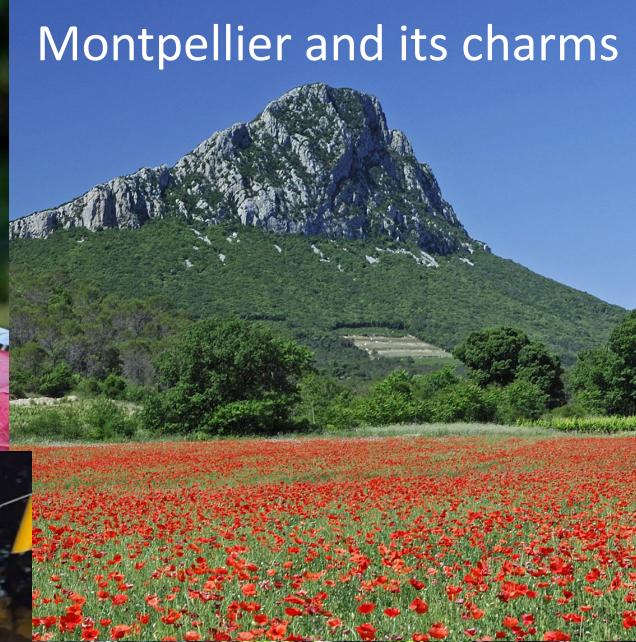




Bayesian integrated population modeling using JAGS

Estimation of survival
probabilities using
capture-recapture data

Montpellier and its charms





CORONAVIRUS DISEASE [COVID-19]



zoom



It is fairly easy to estimate survival, or is it?

In principle:

- Follow individuals across time
- Count individuals at time t say C_t
- Assess how many of them are still alive after time Δt say $L_{t+\Delta t}$
- Survival probability is then $S_{\Delta t} = \frac{L_{t+\Delta t}}{C_t}$



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- Follow individuals across time
- Count individuals at time t say C_t
- Assess how many of them are still alive after time Δt say $L_{t+\Delta t}$
- Survival probability is then $S_{\Delta t} = \frac{L_{t+\Delta t}}{C_t}$

Major issue: all individuals that are still alive, but **not seen**, are counted as **dead**

- Ignoring imperfect detection leads to underestimating survival
- Typically, we do not know $L_{t+\Delta t}$, only $p \cdot L_{t+\Delta t}$, where p is detection probability
- Detection can be estimated & distinguished from survival, when ≥ 3 occasions
- Thus, collect **capture-recapture data**: individual capture/encounter histories

MODELING SURVIVAL AND TESTING BIOLOGICAL HYPOTHESES USING MARKED ANIMALS: A UNIFIED APPROACH WITH CASE STUDIES¹

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REVIEW

A review of Bayesian state-space modelling of capture–recapture–recovery data

Ruth King*

School of Mathematics and Statistics and Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, Fife KY16 9LZ, UK

Traditionally, state-space models are fitted to data where there is uncertainty in the observation or measurement of the system. State-space models are partitioned into an underlying system process describing the transitions of the true states of the system over time and the observation process linking the observations of the system to the true states. Open population capture–recapture–recovery data can be modelled in this framework by regarding the system process as the state of each individual observed within the study in terms of being alive or dead, and the observation process the recapture and/or recovery process. The traditional observation error of a state-space model is incorporated via the recapture/recovery probabilities being less than unity. The models can be fitted using a Bayesian data augmentation approach and in standard BUGS packages. Applying this state-space framework to such data permits additional complexities including individual heterogeneity to be fitted to the data at very little additional programming effort. We consider the efficiency of the state-space model fitting approach by considering a random effects model for capture–recapture data relating to dippers and compare different Bayesian model-fitting algorithms within WinBUGS.

Keywords: Bayesian approach; BUGS; data augmentation; hierarchical model; individual heterogeneity; mixed effects models

Marking, recaptures and resightings



Artificial marks

Marking, recaptures and resightings



Artificial marks

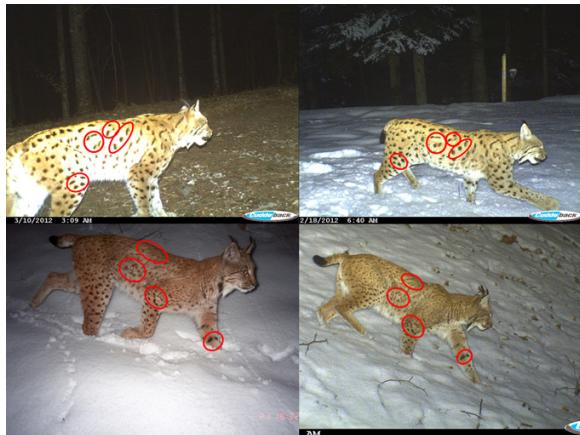


Natural marks

Marking, recaptures and resightings



Artificial marks



Natural marks

... also genetic & acoustic marks

Individual capture histories – longitudinal monitoring

ID	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0
2	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0
5	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
12	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0

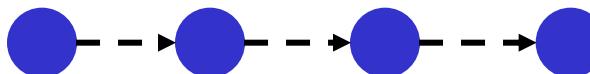


S. Wanless, J. Lahoz-Monfort
<https://bit.ly/390ABBu>

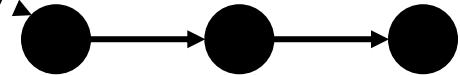
Individual capture history: result of two processes

