

# Capture-recapture experiments

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## Inference in finite populations

Problem of estimating an unknown population size,  $N$ , based on partial observation of this population: domain of *survey sampling*

### Warning

We do not cover the official Statistics/stratified type of survey based on a preliminary knowledge of the structure of the population

## Numerous applications

- *Biology & Ecology* for estimating the size of herds, of fish or whale populations, etc.
- *Sociology & Demography* for estimating the size of populations at risk, including homeless people, prostitutes, illegal migrants, drug addicts, etc.
- *official Statistics* in the U.S. and French census undercount procedures
- *Economics & Finance* in credit scoring, defaulting companies, etc.,
- *Fraud detection* phone, credit card, etc.
- *Document authentication* historical documents, forgery, etc.,
- *Software debugging*

## Setup

Size  $N$  of the whole population is unknown but samples (with fixed or random sizes) can be extracted from the population.

## The binomial capture model

Simplest model of all: joint capture of  $n^+$  individuals from a population of size  $N$ .

Population size  $N \in \mathbb{N}^*$  is the parameter of interest, but there exists a nuisance parameter, the probability  $p \in [0, 1]$  of capture [under assumption of independent captures]

Sampling model

$$n^+ \sim \mathcal{B}(N, p)$$

and corresponding likelihood

$$\ell(N, p | n^+) = \binom{N}{n^+} p^{n^+} (1 - p)^{N - n^+} \mathbb{I}_{N \geq n^+}.$$

## Bayesian inference (1)

Under vague prior

$$\pi(N, p) \propto N^{-1} \mathbb{I}_{\mathbb{N}^*}(N) \mathbb{I}_{[0,1]}(p),$$

posterior distribution of  $N$  is

$$\begin{aligned} \pi(N|n^+) &\propto \frac{N!}{(N-n^+)!} N^{-1} \mathbb{I}_{N \geq n^+} \mathbb{I}_{\mathbb{N}^*}(N) \int_0^1 p^{n^+} (1-p)^{N-n^+} dp \\ &\propto \frac{(N-1)!}{(N-n^+)!} \frac{(N-n^+)!}{(N+1)!} \mathbb{I}_{N \geq n^+ \vee 1} \\ &= \frac{1}{N(N+1)} \mathbb{I}_{N \geq n^+ \vee 1}. \end{aligned}$$

where  $n^+ \vee 1 = \max(n^+, 1)$

## Bayesian inference (2)

If we use the uniform prior

$$\pi(N, p) \propto \mathbb{I}_{\{1, \dots, S\}}(N) \mathbb{I}_{[0, 1]}(p),$$

the posterior distribution of  $N$  is

$$\pi(N | n^+) \propto \frac{1}{N + 1} \mathbb{I}_{\{n^+ + 1, \dots, S\}}(N).$$

## Capture-recapture data

### European dippers

Birds closely dependent on streams, feeding on underwater invertebrates

Capture-recapture data on dippers over years 1981–1987 in 3 zone of 200 km<sup>2</sup> in eastern France with markings and recaptures of breeding adults each year, during the breeding period from early March to early June.



## eurodip

Each row of 7 digits corresponds to a capture-recapture story: 0 stands for absence of capture and, else, 1, 2 or 3 represents the zone of capture.

E.g.

1 0 0 0 0 0 0

1 3 0 0 0 0 0

0 2 2 2 1 2 2

means: first dipper only captured the first year [in zone 1], second dipper captured in years 1981–1982 and moved from zone 1 to zone 3 between those years, third dipper captured in years 1982–1987 in zone 2

## The two-stage capture-recapture experiment

Extension to the above with two capture periods plus a marking stage:

- ①  $n_1$  individuals from a population of size  $N$  captured [*sampled without replacement*]
- ② captured individuals marked and released
- ③  $n_2$  individuals captured during second identical sampling experiment
- ④  $m_2$  individuals out of the  $n_2$ 's bear the identification mark [*captured twice*]

