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Bayesian inference on age-specific survival for censored and truncated data

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Summary

1. Traditional estimation of age-specific survival and mortality rates in vertebrates is limited to individuals with known age. Although this subject has been studied extensively using effective capture–recapture and capture–recovery models, inference remains challenging because of large numbers of incomplete records (i.e. unknown age of many individuals) and because of the inadequate duration of the studies.

2. Here, we present a hierarchical model for capture–recapture/recovery (CRR) data sets with large proportions of unknown times of birth and death. The model uses a Bayesian framework to draw inference on population-level age-specific demographic rates using parametric survival functions and applies this information to reconstruct times of birth and death for individuals with unknown age.

3. We simulated a set of CRR data sets with varying study span and proportions of individuals with known age, and varying recapture and recovery probabilities. We used these data sets to compare our method to a traditional CRR model, which requires knowledge of individual ages. Subsequently, we applied our method to a subset of a long-term CRR data set on Soay sheep.

4. Our results show that this method performs better than the common CRR model when sample sizes are low. Still, our model is sensitive to the choice of priors with low recapture probability and short studies. In such cases, priors that overestimate survival perform better than those that underestimate it. Also, the model was able to estimate accurately ages at death for Soay sheep, with an average error of 0·94 years and to identify differences in mortality rate between sexes.

5. Although many of the problems in the estimation of age-specific survival can be reduced through more efficient sampling schemes, most ecological data sets are still sparse and with a large proportion of missing records. Thus, improved sampling needs still to be combined with statistical models capable of overcoming the unavoidable limitations of any fieldwork. We show that our approach provides reliable estimates of parameters and unknown times of birth and death even with the most incomplete data sets while being flexible enough to accommodate multiple recapture probabilities and covariates.

Key-words: age-specific survival, Bayesian inference, capture–recapture/recovery data, maximum likelihood

Introduction

An understanding of how mortality risk changes with age is needed to anticipate population dynamics (Pollock 1981). Projections of population declines because of climate change, habitat loss and over-exploitation based on assumptions of constant risk or estimates that omit important sources of uncertainty could have disastrous implications for management and conservation. However, studying age-specific mortality (or survival) rates in the wild is challenging because of scarcity of old individuals (Ricklefs & Scheuerlein 2001; Metcalf *et al.* 2009) and unknown times of birth and death for most individuals (Nisbet 2001). Field studies typically span the lifetimes of few individuals, and ages for a large portion of the population are unknown (Frederiksen, Wanless & Harris 2004). All these data constraints stress the need to

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develop further analytical methods that can account for the sources of uncertainty associated with limited data while extracting the (hidden) demographic processes.

Capture–recapture/recovery (CRR) studies are based on the repeated sampling of a population in which individuals are first marked and released, and, at each subsequent occasion, they are either recaptured, not detected, or recovered dead (Catchpole *et al*. 1998). Observations consist of longitudinal *individual histories* of capture, ideally bounded by times of birth and death (i.e. uncensored records). However, most CRR data sets include individuals with unknown time of birth, some of which could have been born before the study (left-truncated), and individuals with unknown time of death, including (but not restricted to) individuals that died after the termination of the study (right-censored). Models derived from the Cormack–Jolly–Seber framework (CJS; after Cormack 1964; Jolly 1965; Seber 1965) can accommodate both uncensored and right-censored records. This treatment recognizes that both types of observations need inclusion and that each contributes different information (White & Burnham 1999). Often, left-truncated records are included either by assuming that mortality is only time dependent (i.e. constant with age; Aebischer & Coulson 1990) or by using time at first capture as a surrogate for age at maturity (Crespin *et al*. 2006; Reed *et al*. 2008); both treatments bear strong assumptions that can potentially mislead inference on age-specific survival. As a result, in most cases, left-truncated records are discarded. Without left-truncated records, the remaining subset of the population can be small, consisting only of individuals born since the study began. For long-lived species, decades might be required before known-age individuals become a substantial fraction of the population. Yet, deaths may be observed for a variety of individuals, not just those of known age. Although the consequences for inference of ignoring observations on much of the population could be substantial, there is rare opportunity to compare estimates against those that might come from more complete observations.