State process

Alive



Dead



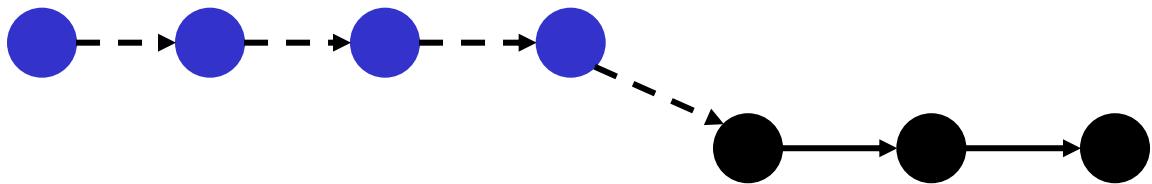
→ Stochastic process

→ Deterministic process

Individual capture history: result of two processes

State process

Alive



Dead

Actual states: AAAADDD

→ Stochastic process

→ Deterministic process

Individual capture history: result of two processes

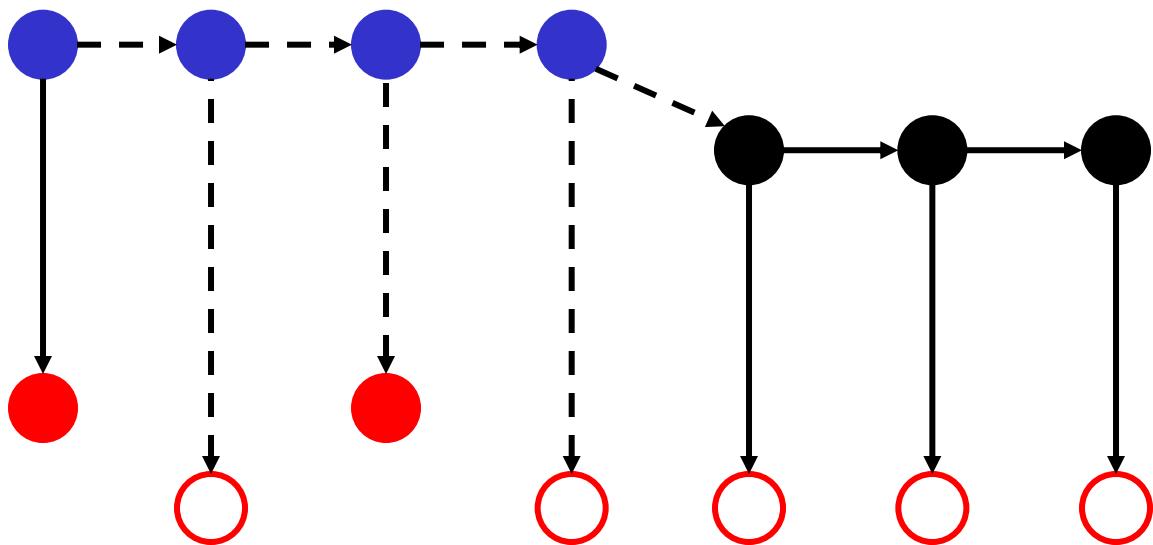
State process

Alive

Dead

Seen

Not seen



Observation process

—→ Stochastic process

—→ Deterministic process

Individual capture history: result of two processes

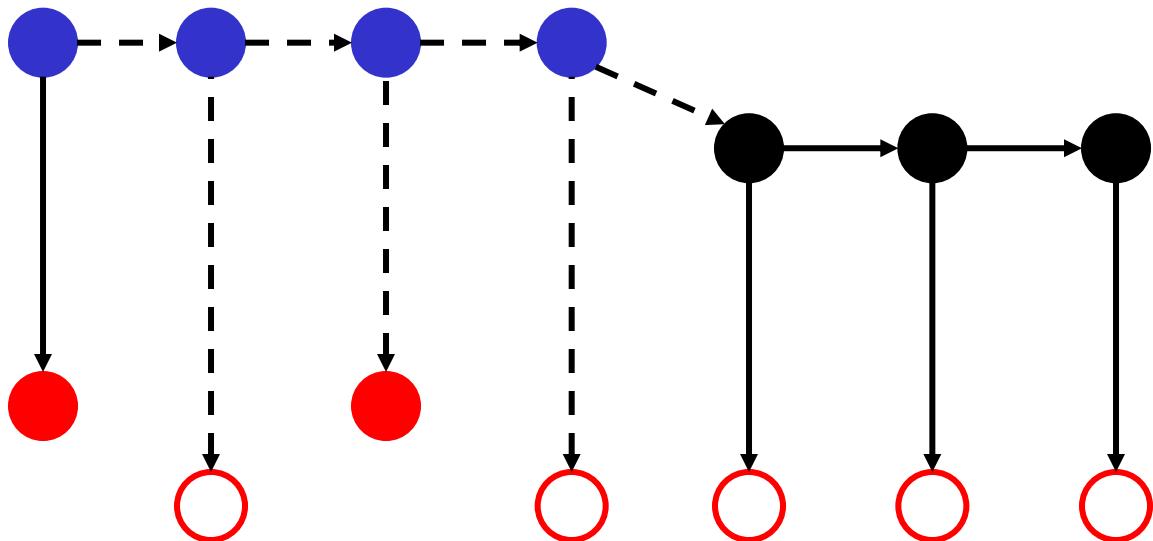
State process

Alive

Dead

Seen

Not seen



Observation process

- Stochastic process
- Deterministic process

Actual states: AAAADDD
Observations are: 1010000

State-space likelihood to analyse CR data

1. State process corresponding to survival

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

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

State-space likelihood to analyse CR data

1. State process corresponding to survival

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

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

where,

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

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

If $z_{i,t-1} = 0$ (i is dead at $t-1$) then $z_{i,t} \sim \text{Bernoulli}(0)$
that is $z_{i,t} = 0$ with certainty (no zombies)

State-space likelihood to analyse CR data

1. State process corresponding to survival

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

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

where,

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

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

If $z_{i,t-1} = 1$ (i is alive at $t-1$) then $z_{i,t} \sim \text{Bernoulli}(\phi_{i,t-1})$
that is $z_{i,t} = 1$ with prob $\phi_{i,t-1}$ and $z_{i,t} = 0$ with prob $(1-\phi_{i,t-1})$

State-space likelihood to analyse CR data

1. State process corresponding to survival

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

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

where,

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

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

2. Observation process corresponding to detection

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

where,

$y_{i,t}$: is the event of capture for individual i at time t ($y = 1$ if detected, 0 otherwise)

$p_{i,t}$: 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

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

Data

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

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Data

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

Parameters

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

$$\boldsymbol{p}_{i,t} = \begin{matrix} NA & p_{1,3} & p_{1,4} & p_{1,5} \\ p_{2,2} & p_{2,3} & p_{2,4} & p_{2,5} \\ NA & NA & p_{3,4} & p_{3,5} \\ \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots \end{matrix}$$