## The two-stage capture-recapture model

For *closed populations* [fixed population size  $N$  throughout experiment, constant capture probability  $p$  for all individuals, and independence between individuals/captures], binomial models:

$$n_1 \sim \mathcal{B}(N, p), \quad m_2 | n_1 \sim \mathcal{B}(n_1, p) \quad \text{and}$$

$$n_2 - m_2 | n_1, m_2 \sim \mathcal{B}(N - n_1, p).$$

## The two-stage capture-recapture likelihood

Corresponding likelihood  $\ell(N, p | n_1, n_2, m_2)$

$$\begin{aligned}
 & \binom{N - n_1}{n_2 - m_2} p^{n_2 - m_2} (1 - p)^{N - n_1 - n_2 + m_2} \mathbb{I}_{\{0, \dots, N - n_1\}}(n_2 - m_2) \\
 & \quad \times \binom{n_1}{m_2} p^{m_2} (1 - p)^{n_1 - m_2} \binom{N}{n_1} p^{n_1} (1 - p)^{N - n_1} \mathbb{I}_{\{0, \dots, N\}}(n_1) \\
 & \propto \frac{N!}{(N - n_1 - n_2 + m_2)!} p^{n_1 + n_2} (1 - p)^{2N - n_1 - n_2} \mathbb{I}_{N \geq n^+} \\
 & \propto \binom{N}{n^+} p^{n^c} (1 - p)^{2N - n^c} \mathbb{I}_{N \geq n^+}
 \end{aligned}$$

where  $n^c = n_1 + n_2$  and  $n^+ = n_1 + (n_2 - m_2)$  are total number of captures/captured individuals over both periods

## Bayesian inference (1)

Under prior  $\pi(N, p) = \pi(N)\pi(p)$  where  $\pi(p)$  is  $\mathcal{U}([0, 1])$ , conditional posterior distribution on  $p$  is

$$\pi(p|N, n_1, n_2, m_2) = \pi(p|N, n^c) \propto p^{n^c} (1-p)^{2N-n^c},$$

that is,

$$p|N, n^c \sim \mathcal{Be}(n^c + 1, 2N - n^c + 1).$$

Marginal posterior distribution of  $N$  more complicated. If  $\pi(N) = \mathbb{I}_{\mathbb{N}^*}(N)$ ,

$$\pi(N|n_1, n_2, m_2) \propto \binom{N}{n^+} B(n^c + 1, 2N - n^c + 1) \mathbb{I}_{N \geq n^+ + 1}$$

*[Beta-Pascal distribution]*

## Bayesian inference (2)

Same problem if  $\pi(N) = N^{-1} \mathbb{I}_{\mathbb{N}^*}(N)$ .

### Computations

Since  $N \in \mathbb{N}$ , always possible to approximate the missing normalizing factor in  $\pi(N|n_1, n_2, m_2)$  by summing in  $N$ . Approximation errors become a problem when  $N$  and  $n^+$  are large.

Under proper uniform prior,

$$\pi(N) \propto \mathbb{I}_{\{1, \dots, S\}}(N),$$

posterior distribution of  $N$  proportional to

$$\pi(N|n^+) \propto \binom{N}{n^+} \frac{\Gamma(2N - n^c + 1)}{\Gamma(2N + 2)} \mathbb{I}_{\{n^+ + v_1, \dots, S\}}(N).$$

and can be computed with no approximation error.

## The Darroch model

Simpler version of the above: conditional on both samples sizes  $n_1$  and  $n_2$ ,

$$m_2 | n_1, n_2 \sim \mathcal{H}(N, n_2, n_1/N).$$

Under uniform prior on  $N \sim \mathcal{U}(\{1, \dots, S\})$ , posterior distribution of  $N$

$$\pi(N | m_2) \propto \binom{n_1}{m_2} \binom{N - n_1}{n_2 - m_2} / \binom{N}{n_2} \mathbb{I}_{\{n_1 + v_1, \dots, S\}}(N)$$

and posterior expectations computed numerically by simple summations.

## eurodip

For the two first years and  $S = 400$ , posterior distribution of  $N$  for the Darroch model given by

$$\pi(N|m_2) \propto (n-n_1)!(N-n_2)!/\{(n-n_1-n_2+m_2)!N!\} \mathbb{I}_{\{71,\dots,400\}}(N),$$

with inverse normalization factor

$$\sum_{k=71}^{400} (k-n_1)!(k-n_2)!/\{(k-n_1-n_2+m_2)!k!\}.$$

Influence of prior hyperparameter  $S$  (for  $m_2 = 11$ ):

$S$	100	150	200	250	300	350	400	450	500
$\mathbb{E}[N m_2]$	95	125	141	148	151	151	152	152	152

## Gibbs sampler for 2-stage capture-recapture

If  $n^+ > 0$ , both conditional posterior distributions are standard, since

$$\begin{aligned} p|n^c, N &\sim \mathcal{Be}(n^c + 1, 2N - n^c + 1) \\ N - n^+|n^+, p &\sim \mathcal{Neg}(n^+, 1 - (1 - p)^2). \end{aligned}$$

Therefore, joint distribution of  $(N, p)$  can be approximated by a Gibbs sampler

## $T$ -stage capture-recapture model

Further extension to the two-stage capture-recapture model: series of  $T$  consecutive captures.