The missing data problem in CRR data sets does not only pertain to survival status, but also other state variables. CJS-based models provide the basis to estimate survival probabilities for the single-state case when times of death are unknown (i.e. right-censoring), and when recapture probabilities are < 1, using likelihoods that marginalize over all the possible states that could apply to each individual. Generalizations of the basic CJS framework have been developed to include multiple states, such as location and developmental stage (Arnason 1973; Schwarz, Schweigert & Arnason 1993; Lebreton & Pradel 2002). The likelihoods necessarily become large and complex to accommodate the many combinations of potential states for each individual, but can be simplified conditionally. Dupuis (1995, 2002) used a Bayesian framework to extend the Arnason–Schwartz model to estimate survival and movement probabilities from capture–recapture data that accounted for missing data on locations and capture occasions through data augmentation. King & Brooks (2002) extended Dupuis (1995) approach when competing models were tested by incorporating model averaging to estimate survival parameters and transition probabilities between states using reversible jump Markov Chain Monte Carlo (RJMCMC) algorithms. Clark *et al*. (2005) developed a hierarchical Bayesian framework that combined Dupuis (1995) approach with stage-structured population modelling (Fujiwara & Caswell 2002) where transitions between states could not be associated with specific covariates and were modelled as random effects. Clark *et al*. (2005) showed that conditional modelling of latent (unknown) states vastly simplifies algorithms thereby allowing for more flexible modelling.

Latent state models have been primarily applied to finite numbers of discrete states (e.g. locations, stages). However, the estimation of initial and terminal states such as times of birth and death needs the integration across continuous variables, without known lower (birth) or upper (death) bounds. Frederiksen, Wanless & Harris (2004) sidestepped this problem by modelling age as a quadratic covariate of survival for black-legged kittiwake data that had a large proportion of unknown ages. The assumptions do not describe survival lacking such a quadratic relationship with age making their methods limited to a small range of species. Zajitschek *et al*. (2009), used life-table analysis originally developed by Müller *et al*. (2004), combined with capture–recapture techniques to estimate age-specific survival rates in male and female black field crickets where times of birth and death were unknown. Link & Barker (2005) and Schofield & Barker (2008) applied a Bayesian approach for open mark–recapture populations that combined estimates of population sizes and per capita birth rates to model missing birth times as the multinomial probability of being born in any given interval within the study span. Recently, Pledger *et al*. (2009) developed an extension of the Jolly–Seber and Arnason–Schwartz models to estimate times of arrival and departure at a stopover site, analogous to the estimation of times of birth and death in the previous example. All these approaches (except for Frederiksen, Wanless & Harris 2004) require that the times for the initial and terminal states are approximately known, as with stopover sites or species for which birth and death happen within the same year (e.g. semelparous species). In such cases, it is easier to assume that the population has reached a stable age distribution to approximate survival rates (Zajitschek *et al*. 2009), or to use a maximum-likelihood framework to convolve over all possible initial and terminal states (Link & Barker 2005; Schofield & Barker 2008; Pledger *et al*. 2009). However, in populations consisting of a large number of cohorts with overlapping generations, the marginal likelihood for the estimation of times of birth and death would not be available (see Matechou 2010 for alternatives based on Pledger *et al*. 2009).

Here, we developed an alternative approach that combines estimation of survival parameters and imputation of unknown states (i.e. times of birth and death) within a Bayesian hierarchical framework. The modelling of missing data allowed us to combine what is known from a large number of partially observed individuals to obtain

population-level estimates of survival. By modelling both (past) birth years and (future and unknown) death years as latent variables, combined with a flexible parametric mortality function for the full population, we could readily admit partial observations on individuals of unknown age, extending the types of observations that could be included. We simulated data sets of varying duration, detection and recovery probabilities and proportions of individuals with known time of birth. Under these scenarios, we compared our model to a traditional CRR model (Catchpole *et al.* 1998) and assessed both models on the basis of their ability to predict age-specific survival trends and, for our model, parameter estimates and estimates of ages at death. To illustrate the performance of our model, we applied it to a Soay sheep (*Ovis aries*, L.) CRR data set and extended it to accommodate covariates (i.e. sex). Our results showed that within a hierarchical setting, the assimilation of types of observations that are not typically accommodated by a traditional approach could provide more powerful inference than traditional methods.