1

Data

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

Parameters

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

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Modelling

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

Modelling

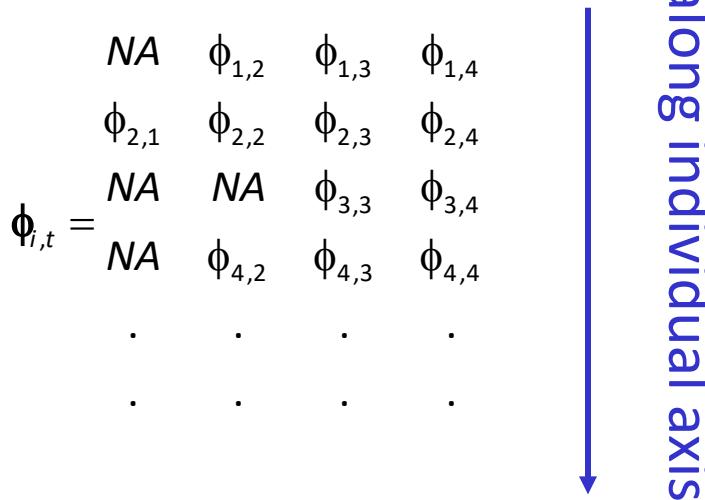
along time axis

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

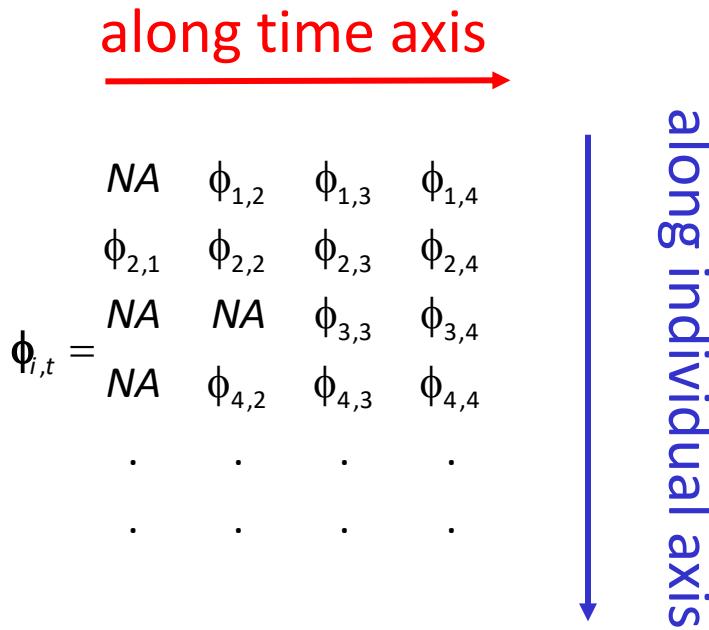
Modelling

along time axis

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



Modelling



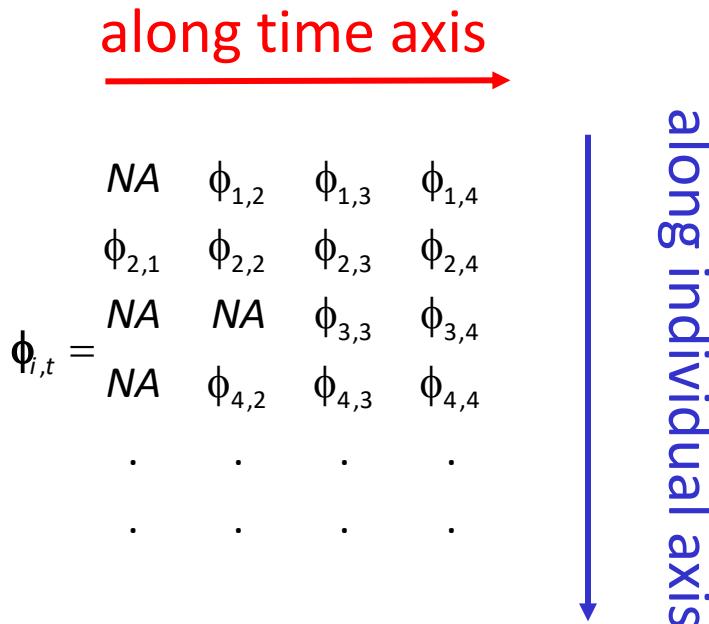
Time axis:

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

Individual axis:

- groups (fixed, random)
- individual covariates

Modelling



Time axis:

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- temporal covariates
- time-constant

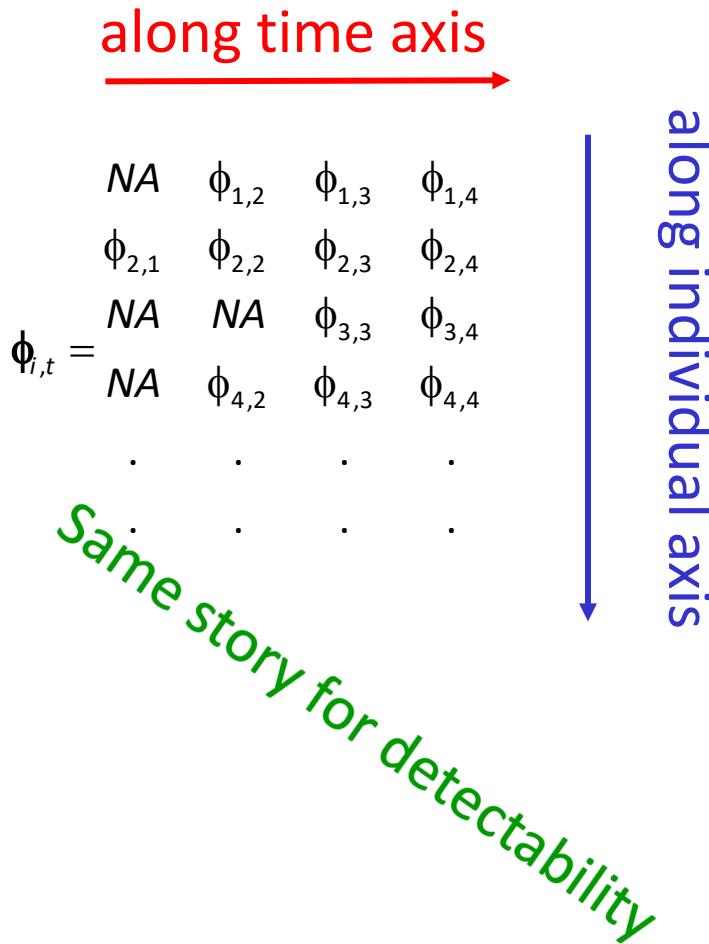
Individual axis:

- groups (fixed, random)
- individual covariates

Interaction of time and individual axes:

- age effect (time since first capture)
- additive effects (group + time)
- cohort effects

Modelling



Time axis:

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

Individual axis:

- groups (fixed, random)
- individual covariates

Interaction of time and individual axes:

- age effect (time since first capture)
- additive effects (group + time)
- cohort effects
- trap-response



A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

$$z_{i,t} : \text{Bern}(z_{i,t-1}\phi)$$

$$y_{i,t} : \text{Bern}(z_{i,t}p)$$

A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

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

$$z_{i,t} : Bern(z_{i,t-1}\phi)$$

$$y_{i,t} : Bern(z_{i,t}p)$$

```
}
```

A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

    # Define latent state at first capture
    z[i,f[i]] <- 1
```

$z_{i,first_i} = 1$

$z_{i,t} : Bern(z_{i,t-1}\phi)$

$y_{i,t} : Bern(z_{i,t}p)$

```
}
```

A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

  # Define latent state at first capture
  z[i,f[i]] <- 1
   $z_{i,first_i} = 1$ 
  for (t in (f[i]+1):n.occasions) {
     $z_{i,t} : Bern(z_{i,t-1}\phi)$ 
     $y_{i,t} : Bern(z_{i,t}p)$ 
  }
  #t
} #i
```

A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

  # Define latent state at first capture
  z[i,f[i]] <- 1
   $z_{i,first_i} = 1$ 

  for (t in (f[i]+1):n.occasions) {
    # State process
    z[i,t] ~ dbern(phi * z[i,t-1])
     $z_{i,t} : Bern(z_{i,t-1}\phi)$ 
     $y_{i,t} : Bern(z_{i,t}p)$ 

  } #t
} #i
```

A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

    # Define latent state at first capture
    z[i,f[i]] <- 1
     $z_{i,first_i} = 1$ 

    for (t in (f[i]+1):n.occasions) {
        # State process
        z[i,t] ~ dbern(phi * z[i,t-1])
         $z_{i,t} : Bern(z_{i,t-1}\phi)$ 

        # Observation process
        y[i,t] ~ dbern(p * z[i,t])
         $y_{i,t} : Bern(z_{i,t}p)$ 
    } #t
} #i
```

A model with constant parameters: $\phi(\cdot)$, $p(\cdot)$

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

  # Define latent state at first capture
  z[i,f[i]] <- 1
  zi,firsti = 1
  for (t in (f[i]+1):n.occasions) {
    # State process
    z[i,t] ~ dbern(phi * z[i,t-1])
    zi,t : Bern(zi,t-1φ)
    yi,t : Bern(zi,tp)
    # Observation process
    y[i,t] ~ dbern(p * z[i,t])
    } #t
  } #i
phi ~ dunif(0,1) # Prior for survival
p ~ dunif(0,1) # Prior for recapture
```

The Cormack-Jolly-Seber model: $\phi(t)$, $p(t)$

$$z_{i, \text{first}_i} = 1$$

$$z_{i,t} : \text{Bern}(z_{i,t-1} \phi_{t-1})$$

$$y_{i,t} : \text{Bern}(z_{i,t} p_t)$$

The Cormack-Jolly-Seber model: $\phi(t)$, $p(t)$

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

  # Define latent state at first capture
  z[i,f[i]] <- 1

  for (t in (f[i]+1):n.occasions) {
    # State process
    z[i,t] ~ dbern(phi[t-1] * z[i,t-1])

    # Observation process
    y[i,t] ~ dbern(p[t-1] * z[i,t])
  } #t
} #i
```

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

$$z_{i,t} : Bern(z_{i,t-1}\phi_{t-1})$$

$$y_{i,t} : Bern(z_{i,t}p_t)$$

The Cormack-Jolly-Seber model: $\phi(t)$, $p(t)$

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

  # Define latent state at first capture
  z[i,f[i]] <- 1

  for (t in (f[i]+1):n.occasions) {
    # State process
    z[i,t] ~ dbern(phi[t-1] * z[i,t-1])

    # Observation process
    y[i,t] ~ dbern(p[t-1] * z[i,t])
  } #t
} #i
for (t in 1:n.occasions) {
  phi[t] ~ dunif(0,1) # Prior for survival
  p[t] ~ dunif(0,1)} # Prior for recapture
```

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

$$z_{i,t} : Bern(z_{i,t-1}\phi_{t-1})$$

$$y_{i,t} : Bern(z_{i,t}p_t)$$

A general structure with individual & time dependence

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

    # Define latent state at first capture
    z[i,f[i]] <- 1

    for (t in (f[i]+1):n.occasions) {
        # State process
        z[i,t] ~ dbern(phi[i,t-1] * z[i,t-1])

        # Observation process
        y[i,t] ~ dbern(p[i,t-1] * z[i,t])
    } #t
} #i
```

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

$$z_{i,t} : Bern(z_{i,t-1}\phi_{i,t-1})$$

$$y_{i,t} : Bern(z_{i,t}p_{i,t})$$

Build simpler models from this general structure



Note: Same idea in, e.g., MARK, unmarked and E-SURGE

Same likelihood structure

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

  # Define latent state at first capture
  z[i,f[i]] <- 1

  for (t in (f[i]+1):n.occasions){
    # State process
    z[i,t] ~ dbern(phi[i,t-1] * z[i,t-1])