$n_t$  individuals captured at period  $1 \leq t \leq T$ , and  $m_t$  recaptured individuals (with the convention that  $m_1 = 0$ )

$$n_1 \sim \mathcal{B}(N, p)$$

and, conditional on earlier captures/recaptures ( $2 \leq j \leq T$ ),

$$m_j \sim \mathcal{B} \left( \sum_{t=1}^{j-1} (n_t - m_t), p \right) \quad \text{and}$$

$$n_j - m_j \sim \mathcal{B} \left( N - \sum_{t=1}^{j-1} (n_t - m_t), p \right).$$

## $T$ -stage capture-recapture likelihood

Likelihood  $\ell(N, p | n_1, n_2, m_2, \dots, n_T, m_T)$  given by

$$\begin{aligned} & \binom{N}{n_1} p^{n_1} (1-p)^{N-n_1} \prod_{j=2}^T \left[ \binom{N - \sum_{t=1}^{j-1} (n_t - m_t)}{n_j - m_j} p^{n_j - m_j} \right. \\ & \quad \times (1-p)^{N - \sum_{t=1}^j (n_t - m_t)} \binom{\sum_{t=1}^{j-1} (n_t - m_t)}{m_j} \\ & \quad \left. \times p^{m_j} (1-p)^{\sum_{t=1}^{j-1} (n_t - m_t) - m_j} \right]. \end{aligned}$$

## Sufficient statistics

Simplifies into

$$\ell(N, p | n_1, n_2, m_2, \dots, n_T, m_T) \propto \frac{N!}{(N - n^+)!} p^{n^c} (1-p)^{TN - n^c} \mathbb{I}_{N \geq n^+}$$

with the sufficient statistics

$$n^+ = \sum_{t=1}^T (n_t - m_t) \quad \text{and} \quad n^c = \sum_{t=1}^T n_t,$$

total number of captured individuals/captures over the  $T$  periods

## Bayesian inference (1)

Under noninformative prior  $\pi(N, p) = 1/N$ , joint posterior

$$\pi(N, p | n^+, n^c) \propto \frac{(N-1)!}{(N-n^+)!} p^{n^c} (1-p)^{TN-n^c} \mathbb{I}_{N \geq n^+ + 1}.$$

leads to conditional posterior

$$p | N, n^+, n^c \sim \mathcal{B}e(n^c + 1, TN - n^c + 1)$$

and marginal posterior

$$\pi(N | n^+, n^c) \propto \frac{(N-1)!}{(N-n^+)!} \frac{(TN - n^c)!}{(TN + 1)!} \mathbb{I}_{N \geq n^+ + 1}$$

which is computable [*under previous provisions*].

Alternative Gibbs sampler also available.

## Bayesian inference (2)

Under prior  $N \sim \mathcal{U}(\{1, \dots, S\})$  and  $p \sim \mathcal{U}([0, 1])$ ,

$$\pi(N|n^+) \propto \binom{N}{n^+} \frac{(TN - n^c)!}{(TN + 1)!} \mathbb{I}_{\{n^+ \vee 1, \dots, S\}}(N).$$

### eurodip

For the whole set of observations,  $T = 7$ ,  $n^+ = 294$  and  $n^c = 519$ .

For  $S = 400$ , the posterior expectation of  $N$  is equal to 372.89.

For  $S = 2500$ , it is 373.99.

## Computational difficulties

E.g., heterogeneous capture–recapture model where individuals are captured at time  $1 \leq t \leq T$  with probability  $p_t$  with both  $N$  and the  $p_t$ 's are unknown.

Corresponding likelihood

$$\begin{aligned} \ell(N, p_1, \dots, p_T | n_1, n_2, m_2, \dots, n_T, m_T) \\ \propto \frac{N!}{(N - n^+)!} \prod_{t=1}^T p_t^{n_t} (1 - p_t)^{N - n_t}. \end{aligned}$$

## Computational difficulties (cont'd)

Associated prior  $N \sim \mathcal{P}(\lambda)$  and

$$\alpha_t = \log(p_t/1 - p_t) \sim \mathcal{N}(\mu_t, \sigma^2),$$

where the  $\mu_t$ 's and  $\sigma$  are known.