Materials and methods

MISSING DATA IN CRR STUDIES

In CRR studies, missing data on individual times of birth (b_i) and death (d_i) can occur in response to different processes. When modelling age-specific mortality through estimating the unobservable age states, these sources of 'missingness' need to be clearly acknowledged. Ideally, CRR data sets should include a large proportion of uncensored records (i.e. with known times of birth and death). However, as we mentioned above, both left-truncated and right-censored records can be common, while their prevalence can be tightly linked to the duration of the study. Furthermore, low recapture and/or recovery probabilities limit the number of detections and introduce uncertainty about status.

Commonly, data collection for CRR studies consists of population sampling at discrete intervals spanning an interval $[t_1,\ldots, t_T]$, where t_1 and t_T correspond to the first and last sampling occasions, respectively. At each sampling occasion, new individuals are marked and released while previously marked ones are recaptured when they are alive or recovered when they die. The event of an individual i being detected (captured) or not at each occasion t is defined by the indicator $y_{i,t}$, which assigns 1 if the individual is recaptured and 0 otherwise. The resulting capture history vector is $\mathbf{y}_i$, with maximum possible length equal to the study span T. Thus, for a study span of $T = t_T - t_1 + 1$ years, the vector $\mathbf{y}_i$ for an individual with unknown times of birth and death is the T-sequence of binary indicators that takes values on the discrete space $\{0,1\}^T$. We define the first time an individual is detected as f_i, the last time as l_i, and the total number of years it was observed as o_i. Thus for the observation vector $\mathbf{y}_i = [1, 0, 1, 0, 0]$, we have $T = 5$ and $o_i = \sum_{t=1}^{T} y_{i,t} = 2, f_i = 1$ and $l_i = 3$. However, the entire *individual history* is not always bound by the study span, because births and deaths can occur before and after the study, respectively. Therefore, each individual history combines the vector $\mathbf{y}_i$ with the respective times of birth (b_i) and death (d_i). For example, an individual history given by the vector $[b_i, 1, 1, 0, d_i]$ corresponds to an individual known to be born at a time $b_i = t$, defined within the interval $[t, t + \Delta x]$, that died at a time $d_i = t + 4$, and was recaptured at times $t + 1$ and $t + 2$. This uncensored record contains all the information required to estimate age-specific survival probability, while the missing observation at occasion 4 contributes to the data model that we describe below. A data set consists of n individual histories, where n corresponds to the total number of individuals recorded.

A HIERARCHICAL FRAMEWORK FOR TRUNCATED AND CENSORED RECORDS

Analysis of age-specific survival is traditionally applied to capture–mark–recapture data sets by combining models for survival and recapture probability. Let x represent age and X be the random variable for age at death. The age at death for an individual i is calculated as the difference between the times of death and birth ($X_i = d_i - b_i$). Because observations are often annual, we discuss data in terms of discrete time increments of duration $\Delta x = 1$ year.

Parametric models are commonly used for inference on lifetime survival. A model for continuous age x is expressed in terms of an age-specific rate of mortality, or hazard rate, $\mu(x|\theta) = \lim_{\mathrm{d}x\to 0} \Pr(x \le X < (x+\Delta x)|x \le X, \theta)/\mathrm{d}x$, where parameters are represented by θ. This estimate of mortality rate can be used to calculate the probability of survival until age x, or survivor function,

$$S(x|\theta) = \Pr(X \ge x) = \exp\left[-\int_0^x \mu(z|\theta)\,\mathrm{d}z\right] \qquad \text{eqn 1a}$$

the probability that death occurs before age x,

$$F(x|\theta) = \Pr(X < x) = 1 - S(x|\theta) \qquad \text{eqn 1b}$$

and the probability density function (pdf) of ages at death,

$$f(x|\theta) = \Pr(x \le X < (x+\Delta x)) = S(x|\theta)\mu(x|\theta) \qquad \text{eqn 1c}$$

