

Taken from the working paper:

Died or left? Bayesian inference on male and female survival for data with uncertain male fates due to male natal dispersal

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Methods

We focus on species in which males disperse only once at around the age of maturity ("natal dispersal"). To isolate the effect of uncertain male records on estimates of survival from other effects, we focus on data that are mostly free of other issues. We therefore assume that individuals are re-sighted with certainty if they are alive and in the study area, that individuals are only observed at one location, and that survival probabilities only depend on age and sex and not on any other covariates. We further assume that survival probabilities in- and outside of the study area are equal and that individuals born outside of the study area disperse into the study area with equal probabilities as individuals born in the study area disperse out of it. We also assume that ages of individuals whose birth was not observed (left-truncated records) can be estimated with sufficient certainty by a trained observer to allow us to not include time of birth as a latent state in the model and to model ages at death as a continuous variable. However, since the data available to us for the empirical application contained individuals that died before sexing was possible, we did construct the model to accommodate this type of record, treating the sex of unsexed individuals as another latent state.

Data structure

The life history data used to estimate age- and sex-specific mortality included records for native-borns and immigrants. Native-borns were born in the study population, defined as all individually recognisable and constantly monitored individuals. Immigrants entered the study population some time after their birth either due to migration, or being alive at the start of the study (Figure 1.1). The recorded types of departure from the population included death, censoring due to being alive at the end of the study, or uncertain fate (death or censoring through dispersal). Uncertain fates through dispersal were only caused by dispersals from the study population to an external population, and not by dispersals within the study population. Here, we refer to this out-migration from the study population when we use the term "dispersal".

Model variables and functions

We used a Bayesian approach that allowed us to estimate not only parameters for mortality and dispersal but also the different latent states such as dispersal state and sex. We defined the random variables X for ages at death and Y for ages at natal dispersal. We also defined

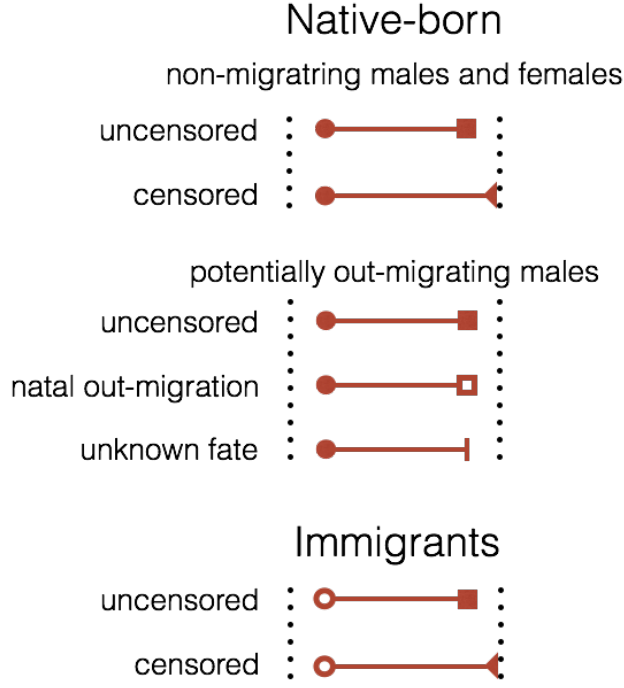


Figure 1.1. Example of types of records in the lion datasets. Circles represent times of entry, where the entry type for filled circles corresponds to known times of birth and open circles are entries after birth (i.e. immigration or birth before the study started). Squares are departure times where filled squares are known times of death and open squares are dispersal. Filled triangles indicate individuals known to be alive at the end of the study and vertical bars indicate that the type of departure from the study population is uncertain (i.e. either death or dispersal).

a dispersal state D which assigned 1 if an individual i , born at b_i and last detected at t_i^L , dispersed in its last detection age, $x_i^L = t_i^L - b_i$, and 0 if otherwise. We treated D as a latent variable for all individuals with uncertain fate. We also defined a variable S that assigned 1 if an individual was female and 0 otherwise.