    # Observation process
    y[i,t] ~ dbern(p[i,t-1] * z[i,t])
  } #t
} #i
```

Apply constraints on parameters

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

  # Define latent state at first capture
  z[i,f[i]] <- 1

  for (t in (f[i]+1):n.occasions){
    # State process
    z[i,t] ~ dbern(phi[i,t-1] * z[i,t-1])

    # Observation process
    y[i,t] ~ dbern(p[i,t-1] * z[i,t])
  } #t
} #i
```

Example for $\phi(\cdot)$, $p(\cdot)$:

```
# Priors and constraints
for (i in 1:nind) {
  for (t in 1:(n.occasions-1)) {
    phi[i,t] <- mean.phi
    p[i,t] <- mean.p
  } #t
} #i
```

Apply constraints on parameters

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

  # Define latent state at first capture
  z[i,f[i]] <- 1

  for (t in (f[i]+1):n.occasions){
    # State process
    z[i,t] ~ dbern(phi[i,t-1] * z[i,t-1])

    # Observation process
    y[i,t] ~ dbern(p[i,t-1] * z[i,t])
  } #t
} #i
```

Example for $\phi(\cdot)$, $p(\cdot)$:

```
# Priors and constraints
for (i in 1:nind){
  for (t in 1:(n.occasions-1)) {
    phi[i,t] <- mean.phi
    p[i,t] <- mean.p
  } #t
} #i