Posterior

$$\begin{aligned} \pi(\alpha_1, \dots, \alpha_T, N | n_1, \dots, n_T) &\propto \frac{N!}{(N - n^+)!} \frac{\lambda^N}{N!} \prod_{t=1}^T (1 + e^{\alpha_t})^{-N} \\ &\quad \times \prod_{t=1}^T \exp \left\{ \alpha_t n_t - \frac{1}{2\sigma^2} (\alpha_t - \mu_t)^2 \right\}. \end{aligned}$$

much less manageable computationally.

## Open populations

More realistically, population size does not remain fixed over time: probability  $q$  for each individual to leave the population at each time [or between each capture episode]

First occurrence of missing variable model.

Simplified version where only individuals captured during the first experiment are marked and their subsequent recaptures are registered.

## Working example

Three successive capture experiments with

$$n_1 \sim \mathcal{B}(N, p),$$

$$r_1 | n_1 \sim \mathcal{B}(n_1, q),$$

$$c_2 | n_1, r_1 \sim \mathcal{B}(n_1 - r_1, p),$$

$$r_2 | n_1, r_1 \sim \mathcal{B}(n_1 - r_1, q)$$

$$c_3 | n_1, r_1, r_2 \sim \mathcal{B}(n_1 - r_1 - r_2, p)$$

where only  $n_1$ ,  $c_2$  and  $c_3$  are observed.

Variables  $r_1$  and  $r_2$  not available and therefore part of unknowns like parameters  $N$ ,  $p$  and  $q$ .

## Bayesian inference

### Likelihood

$$\binom{N}{n_1} p^{n_1} (1-p)^{N-n_1} \binom{n_1}{r_1} q^{r_1} (1-q)^{n_1-r_1} \binom{n_1-r_1}{c_2} p^{c_2} (1-p)^{n_1-r_1-c_2} \\ \binom{n_1-r_1}{r_2} q^{r_2} (1-q)^{n_1-r_1-r_2} \binom{n_1-r_1-r_2}{c_3} p^{c_3} (1-p)^{n_1-r_1-r_2-c_3}$$

and prior

$$\pi(N, p, q) = N^{-1} \mathbb{I}_{[0,1]}(p) \mathbb{I}_{[0,1]}(q)$$

## Full conditionals for Gibbs sampling

$$\pi(p|N, q, \mathcal{D}^*) \propto p^{n_+} (1-p)^{u_+}$$

$$\pi(q|N, p, \mathcal{D}^*) \propto q^{c_1+c_2} (1-q)^{2n_1-2r_1-r_2}$$

$$\pi(N|p, q, \mathcal{D}^*) \propto \frac{(N-1)!}{(N-n_1)!} (1-p)^N \mathbb{I}_{N \geq n_1}$$

$$\pi(r_1|p, q, n_1, c_2, c_3, r_2) \propto \frac{(n_1 - r_1)! q^{r_1} (1-q)^{-2r_1} (1-p)^{-2r_1}}{r_1! (n_1 - r_1 - r_2 - c_3)! (n_1 - c_2 - r_1)!}$$

$$\pi(r_2|p, q, n_1, c_2, c_3, r_1) \propto \frac{q^{r_2} [(1-p)(1-q)]^{-r_2}}{r_2! (n_1 - r_1 - r_2 - c_3)!}$$