In standard survival analysis, individuals of both known and unknown age at death contribute to estimates, but in different ways (Cox & Oakes 1984). Individuals having known age at death are uncensored and contribute likelihood 1c, while those for which age at death could not be recorded are right-censored and contribute likelihood 1a. Individuals of unknown age (i.e. left-truncated) are typically omitted.

Our treatment extends inference to left-truncated records by imputing times of birth and death, and thus, only the pdf of ages at death (eqn 1c) is required. For right-censored and left-truncated individuals, the imputed age at death substitutes for known age at death. Let $\mathbf{X} = [X_1, \ldots, X_n]$ be the vector for ages at death, and $\mathbf{X}_k \subseteq \mathbf{X}$ and $\mathbf{X}_u \subseteq \mathbf{X}$ are vectors containing the known (uncensored) and unknown (truncated and censored) ages, respectively. These subsets of $\mathbf{X}$ have length $n_k = \sum_i \delta_i$ and $n_u = \sum_i (1 - \delta_i)$, where the level of missingness $n_u < n$ will determine our ability to estimate parameters (see below). Here, δ_i is an indicator that assigns 1 if individual i was uncensored, and 0 otherwise.

The joint distribution of unknowns $p(\theta, \pi, \mathbf{X}_u|\mathbf{y}, \mathbf{X}_k)$ cannot be analysed under a maximum-likelihood framework, because it requires the integration of all the multinomial probabilities for possible recapture histories and the unknown (stochastic) ages. Our hierarchical framework needs only 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 divides the posterior for the joint distribution of unknowns into three sections: (a) estimation of survival

parameters, θ; (b) estimation of unknown ages at death, $\mathbf{X}_u$ and (c) estimation of recapture probability(ies), π.

In Section (a), survival parameters θ conditioned on age $\mathbf{X}$ have density

$$p(\theta|\mathbf{X}_u, \mathbf{X}_k) \propto p(\mathbf{X}_u, \mathbf{X}_k|\theta)p(\theta|\theta_p) \quad \text{eqn 2}$$

The first factor on the right-hand side of eqn 2 is the likelihood for ages at death, and the second factor is the prior distribution for the mortality parameters θ, where θ_p are the prior parameter values. The likelihood is calculated as

$$p(X_i|\theta) \propto \begin{cases} f(X_i|\theta) & \text{if } b_i \geq t_1 \quad \text{(a)} \\ f(X_i|\theta)/S(t_1 - b_i|\theta) & \text{if } b_i < t_1 \quad \text{(b)} \end{cases} \quad \text{eqn 3}$$

where eqn 3b is applied to left-truncated individuals. For these records, the probability of dying (to a discrete approximation) at age $X_i = x$ is conditioned on surviving to the age at truncation t_1-b_i and is derived as

$$\Pr(X_i = x|X_i > t_1 - b_i) = \frac{\Pr(X_i = x)}{\Pr(X_i > t_1 - b_i)} = \frac{f(X_i|\theta)}{S(t_1 - b_i|\theta)}$$

Section (b) estimates the age at death for individuals that are either censored, truncated or both, conditioned on survival and observations, and is calculated as

$$p(\mathbf{X}_u|\mathbf{X}_k, \theta, \mathbf{y}_u, \pi) \propto p(\mathbf{y}_u|\pi, \mathbf{X}_u)p(\mathbf{X}_u|\mathbf{X}_k, \theta)p(\mathbf{X}|\theta_p) \quad \text{eqn 4}$$