mean.phi ~ dunif(0,1) # Prior mean surv
mean.p ~ dunif(0,1)   # Prior mean recap
```

Live demo



Exercise 1

What does *survival* actually mean in capture-recapture ?



- Survival refers to the study area

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- Consequently, apparent survival < true survival unless study area fidelity = 1

Note: Combine with recoveries (Lebreton et al. 1999), or go spatial (Gilroy et al. 2012, Schaub & Royle 2014)

Capture-recapture models rely on assumptions



- Design
 - No mark lost
 - Identity of individuals recorded without error (*no false positives*)
 - Captured individuals are a random sample

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Note: Use goodness-of-fit tests to assess assumptions (Pradel et al. 2005)

Embrace heterogeneity!

Embrace heterogeneity!

Temporal heterogeneity

Individual heterogeneity

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Temporal heterogeneity

- Fixed effect $\text{phi}[i, t] \leftarrow \text{alpha}[t]$

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Temporal heterogeneity

- Fixed effect `phi[i,t] <- alpha[t]`
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`epsilon[t] ~ dnorm(0, tau)`

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- Sex effect `logit(phi[i,t]) <- alpha[group[i]]`
with `group[i] = 1 if i is female, group[i] = 2 otherwise`

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- Age effect: `logit(phi[i,t]) <- alpha[age[i,t]]`
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Both temporal and individual heterogeneity

- Age effect: `logit(phi[i,t]) <- alpha[age[i,t]]`
with `age[i,t] = 1` if individual i is young, `age[i,t] = 2` if adult

Note: In capture-recapture, age corresponds to time elapsed since first encounter. Thus, age in capture-recapture models is true age only for individuals marked at birth.

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Both temporal and individual heterogeneity

- Age effect: `logit(phi[i,t]) <- alpha[age[i,t]]`
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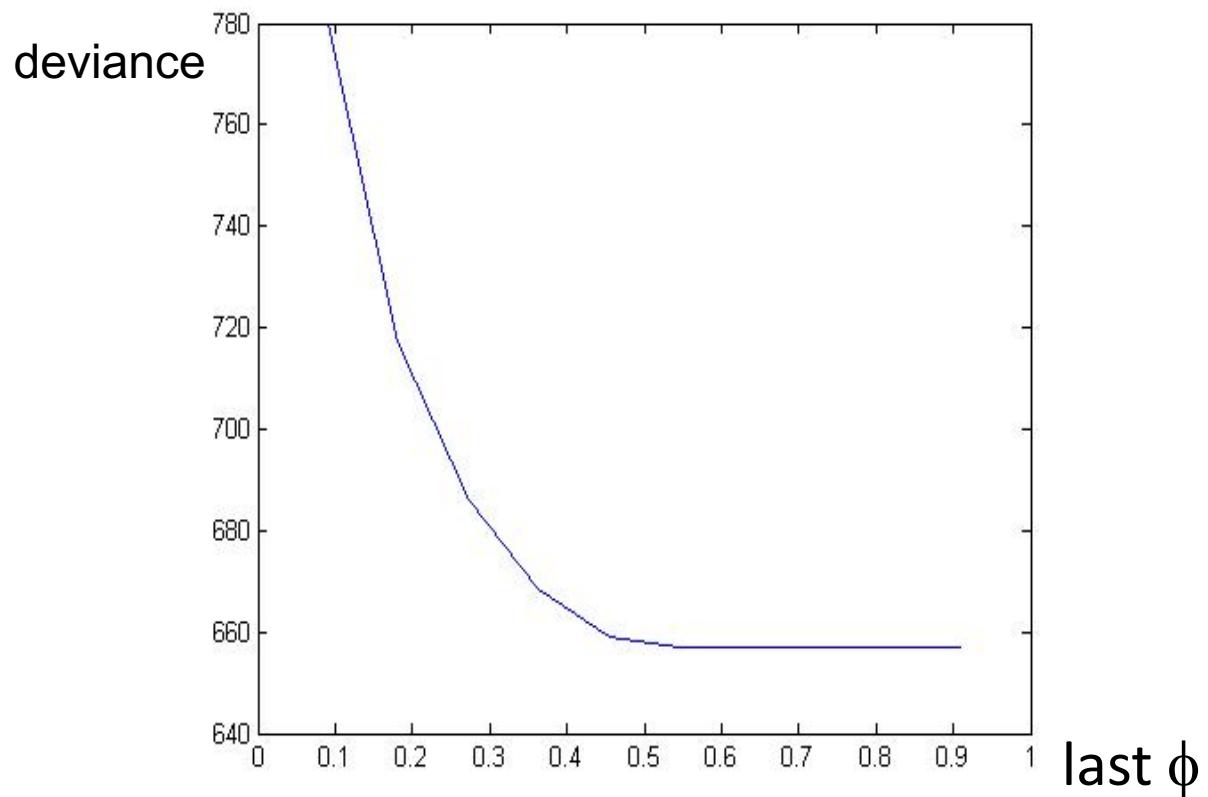
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- Covariate `logit(phi[i,t]) <- beta[1] + beta[2] * x[i,t]`

Note: We need to know the value of covariate at every occasion, even when an individual is not recaptured. If it is not the case, we have missing value(s). The Bayesian framework is useful here, as we can consider a model for the covariate, and fill in the gaps.

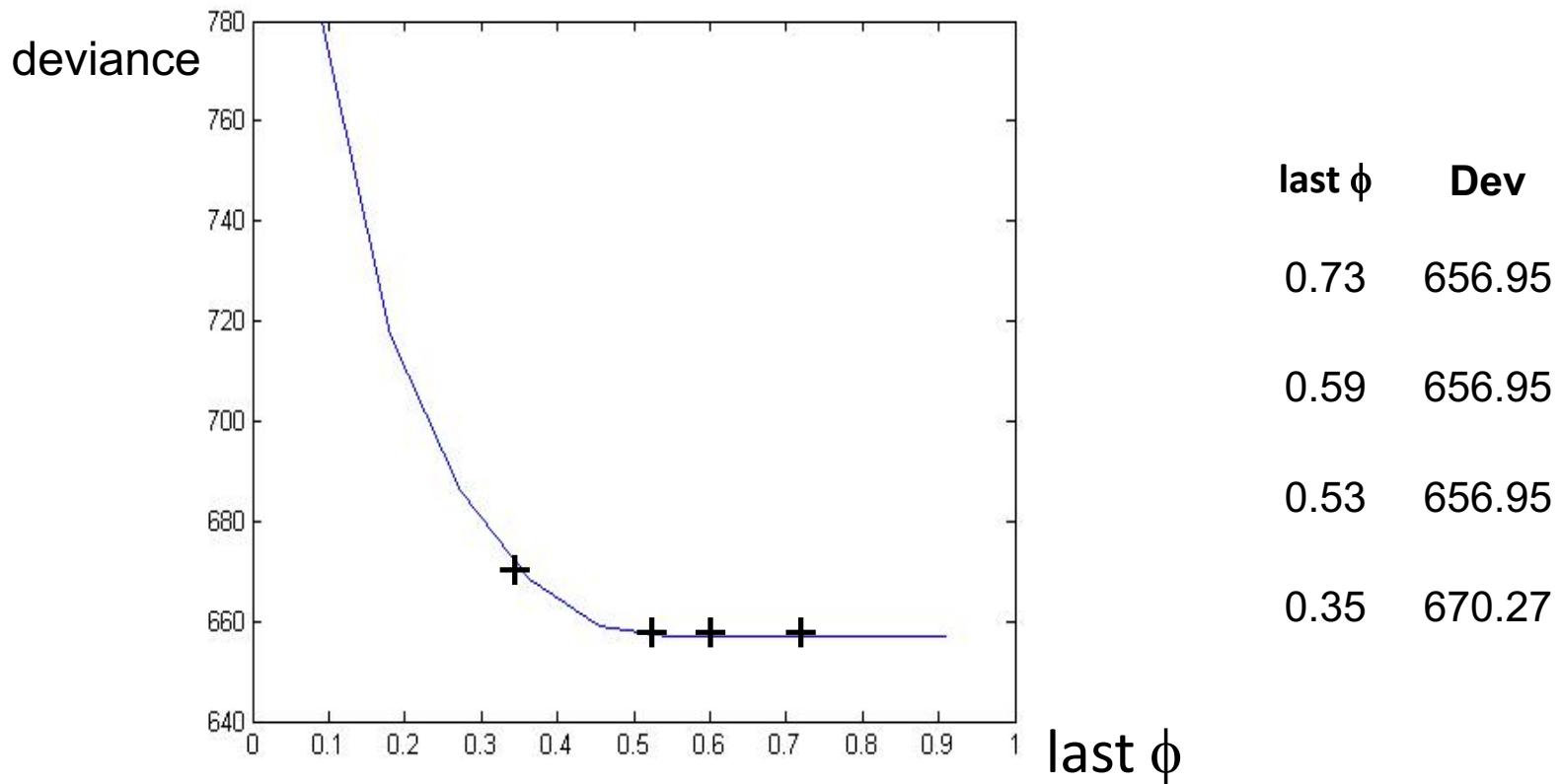
Live demo



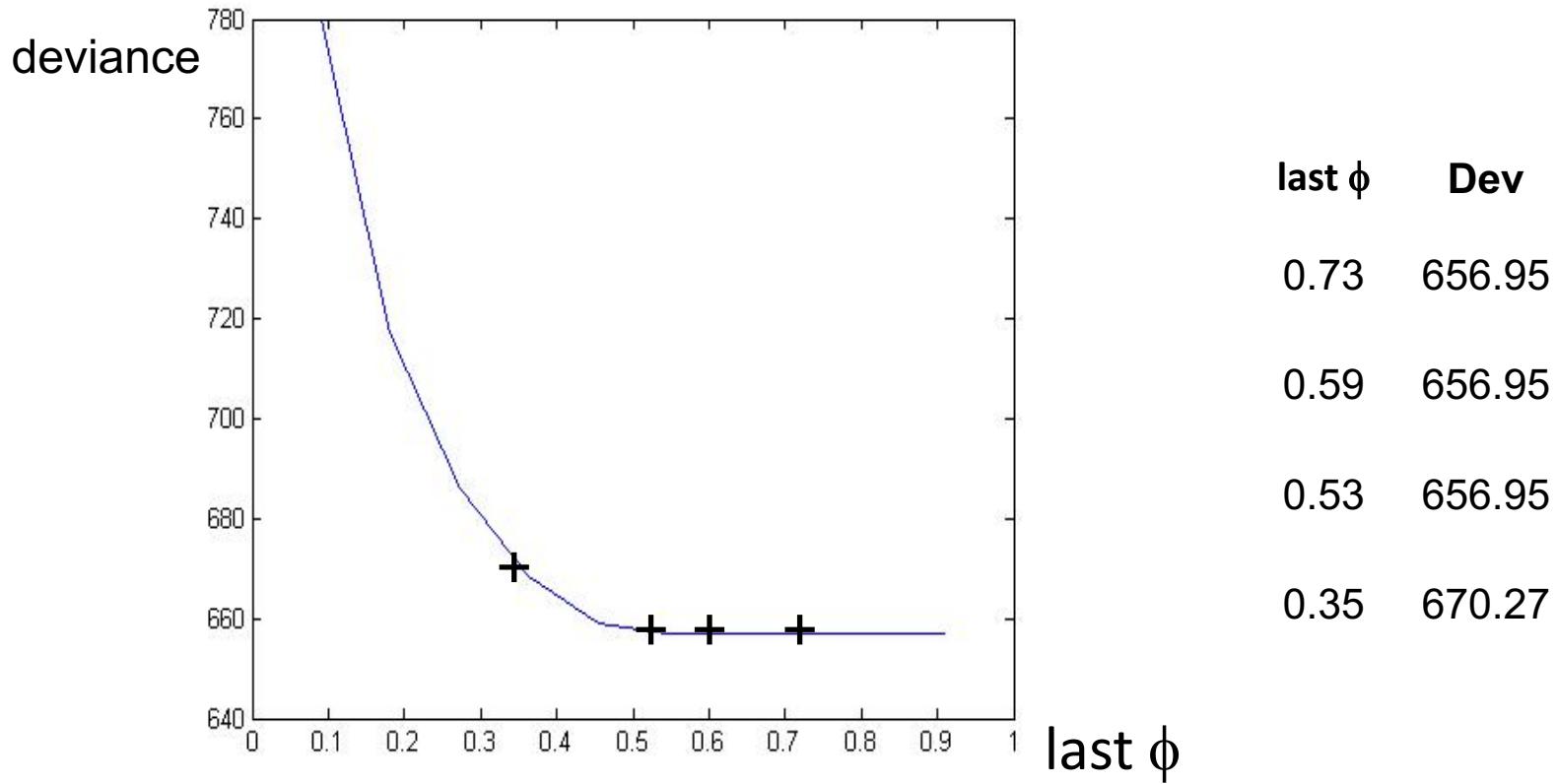
Parameter identifiability: CJS model example



Parameter identifiability: CJS model example



Parameter identifiability: CJS model example