where

$$\mathcal{D}^* = (n_1, c_2, c_3, r_1, r_2)$$

$$u_1 = N - n_1, u_2 = n_1 - r_1 - c_2, u_3 = n_1 - r_1 - r_2 - c_3$$

$$n_+ = n_1 + c_2 + c_3, u_+ = u_1 + u_2 + u_3$$

## Full conditionals (2)

Therefore,

$$p|N, q, \mathcal{D}^* \sim \text{Be}(n_+ + 1, u_+ + 1)$$

$$q|N, p, \mathcal{D}^* \sim \text{Be}(r_1 + r_2 + 1, 2n_1 - 2r_1 - r_2 + 1)$$

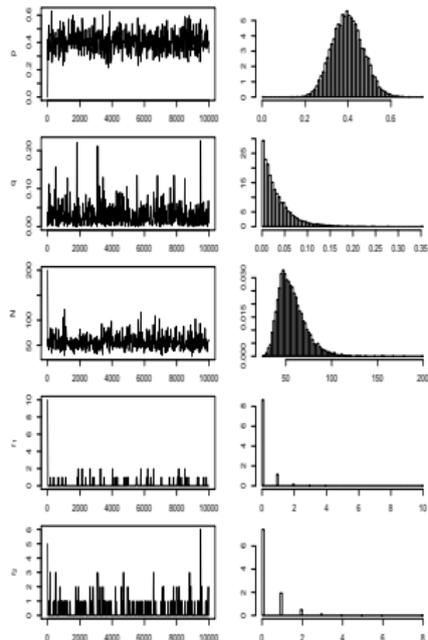
$$N - n_1|p, q, \mathcal{D}^* \sim \text{Neg}(n_1, p)$$

$$r_2|p, q, n_1, c_2, c_3, r_1 \sim \mathcal{B}\left(n_1 - r_1 - c_3, \frac{q}{1 + (1 - q)(1 - p)}\right)$$

$r_1$  has a less conventional distribution, but, since  $n_1$  not extremely large, possible to compute the probability that  $r_1$  is equal to one of the values in  $\{0, 1, \dots, \min(n_1 - r_2 - c_3, n_1 - c_2)\}$ .

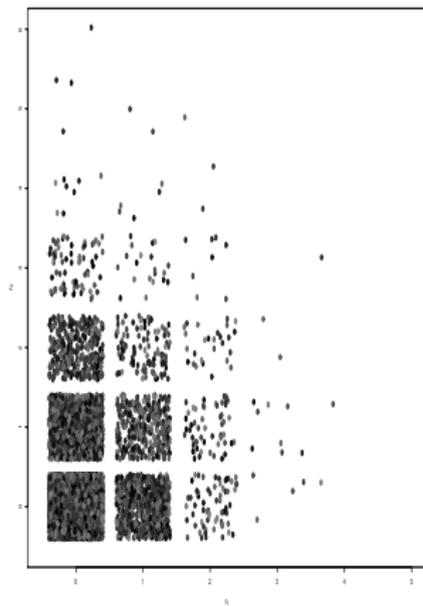
## eurodip

$n_1 = 22$ ,  $c_2 = 11$  and  $c_3 = 6$   
MCMC approximations to the  
posterior expectations of  $N$  and  
 $p$  equal to 57 and 0.40



## eurodip

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posterior expectations of  $N$  and  
 $p$  equal to 57 and 0.40



## Accept-Reject methods

- Many distributions from which it is difficult, or even impossible, to directly simulate.
- Technique that only require us to know the functional form of the target  $\pi$  of interest up to a multiplicative constant.
- Key to this method is to use a proposal density  $g$  [as in *Metropolis-Hastings*]

## Principle

Given a target density  $\pi$ , find a density  $g$  and a constant  $M$  such that

$$\pi(x) \leq Mg(x)$$

on the support of  $\pi$ .

Accept-Reject algorithm is then

- 1 Generate  $X \sim g$ ,  $U \sim \mathcal{U}_{[0,1]}$  ;
- 2 Accept  $Y = X$  if  $U \leq \frac{f(X)}{Mg(X)}$  ;
- 3 Return to 1. otherwise.

## Validation of Accept-Reject

This algorithm produces a variable  $Y$  distributed according to  $f$

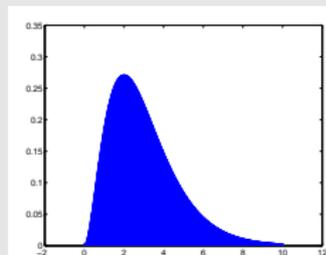
Fundamental theorem of simulation

Simulating

$$X \sim f(x)$$

is equivalent to simulating

$$(X, U) \sim \mathcal{U}\{(x, u) : 0 < u < \pi(x)\}$$



## Two interesting properties:

- First, Accept-Reject provides a generic method to simulate from any density  $\pi$  that is known *up to a multiplicative factor*. Particularly important for Bayesian calculations since

$$\pi(\theta|x) \propto \pi(\theta) f(x|\theta) .$$

is specified up to a normalizing constant

- Second, the probability of acceptance in the algorithm is  $1/M$ , e.g., expected number of trials until a variable is accepted is  $M$

## Application to the open population model

Since full conditional distribution of  $r_1$  non-standard, rather than using exhaustive enumeration of all probabilities  $\mathbb{P}(m_1 = k) = \pi(k)$  and then sampling from this distribution, try to use a proposal based on a binomial upper bound.