The first factor evaluates the probability that an individual is not detected for η_i years before the first capture (for truncated records) and after the last capture (for censored records) and is calculated as

$$p(\mathbf{y}_i|\pi, X_i) \propto (1 - \pi)^{\eta_i(1-\delta_i)} \quad \text{eqn 5}$$

where η_i is calculated as

$$\eta_i = (f_i - 1) - \max[t_1, (b_i + 1)] + \min[t_T, (d_i - 1)] - (l_i + 1)$$

The second factor in eqn 4 is the density of deaths (as in eqn 1c) conditional on estimated times of birth and death. The last factor is the prior age distribution, which is constructed from the prior parameters θ_p

$$p(X|\theta_p) = \frac{S(X|\theta_p)}{E(x|\theta_p)}$$

where life expectancy (i.e. expected age at death) is calculated as $E(x|\theta_p) = \int_0^\infty xf(x|\theta_p)\,\mathrm{d}x$. Prior dependence introduced by the parametric model allows for imputation of times and ages at death for censored and truncated individuals using a Metropolis step. CRR data sets consist of discrete observations separated by intervals of time where no records are taken. However, mortality is a process that happens continuously in time – individuals can die at anytime between consecutive observations. To account for this discretization in mortality with age, we used a mid-point approximation of ages at death when estimating the survival and mortality functions. This means that the probability that an individual i dies at age X_i, this is $\Pr(x < X_i < x + \Delta x)$, is evaluated at the mid-point of the interval, namely at age $x + (\Delta x * 0{\cdot}5)$ (see Appendix S1 for details of the implementation).

Section (c) estimates detection probability π with conditional posterior constructed as the product of a binomial density, which is the likelihood for the number of years an individual i is observed (o_i) given the number of years it is imputed to be alive (n_i) within the study, and a Beta prior distribution for π with hyper-parameters ρ_1 and ρ_2. The result is a conjugate Beta conditional posterior

$$p(\pi|\mathbf{o}, \mathbf{n}, \rho_1, \rho_2) \propto \beta\left(\pi \middle| \rho_1 + \sum_{i=1}^{n} o_i; \rho_2 + \sum_{i=1}^{n} \left[\sum_{x=\max(b_i+1, T_f)}^{\min(d_i-1, T_l)} (1 - y_{i,x})\right]\right) \quad \text{eqn 6}$$

Section (c) can be extended to estimate multiple recapture probabilities through a multivariate Beta conditional posterior (e.g. different recapture probabilities by year or age; see Appendix S1 for an implementation in the code), or by treating the recapture probability as a binomial GLM with a link function that relates it with categorical or continuous explanatory variables (e.g. year, age, random individual effects, etc.).

In summary, the three sections described above are introduced into a Gibbs sampler algorithm as follows:

Section a: Metropolis Sampling for the two potential vectors of survival parameters θ and θ 'given the real and proposed ages at death with acceptance probability

$$p(\theta, \theta') = \min\left\{1, \frac{\prod_{i=1}^{n} [f(X_i|\theta')]p(\theta'|\theta_p)}{\prod_{i=1}^{n} [f(X_i|\theta)]p(\theta|\theta_p)}\right\}$$

Section b: Metropolis sampling between two potential ages at death X_i and X_i', and the associated times of birth and death (d_i and b_i), with acceptance probability

$$p(X_i, X'_i) = \min\left\{1, \frac{(1 - \pi)^{\eta'_i} f(X'_i|\theta)p(X'_i|\theta_p)}{(1 - \pi)^{\eta_i} f(X_i|\theta)p(X_i|\theta_p)}\right\}.$$

Section c: Direct sampling for recapture probability from the Beta distribution in eqn 6. If multiple recaptures are evaluated using a link function within a GLM framework, Metropolis sampling would be required if the distributions of the link function parameters are not conjugate with the binomial recapture probabilities (Clark 2007).

The outputs for this model are converged sequences of estimates for parameters (i.e.$\hat{\theta}$ and $\hat{\pi}$) and for missing birth and death years ($\hat{b}_i$and $\hat{d}_i$) with the corresponding vector of ages at death $\hat{\mathbf{X}}_u$. Mean values and 95% credible intervals can be calculated from these converged sequences. In Appendix S1, we include a detailed description of the R code used with the model.