Last survival and recapture probabilities cannot be estimated separately.

Parameter identifiability

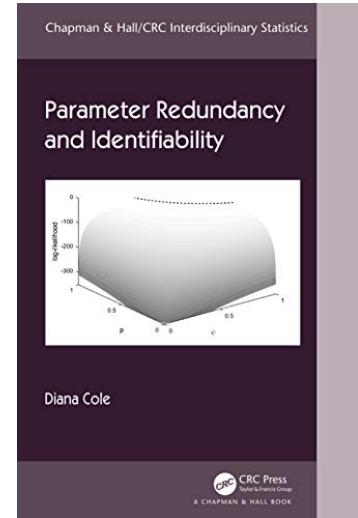
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 - Feature of the model

Parameter identifiability

- **Intrinsic** non-identifiability
 - Likelihood can be expressed by a smaller number of parameters
 - Feature of the model
- **Extrinsic** non-identifiability
 - Model structure is fine
 - But lack of data makes a parameter non-estimable
 - Feature of the data

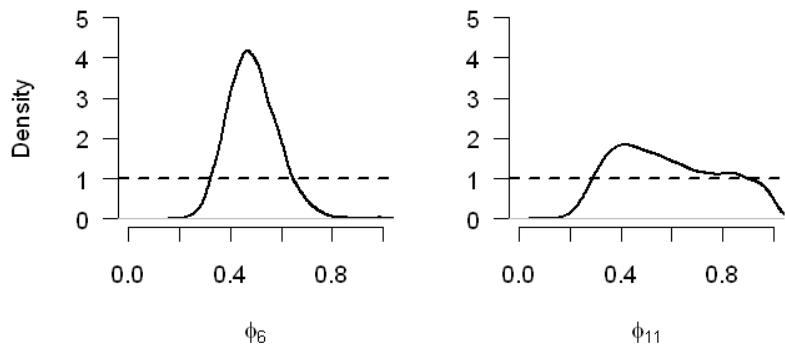
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Parameter identifiability in a Bayesian framework?

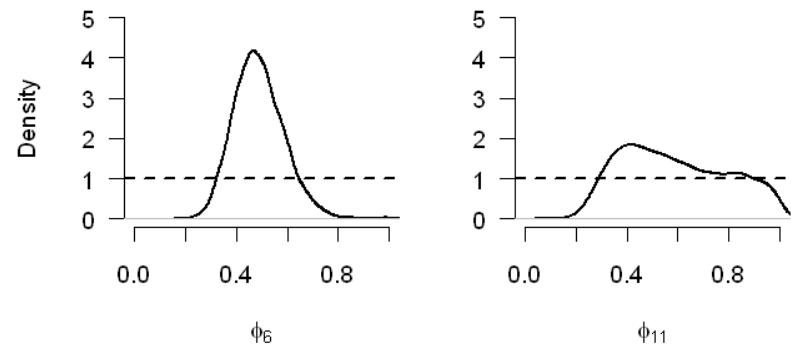
Parameter identifiability in a Bayesian framework?



CJS model (ϕ_t, p_t) with 12 years
and uniform priors

Parameter identifiability in a Bayesian framework?

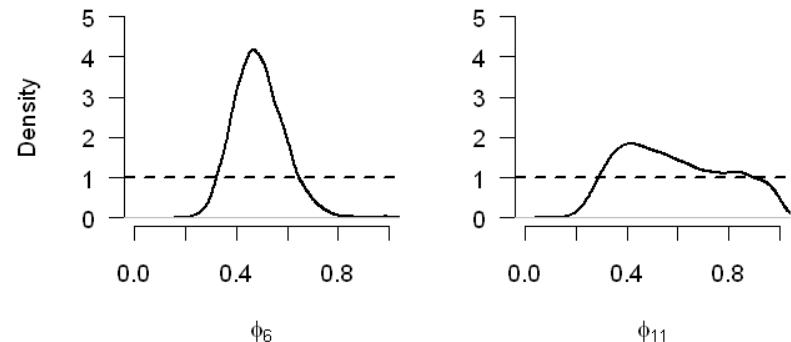
- Compare prior and posterior



CJS model (ϕ_t, p_t) with 12 years
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Parameter identifiability in a Bayesian framework?

- Compare prior and posterior
- Prior knowledge can be used to make parameters identifiable



CJS model (ϕ_t, p_t) with 12 years
and uniform priors

Exercise 2

Bonus

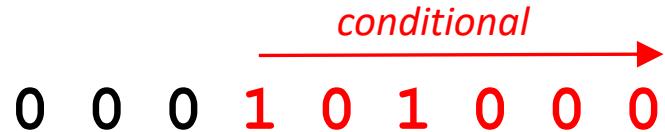
Jolly-Seber model

- The CJS model is *conditional* on first capture

0 0 0 1 0 1 0 0 0

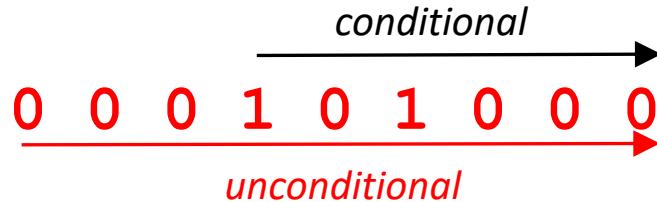
Jolly-Seber model

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Jolly-Seber model

- The CJS model is *conditional* on first capture



- The Jolly-Seber model is *unconditional*
- Estimation of *recruitment* and *population size* is possible
- Requires an additional assumption (capture = recapture)
- See chapter 10 in BPA book

Multinomial model for capture-recapture 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	-
2	-	-	-	-
3	-	-	-	-

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

Multinomial model for capture-recapture data

Cell probabilities of the m-array:

	Recapture occ.					
Rel.	2	3	4		Never	
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:

$$\mathbf{m}_t : \text{Multinomial}(\mathbf{q}_t, R_t)$$

where

$\mathbf{m}_t = t^{\text{th}}$ row of m-array

\mathbf{q}_t = cell probabilities of the m-array for release occasion t

R_t = number of released individuals at occasion t

Bayesian GOF: Posterior predictive check (PPC)

- Several Bayesian GOF are possible (reviewed by Conn *et al.* 2018)
- Here we use a general and very common Bayesian model-checking procedure, the **posterior predictive check**
- In a nutshell:
 - Quantify how different the **observed** data is compared to what we **expect** from the estimated parameters [measure of **discrepancy**]