Take  $g$  equal to the binomial  $\mathcal{B}(n_1, q_1)$  with

$$q_1 = q / (1 - q)^2 (1 - p)^2$$

## Proposal bound

$\pi(k)/g(k)$  proportional to

$$\frac{\binom{n_1 - c_2}{k} (1 - q_1)^k \binom{n_1 - k}{r_2 + c_3}}{\binom{n_1}{k}} = \frac{(n_1 - c_2)!}{(r_2 + c_3)! n_1!} \frac{((n_1 - k)!)^2 (1 - q_1)^k}{(n_1 - c_2 - k)! (n_1 - r_2 - c_3 - k)!}$$

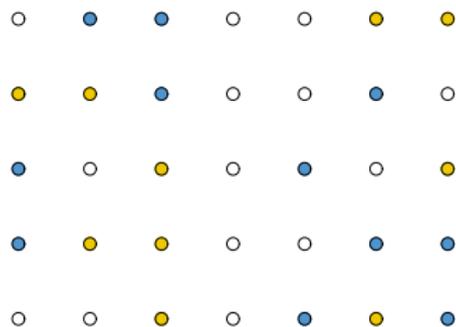
decreasing in  $k$ , therefore bounded by

$$\frac{(n_1 - c_2)!}{(r_2 + c_3)!} \frac{n_1!}{(n_1 - c_2)! (n_1 - r_2 - c_3)!} = \binom{n_1}{r_2 + c_3}.$$

- ⚡ This is *not* the constant  $M$  because of unnormalised densities [ $M$  may also depend on  $q_1$ ]. Therefore the average acceptance rate is undetermined and requires an extra Monte Carlo experiment

## Arnason-Schwarz Model

Representation of a capture recapture experiment as a collection of individual histories: for each individual captured at least once, individual characteristics of interest (location, weight, social status, &tc.) registered at each capture.



Possibility that individuals vanish from the *[open]* population between two capture experiments.

## Parameters of interest

Study the movements of individuals between zones/strata rather than estimating population size.

Two types of variables associated with each individual  $i = 1, \dots, n$

- 1 a variable for its location [*partly observed*],

$$\mathbf{z}_i = (z_{(i,t)}, t = 1, \dots, \tau)$$

where  $\tau$  is the number of capture periods,

- 2 a binary variable for its capture history [*completely observed*],

$$\mathbf{x}_i = (x_{(i,t)}, t = 1, \dots, \tau).$$

## Migration & deaths

$z_{(i,t)} = r$  when individual  $i$  is alive in stratum  $r$  at time  $t$  and denote  $z_{(i,t)} = \dagger$  for the case when it is dead at time  $t$ .

Variable  $\mathbf{z}_i$  sometimes called *migration* process of individual  $i$  as when animals moving between geographical zones.

E.g.,

$$\mathbf{x}_i = 1 \ 1 \ 0 \ 1 \ 1 \ 1 \ 0 \ 0 \ 0 \quad \text{and} \quad \mathbf{z}_i = 1 \ 2 \cdot 3 \ 1 \ 1 \cdot \dots$$

for which a possible completed  $\mathbf{z}_i$  is

$$\mathbf{z}_i = 1 \ 2 \ 1 \ 3 \ 1 \ 1 \ 2 \ \dagger \ \dagger$$

meaning that animal died between 7th and 8th captures

## No tag recovery

We assume that

- $\dagger$  is absorbing
- $z_{(i,t)} = \dagger$  always corresponds to  $x_{(i,t)} = 0$ .
- the  $(\mathbf{x}_i, \mathbf{z}_i)$ 's ( $i = 1, \dots, n$ ) are independent
- each vector  $\mathbf{z}_i$  is a Markov chain on  $\mathcal{R} \cup \{\dagger\}$  with uniform initial probability on  $\mathcal{R}$ .

