t} + N_{ad,t}$

Parameters

S: survival probability

f: productivity

N_1 : population size of 1y

N_{ad} : population size of adults

2. Likelihood for the different data sets

A. Counts: state-space model

State process equations:

$$N_{1,t+1} \sim \text{Po} \left((N_{1,t} + N_{ad,t}) S_{1,t} \frac{f_t}{2} \right)$$

$$N_{ad,t+1} \sim \text{Bin} (N_{1,t} + N_{ad,t}, S_{ad,t})$$

Observation process equation:

$$y_t \sim \text{N} \left((N_{1,t} + N_{ad,t}), \sigma_y^2 \right)$$

Likelihood:

$$L_{SS} \left(\mathbf{y} \mid \mathbf{N}, \mathbf{S}_{\text{juv}}, \mathbf{S}_{\text{ad}}, \mathbf{f}, \sigma_y^2 \right) = L_{OB} \left(\mathbf{y} \mid \mathbf{N}, \sigma_y^2 \right) \times L_{SY} \left(\mathbf{N} \mid \mathbf{S}_{\text{juv}}, \mathbf{S}_{\text{ad}}, \mathbf{f} \right)$$

Parameters

S: survival probability

f: productivity

N_1 : population size of 1y

N_{ad} : population size of adults

σ_y^2 : census/residual error

Data

y: counts

B. Capture-recapture data

- As introduced in chapter 7
- Better use multinomial likelihood

Likelihood:

$$L_{CMR}(\mathbf{m} | \mathbf{S}_{juv}, \mathbf{S}_{ad}, \mathbf{p})$$

C. Data on reproductive output

- Poisson regression model

$$J_t \sim Pois(R_t f_t)$$

Likelihood:

$$L_{RS}(J, R | f)$$

Parameters

S: survival probability
p: recapture probability
f: productivity

Data

m: m-array
J: # nestlings
R: # broods

3. Joint likelihood

- Assume independence among data sets
- Joint likelihood

$$L_{IPM}(\mathbf{y}, \mathbf{m}, \mathbf{J}, \mathbf{R} | \mathbf{N}, \mathbf{S}_{juv}, \mathbf{S}_{ad}, \mathbf{f}, \mathbf{p}, \sigma_y^2) = L_{OB}(\mathbf{y} | \mathbf{N}, \sigma_y^2) \times L_{SY}(\mathbf{N} | \mathbf{S}_{juv}, \mathbf{S}_{ad}, \mathbf{f}) \times \\ L_{CMR}(\mathbf{m} | \mathbf{S}_{juv}, \mathbf{S}_{ad}, \mathbf{p}) \times L_{RS}(\mathbf{J}, \mathbf{R} | \mathbf{f})$$

Parameters

S: survival probability

p: recapture probability

f: productivity

N_1 : population size of 1y

N_{ad} : population size of adults

σ_y^2 : census/residual error

Data

y: counts

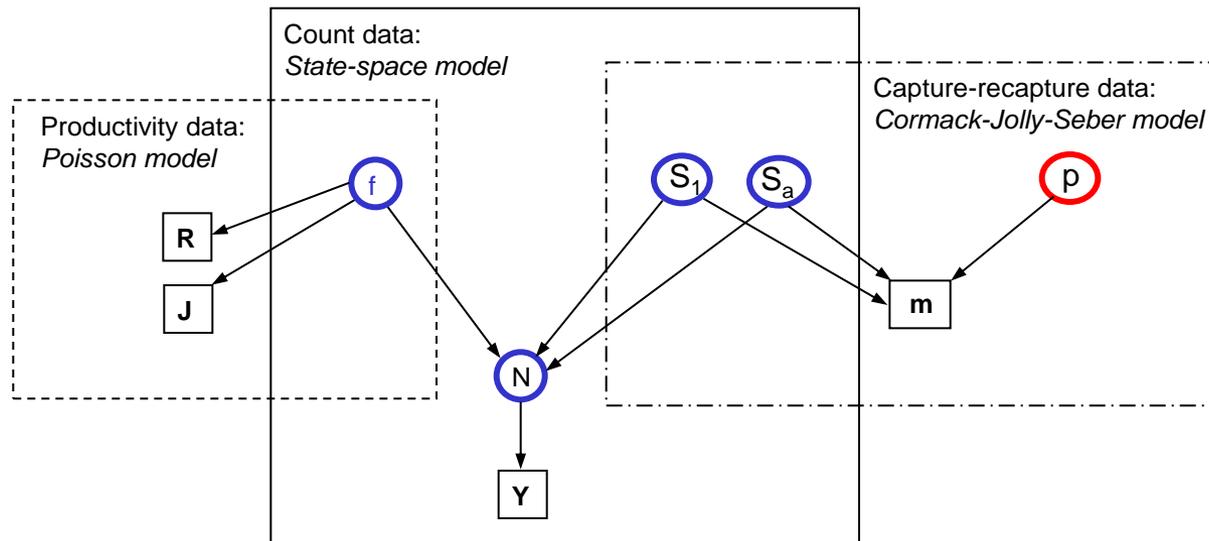
m: m-array

J: # nestlings

R: # broods

3. Joint likelihood

Graphical relationship between data and parameters:
(Directed acyclic graph (DAG) without priors)



Parameters

S : survival probability
 p : recapture probability
 f : productivity
 N_1 : population size of 1y
 N_{ad} : population size of adults
 σ^2_y : census/residual error

Data

y : counts
 m : m-array
 J : # nestlings
 R : # broods