 - To assess how “bad” or “good” that difference is, compare to the same measure of discrepancy obtained for ideal data **simulated** from the estimated parameters
 - This double comparison is done for each sample of the MCMC chains
- Generally straightforward to implement in BUGS or in R after the analysis (from the MCMC chains)

Bayesian GOF: Posterior predictive check (PPC)

Basic algorithm:

At each MCMC iteration t :

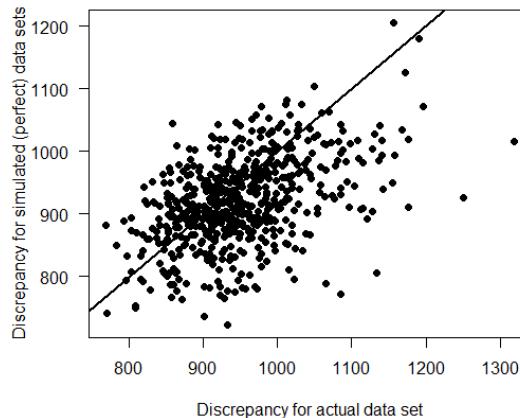
- 1) Calculate a **discrepancy statistic** $D(x; e_t)$ to measure some “distance” between the **observed data** x and the corresponding expected values, e_t at that iteration (based on the MCMC chain values of the parameters)
- 2) Generate a new data set x_t from the fitted model (using the MCMC chain value of the parameters)
- 3) Calculate a discrepancy statistic $D(x_t; e_t)$ to measure the “distance” between the **simulated data** x_t and the corresponding expected values, e_t at that iteration

Bayesian GOF: Posterior predictive check (PPC)

Then, use the values of $D(x; e_t)$ and $D(x_t; e_t)$ to check the fit...

1) ...graphically: scatterplot of $D(x; e_t)$ and $D(x_t; e_t)$

No evidence of lack of fit
if $\sim\frac{1}{2}$ points above and
 $\sim\frac{1}{2}$ below a 1:1 line



2) ...numerically by calculating a **Bayesian p-value** = proportion of times that $D(x; e_t) < D(x_t; e_t)$

→ close to 0.5: good fit

→ close to 0 or 1: suggests doubtful fit

Bayesian GOF: Posterior predictive check (PPC)

On what response to define *observed* and *expected* values?

- Not on binary responses (i.e. detection histories) themselves
- Use some aggregating: **m-array in CR data**

What measure of discrepancy?

- Different options, e.g.
 - Pearson chi-squared statistic
 - Freeman-Tukey statistic
 - Different measures sensible to different kinds of lack of fit; resulting P-values may differ substantially
 - Normally assess some global measure of lack of fit; can also assess particular features of the model (e.g. extreme values)
-
- The diagram consists of two arrows originating from the text 'Pearson chi-squared statistic' and 'Freeman-Tukey statistic' respectively, and pointing towards the right. To the right of the first arrow is the formula for the Pearson chi-squared statistic: $D(x_t, e_t) = \sum_i \frac{(x_i - e_i)^2}{e_i}$. To the right of the second arrow is the formula for the Freeman-Tukey statistic: $D(x_t, e_t) = \sum_i (\sqrt{x_i} - \sqrt{e_i})^2$.

Bayesian GOF: Posterior predictive check (PPC)

- Implicitly depend on priors
 - Bayesian P-values have been criticised
 - They use data twice:
simulate data; compare them to these data
 - Not clear what values represent a good fit
- Descriptive only! (not for model selection)