## Reparameterisation

Parameters of the Arnason-Schwarz model are

- ① capture probabilities

$$p_t(r) = \mathbb{P}(x_{(i,t)} = 1 | z_{(i,t)} = r)$$

- ② transition probabilities

$$q_t(r, s) = \mathbb{P}(z_{(i,t+1)} = s | z_{(i,t)} = r) \quad r \in \mathfrak{K}, s \in \mathfrak{K} \cup \{\dagger\}, \quad q_t(\dagger, \dagger) = 1$$

- ③ *survival* probabilities  $\phi_t(r) = 1 - q_t(r, \dagger)$

- ④ inter-strata *movement* probabilities  $\psi_t(r, s)$  such that

$$q_t(r, s) = \phi_t(r) \times \psi_t(r, s) \quad r \in \mathfrak{K}, s \in \mathfrak{K}.$$

# Modelling

## Likelihood

$$\ell((\mathbf{x}_1, \mathbf{z}_1), \dots, (\mathbf{x}_n, \mathbf{z}_n)) \propto \prod_{i=1}^n \left[ \prod_{t=1}^{\tau} p_t(z_{(i,t)})^{x_{(i,t)}} (1 - p_t(z_{(i,t)}))^{1-x_{(i,t)}} \times \prod_{t=1}^{\tau-1} q_t(z_{(i,t)}, z_{(i,t+1)}) \right].$$

## Conjugate priors

Capture and survival parameters

$$p_t(r) \sim \mathcal{Be}(a_t(r), b_t(r)), \quad \phi_t(r) \sim \mathcal{Be}(\alpha_t(r), \beta_t(r)),$$

where  $a_t(r), \dots$  depend on both time  $t$  and location  $r$ ,

For movement probabilities/Markov transitions

$$\psi_t(r) = (\psi_t(r, s); s \in \mathfrak{K}),$$

$$\psi_t(r) \sim \mathcal{Dir}(\gamma_t(r)),$$

since

$$\sum_{s \in \mathfrak{K}} \psi_t(r, s) = 1,$$

where  $\gamma_t(r) = (\gamma_t(r, s); s \in \mathfrak{K})$ .

## lizards

Capture-recapture experiment on the migrations of lizards between three adjacent zones, with six capture episodes.

Prior information provided by biologists on  $p_t$  (which are assumed to be zone independent) and  $\phi_t(r)$ , in the format of prior expectations and prior confidence intervals.

Differences in prior on  $p_t$  due to differences in capture efforts  
differences between episodes 1, 3, 5 and 2, 4 due to different mortality rates over winter.

## Prior information

Episode		2	3	4	5	6
$p_t$	Mean	0.3	0.4	0.5	0.2	0.2
	95% int.	[0.1,0.5]	[0.2,0.6]	[0.3,0.7]	[0.05,0.4]	[0.05,0.4]
Site		A			B,C	
Episode		t=1,3,5		t=2,4	t=1,3,5	t=2,4
$\phi_t(r)$	Mean	0.7		0.65	0.7	0.7
	95% int.	[0.4,0.95]		[0.35,0.9]	[0.4,0.95]	[0.4,0.95]

## Prior equivalence

Prior information that can be translated in a collection of beta priors

Episode	2	3	4	5	6
Dist.	$Be(6, 14)$	$Be(8, 12)$	$Be(12, 12)$	$Be(3.5, 14)$	$Be(3.5, 14)$
Site	A			B	
Episode	t=1,3,5	t=2,4		t=1,3,5	t=2,4
Dist.	$Be(6.0, 2.5)$	$Be(6.5, 3.5)$		$Be(6.0, 2.5)$	$Be(6.0, 2.5)$

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Prior belief that the capture and survival rates should be constant over time

$$p_t(r) = p(r) \quad \text{and} \quad \phi_t(r) = \phi(r)$$

Assuming in addition that movement probabilities are time-independent,

$$\psi_t(r) = \psi(r)$$

we are left with  $3[p(r)] + 3[\phi(r)] + 3 \times 2[\phi_t(r)] = 12$  parameters.

Use non-informative priors with

$$a(r) = b(r) = \alpha(r) = \beta(r) = \gamma(r, s) = 1$$

## Gibbs sampling

Needs to account for the missing parts in the  $\mathbf{z}_i$ 's, in order to simulate the parameters from the full conditional distributions

$$\pi(\theta|\mathbf{x}, \mathbf{z}) \propto \ell(\theta|\mathbf{x}, \mathbf{z}) \times \pi(\theta),$$

where  $\mathbf{x}$  and  $\mathbf{z}$  are the collections of the vectors of capture indicators and locations.