We used a parametric model to infer age-specific mortality. This is expressed for continuous age x as the mortality rate, or hazard of death,

$$\mu(x|\boldsymbol{\theta}) = \lim_{\Delta x \rightarrow 0} \frac{\Pr(x \leq X < x + \Delta x \mid x \leq X, \boldsymbol{\theta})}{\Delta x}, \quad (1.1)$$

where $\boldsymbol{\theta}$ is a vector of mortality parameters to be estimated. The estimated mortality rate can be used to calculate the probability to survive from birth to age x , or survivor function,

$$S(x|\boldsymbol{\theta}) = \Pr(X \geq x) = \exp \left[- \int_0^x \mu(z|\boldsymbol{\theta}) dz \right], \quad (1.2a)$$

the probability that death occurs before age x , or the cumulative density function (CDF),

$$F(x|\boldsymbol{\theta}) = \Pr(X < x) = 1 - S(x|\boldsymbol{\theta}), \quad (1.2b)$$

and the probability density function (PDF) for age at death

$$f(x|\boldsymbol{\theta}) = \frac{d}{dx} F(x|\boldsymbol{\theta}) = S(x|\boldsymbol{\theta}) \mu(x|\boldsymbol{\theta}). \quad (1.2c)$$

To capture the bathtub-shaped mortality rate typical of large mammals, we used the Siler

model (Siler 1979) in the form

$$\mu(x|\boldsymbol{\theta}) = e^{a_0 - a_1 x} + c + e^{b_0 + b_1 x}, \quad (1.3)$$

where $\boldsymbol{\theta} = \{a_0, a_1, c, b_0, b_1\}$, with $a_0, b_0 \in \mathbb{R}$ and $a_1, c, b_1 > 0$. The Siler model is a competing risk model constituted of three additive mortality hazards. For modelling the ages at dispersal, we used a gamma distribution and defined the PDF as $g(y|\boldsymbol{\gamma})$ with CDF $G(y|\boldsymbol{\gamma})$, where $\boldsymbol{\gamma}$ is a vector of parameters to be estimated. A summary of all the functions, parameters, indicators and variables is provided in Table 1.1.

Table 1.1. Description of random variables, observed variables and indicators.

<i>Modeled random variables</i>	
X	Random variable for ages at death, where x is any age element
Y	Random variable for ages at natal dispersal with elements y
D	Binary random variable for disperser or non-disperser
S	Binary random variable for sex
<i>Observed variables and indicators</i>	
\mathbf{x}^F	Vector of ages at first detection
\mathbf{x}^L	Vector of ages at last detection
\mathbf{m}	Indicator vector for immigrants ($m_i = 1$ if immigrant)
<i>Updated indicators</i>	
\mathbf{d}	Indicator vector for dispersers ($d_i = 1$ if disperser and $d_i = 0$ otherwise)
\mathbf{s}	Indicator vector for sex ($s_i = 1$ if female and $s_i = 0$ otherwise)
$\boldsymbol{\omega}$	Indicator for potential dispersers
<i>Parameters</i>	
$\boldsymbol{\theta}$	Vector of mortality parameters
$\boldsymbol{\gamma}$	Vector of natal dispersal parameters
<i>Functions</i>	
<i>Mortality</i>	
$\mu(x \boldsymbol{\theta})$	Mortality (Siler model)
$S(x \boldsymbol{\theta})$	Survival
$F(x \boldsymbol{\theta})$	CDF for age at death ($F(x) = 1 - S(x)$)
$f(x \boldsymbol{\theta})$	PDF for age at death
<i>Dispersal</i>	
$g(x \boldsymbol{\gamma})$	PDF for age at natal dispersal (gamma)
$G(x \boldsymbol{\gamma})$	CDF for age at natal dispersal

Likelihood and posterior

To construct the likelihood for our Bayesian model, we assigned a different probability to each type of record in Figure 1.1. The likelihood for females and non-migrating native-born males was

$$p(D, x^F, x^L; \boldsymbol{\theta}) = \begin{cases} \Pr(X = x^L | X > x^F) & \text{if uncensored} \\ \Pr(X > x^L | X > x^F) & \text{if censored,} \end{cases} \quad (1.4a)$$

where x^L corresponds to the age at last detection and x^F is the age at first detection (i.e., $x^F = 0$ for individuals born in the study area and $x^F > 0$ for immigrants or individuals born

before the study started), while for dispersers the likelihood was constructed as

$$p(D, x^F, x^L; \theta) = \begin{cases} \Pr(X = x^L, Y > x^L \mid X > x^F) & \text{if uncensored} \\ \Pr(X > x^L, Y > x^L \mid X > x^F) & \text{if censored} \\ \Pr(X > x^L, Y = x^L \mid X > x^F) & \text{if dispersed.} \end{cases} \quad (1.4b)$$