Particular case of *data augmentation*, where the missing data  $\mathbf{z}$  is simulated at each step  $t$  in order to reconstitute a complete sample  $(\mathbf{x}, \mathbf{z}^{(t)})$  with two steps:

- Parameter simulation
- Missing location simulation

# Arnason-Schwarz Gibbs sampler

## Algorithm

Iteration  $l$  ( $l \geq 1$ )

① **Parameter simulation**

simulate  $\theta^{(l)} \sim \pi(\theta | \mathbf{z}^{(l-1)}, \mathbf{x})$  as  $(t = 1, \dots, \tau)$

$$p_t^{(l)}(r) | \mathbf{x}, \mathbf{z}^{(l-1)} \sim \mathcal{Be} \left( a_t(r) + u_t(r), b_t(r) + v_t^{(l)}(r) \right)$$

$$\phi_t^{(l)}(r) | \mathbf{x}, \mathbf{z}^{(l-1)} \sim \mathcal{Be} \left( \alpha_t(r) + \sum_{j \in \mathfrak{K}} w_t^{(l)}(r, j), \beta_t(r) + w_t^{(l)}(r, \dagger) \right)$$

$$\psi_t^{(l)}(r) | \mathbf{x}, \mathbf{z}^{(l-1)} \sim \mathcal{Dir} \left( \gamma_t(r, s) + w_t^{(l)}(r, s); s \in \mathfrak{K} \right)$$

## Arnason-Schwarz Gibbs sampler (cont'd)

where

$$w_t^{(l)}(r, s) = \sum_{i=1}^n \mathbb{I}(z_{(i,t)}^{(l-1)} = r, z_{(i,t+1)}^{(l-1)} = s)$$

$$u_t^{(l)}(r) = \sum_{i=1}^n \mathbb{I}(x_{(i,t)} = 1, z_{(i,t)}^{(l-1)} = r)$$

$$v_t^{(l)}(r) = \sum_{i=1}^n \mathbb{I}(x_{(i,t)} = 0, z_{(i,t)}^{(l-1)} = r)$$

## Arnason-Schwarz Gibbs sampler (cont'd)

### ② Missing location simulation

generate the unobserved  $z_{(i,t)}^{(l)}$ 's from the full conditional distributions

$$\mathbb{P}(z_{(i,1)}^{(l)} = s | x_{(i,1)}, z_{(i,2)}^{(l-1)}, \theta^{(l)}) \propto q_1^{(l)}(s, z_{(i,2)}^{(l-1)})(1 - p_1^{(l)}(s)),$$

$$\begin{aligned} \mathbb{P}(z_{(i,t)}^{(l)} = s | x_{(i,t)}, z_{(i,t-1)}^{(l)}, z_{(i,t+1)}^{(l-1)}, \theta^{(l)}) &\propto q_{t-1}^{(l)}(z_{(i,t-1)}^{(l)}, s) \\ &\times q_t(s, z_{(i,t+1)}^{(l-1)})(1 - p_t^{(l)}(s)), \end{aligned}$$

$$\mathbb{P}(z_{(i,\tau)}^{(l)} = s | x_{(i,\tau)}, z_{(i,\tau-1)}^{(l)}, \theta^{(l)}) \propto q_{\tau-1}^{(l)}(z_{(i,\tau-1)}^{(l)}, s)(1 - p_\tau(s)^{(l)}).$$

## Gibbs sampler illustrated

Take  $\mathcal{K} = \{1, 2\}$ ,  $n = 4$ ,  $m = 8$  and ,for  $\mathbf{x}$ ,

1		1	1	.	.	1	.	.	.
2		1	.	1	.	1	.	2	1
3		2	1	.	1	2	.	.	1
4		1	.	.	1	2	1	1	2

Take all hyperparameters equal to 1

## Gibbs sampler illust'd (cont'd)

One instance of simulated  $\mathbf{z}$  is

1	1	1	2	1	1	2	†
1	1	1	2	1	1	1	2
2	1	2	1	2	1	1	1
1	2	1	1	2	1	1	2

which leads to the simulation of the parameters:

$$p_4^{(l)}(1) | \mathbf{x}, \mathbf{z}^{(l-1)} \sim \mathcal{Be}(1 + 2, 1 + 0)$$

$$\phi_7^{(l)}(2) | \mathbf{x}, \mathbf{z}^{(l-1)} \sim \mathcal{Be}(1 + 0, 1 + 1)$$

$$\psi_2^{(l)}(1, 2) | \mathbf{x}, \mathbf{z}^{(l-1)} \sim \mathcal{Be}(1 + 1, 1 + 2)$$

in the Gibbs sampler.

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## Fast convergence