As we will show below, the dispersal state D for individuals with uncertain fate was treated as a latent variable that needed to be estimated. The censored and uncensored probabilities for dispersers were used to determine how likely a potential dispersers (i.e., departure type of uncertain fate and age older than minimum age at dispersal) out-migrated (e.g., last expression in equation 1.4b) or died at the age of last detection x_L (e.g., first expression in equation 1.4b). With this, we could construct the full Bayesian model as

$$\begin{aligned} p(\mathbf{d}_u, \mathbf{s}_u, \theta, \gamma \mid \mathbf{d}_k, \mathbf{s}_k, \mathbf{x}^F, \mathbf{x}^L) &\propto \underbrace{p(\mathbf{d}, \mathbf{s}, \mathbf{x}^F, \mathbf{x}^L \mid \theta, \gamma)}_{\text{likelihood}} \\ &\times \underbrace{p(\mathbf{d})p(\mathbf{s})}_{\text{priors for states}} \\ &\times \underbrace{p(\theta)p(\gamma)}_{\text{priors for parameters}}, \end{aligned} \quad (1.5)$$

where \mathbf{d} was the vector of dispersal states (i.e., $d_i = 1$ if individual i dispersed and $d_i = 0$ otherwise) and \mathbf{s} was the indicator vector for sex ($s_i = 1$ if female and $s_i = 0$ if male). Each of these vectors had two subsets represented by the subscripts u for unknown and k for known.

MCMC and conditional posteriors

We used a Markov Chain Monte Carlo (MCMC) algorithm to fit the model in equation 1.5. For all implementations, we ran four parallel MCMC sequences with different randomly drawn starting values and set the number of iterations to 15,000 steps with a burn-in of 5,000 initial steps and a thinning factor of 20. We used a hierarchical framework that only needed the conditionals for posterior simulation by Gibbs sampling, specifically Metropolis-within-Gibbs (Gelfand & Smith 1990; Clark 2007). This means that, for this particular case, the algorithm divided the posterior for the joint distribution of unknowns into four sections: (a) estimation of mortality parameters, (b) estimation of dispersal parameters, (c) estimation of unknown dispersal state, and (d) estimation of unknown sexes. Here we present each section, specifying the conditional posterior and the acceptance probability for the Gibbs Sampler algorithm.

Section a: Posterior for mortality parameters

The conditional posterior to estimate the mortality parameters θ required only the ages at last detection x_i^L and the dispersal states d_i . The posterior for a given individual i was

$$p(\theta \mid x_i^L, d_i) \propto \begin{cases} \frac{f(x_i^L \mid \theta)}{S(x_i^F \mid \theta)} p(\theta \mid \theta_p) & \text{if } d_i = 0 \\ \frac{S(x_i^L \mid \theta)}{S(x_i^F \mid \theta)} p(\theta \mid \theta_p) & \text{if } d_i = 1, \end{cases} \quad (1.6)$$

where θ_p was a vector of prior hyper-parameters and x_i^F the age at first detection. If the individual was a native-born, then $x_i^F = 0$ and the denominator in both expressions was equal to 1. At every iteration and for a given parameter $\theta \in \theta$ with conditional posterior $p(\theta \mid \dots)$, the algorithm proposes a new parameter value for each element of θ' and accepts it with acceptance

probability

$$p(\theta, \theta') = \min \left\{ 1, \frac{\prod_{i=1}^n p(\theta' | \dots)}{\prod_{i=1}^n p(\theta | \dots)} \right\}. \quad (1.7)$$

Section b: Posterior for dispersal parameters

The conditional posterior to estimate the parameters γ for the distribution of ages at first dispersal for a given individual i was

$$p(\gamma | x_i^F - \alpha, x_i^L - \alpha, d_i, \omega_i, m_i) \propto \begin{cases} g(x_i^L - \alpha | \gamma) p(\gamma | \gamma_p) & \text{if } \omega_i = 1, m_i = 0 \text{ \& } d_i = 1 \\ [1 - G(x_i^L - \alpha | \gamma)]; p(\gamma | \gamma_p) & \text{if } \omega_i = 1, m_i = 0 \text{ \& } d_i = 0 \\ \frac{g(x_i^F - \alpha | \gamma)}{S(x_i^F | \theta)} p(\gamma | \gamma_p) & \text{if } m_i = 1 \\ 0 & \text{otherwise,} \end{cases} \quad (1.8)$$

where γ_p was a vector of prior hyper-parameters for γ , ω_i was an indicator that assigns 1 if an individual was a potential disperser (i.e., it belonged to the dispersing sex and disappeared at an age older than the minimum age at dispersal α), and m_i was an indicator for immigrants. We set the minimum age at dispersal to $\alpha = 1.75$ years for the simulated data and $\alpha = 1.5$ for the Serengeti data. The age α corresponded to the earliest age at which immigrants could be detected and potential dispersers could be last seen. For a parameter $\gamma \in \gamma$ with conditional posterior density $p(\gamma | \dots)$ The acceptance probability for a proposed parameter of γ' was

$$p(\gamma', \gamma) = \min \left\{ 1, \frac{\prod_{i=1}^n p(\gamma' | \dots)}{\prod_{i=1}^n p(\gamma | \dots)} \right\}. \quad (1.9)$$

Section c: Posterior for dispersal states

Dispersal state was evaluated on individuals that were potential dispersers (i.e. $\omega_i = 1$) and estimated the joint probabilities

$$p(d_i | x_i^L, d_i, \omega_i, m_i) \propto \begin{cases} f(x^L)(1 - G(x^L)) p(d_i | \theta_p, \gamma_p) & \text{if } \omega_i = 1, m_i = 0, d_i = 0 \\ S(x^L)g(x^L) p(d_i | \theta_p, \gamma_p) & \text{if } \omega_i = 1, m_i = 0, d_i = 1 \\ 0 & \text{otherwise.} \end{cases} \quad (1.10)$$

The first terms on the right hand side of equation 1.10 correspond to the likelihood function as defined in equations 1.4, while the second terms are the priors for dispersal state. For this section the acceptance probability for the Metropolis Sampling given the last seen ages, the dispersal states, the potential disperser states, and the immigration states was

$$p(d_i, d'_i) = \min \left\{ 1, \frac{\prod_{i=1}^n p(d'_i | x_i^L, d_i, \omega_i, m_i)}{\prod_{i=1}^n p(d_i | x_i^L, d_i, \omega_i, m_i)} \right\}. \quad (1.11)$$

Section d: Posterior for unknown sexes

Some individuals disappeared before the minimum age at dispersal without that their sex had been determined. The conditional posterior for the latent state of sex was

$$p(s_i | x_i^L, \theta) \propto p(x_i^L, \theta | s_i) p(s_i), \quad (1.12)$$

where the second term on the right-hand side is a prior for sex based on sex ratio at birth, or if the analysis was condition to survive to age x , then based on the sex ratio at age x (0.5 for the simulated data and 0.51 for the Serengeti data, respectively). The indicator for potential dispersers ω_i (see section c) was updated in each iteration. Individuals of undetermined sex and last seen ages older than the minimum age at dispersal were assigned 1 if imputed to be male and 0 if imputed to be female. The acceptance probability given the last seen ages and the mortality parameters was

$$p(s_i, s'_i) = \min \left\{ 1, \frac{\prod_{i=1}^n p(s'_i | x_i^L, \theta)}{\prod_{i=1}^n p(s_i | x_i^L, \theta)} \right\}. \quad (1.13)$$

Mortality and dispersal priors

We set the Siler parameters for the prior for females to $a_{0p} = -1.4$ ($\sigma = 0.5$), $a_{1p} = 0.65$ ($\sigma = 0.25$), $c_p = 0.07$ ($\sigma = 0.25$), $b_{0p} = -3.8$ ($\sigma = 0.5$), and $b_{1p} = 0.2$ ($\sigma = 0.25$), and for males to $a_{0p} = -1.2$ ($\sigma(a_{0p}) = 0.5$), $a_{1p} = 0.7$ ($\sigma(a_{1p}) = 0.25$), $c_p = 0.16$ ($\sigma(c_p) = 0.25$), $b_{0p} = -3.5$ ($\sigma(b_{0p}) = 0.5$), and $b_{1p} = 0.23$ ($\sigma(b_{1p}) = 0.25$). For dispersal, the Gamma parameters (shape and scale) for the prior were set to $\gamma_p = \{8, 2\}$ with $\sigma(\gamma_p) = \{2, 1\}$. Both the mortality and dispersal priors were uninformative.

Bibliography

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