ALTERNATIVES FOR MODEL SELECTION

Model selection can be achieved using deviance information criterion (DIC; Spiegelhalter *et al.* 2002). This method has been described as an alternative for hierarchical Bayesian models, which combines a measure of goodness-of-fit and a penalization for model complexity. Although DICs are easy to compute from MCMC outputs, its use is still controversial (see responses in Spiegelhalter *et al.* (2002) and Celeux *et al.* (2006) and a correction for over-dispersed counts in Millar 2009). Reversible jump MCMC

(RJMCMC) is a powerful option that combines the estimation of posterior probabilities and posterior parameter distributions when models of differing dimensions are evaluated using model averaging (King & Brooks 2002; Gimenez *et al.* 2009). One clear advantage of RJMCMC is that it does not favour a single model, but assigns different weights to the models considered based on their contribution to the posterior density. Thus, RJMCMC allows efficient exploration of parameter and model space. Considering the hierarchical nature of our model, RJMCMC would be the most appropriate procedure for model selection. Moreover, this method can be extended to calculate Bayesian *P*-values as illustrated by King & Brooks (2002).

SIMULATION STUDY

To test the performance of our model in estimating mortality patterns and the imputed ages at death, we stochastically simulated 10 populations. We simulated each population for 130 years, starting from an initial population of 10 individuals and sex ratio of 1 : 1. Each female could produce one offspring per year, and breeding success was randomly drawn from a Bernouilli distribution with probability 0·5. The sex of the offspring was also determined from a Bernouilli trial with probability 0·5. The age at death for each individual was randomly drawn by inverse sampling from a Gompertz mortality cdf (eqn 1b; Gompertz 1825) with hazard $\mu(x) = \alpha e^{\beta x}$, where α and β are the baseline mortality and shape parameters, respectively. Survival probability is then calculated as

$$S(x|\alpha,\beta) = \exp\left[\frac{\alpha}{\beta}(1-\mathrm{e}^{\beta x})\right] \qquad \text{eqn 7a}$$

and the pdf for ages at death is

$$f(x|\alpha,\beta) = \alpha\exp\left[\beta x + \frac{\alpha}{\beta}(1-\mathrm{e}^{\beta x})\right] \qquad \text{eqn 7b}$$

To reproduce the mortality patterns of a long-lived population, we fixed the Gompertz parameters at $\alpha_r = 0{\cdot}02$ and $\beta_r = 0{\cdot}2$, which incorporates strong age-dependence in the mortality rate. The resulting survival function estimates that only 1% of the initial cohort remains alive by age 20. Because we allowed for variability in reproduction and survival, the final size of each population was different, which allowed us to test the sensitivity of the model to sample size.

For each population, we fixed the start of the study at year 100 and generated two sets of data, one for a short study of $T = 10$ years, and one for a long study of $T = 20$ years. We also varied the proportion of individuals first captured at birth (i.e. known-age individuals), the recapture (π) and recovery (λ) probabilities by randomly drawing from a Binomial distribution with two sets of parameters: a low probability of 0·2 (0·1 for λ) and a high probability of 0·8. As a result, we simulated a total of 16 samples per population, which corresponded to all the possible combinations (scenarios) of short-long study span, and low-high proportion of known ages, recapture and recovery probabilities, adding up to 160 study cases.

To provide a point of comparison with more traditional methods, we compared the results of our model with the CRR model proposed by Catchpole *et al.* (1998). We adapted Catchpole *et al.*'s model for inference on age-specific survival assuming no cohort effects. This model is a product of multinomial distributions for age-specific survival probabilities, ϕ_x, detection probability, π, and recovery probability, λ, applied only to individuals with known age (i.e. left-truncated records are not included) and only for ages up to $X = T$-1. The likelihood for an individual i, $L(\mathbf{u}_i; \Phi, \pi, \lambda)$, where $\mathbf{u}_i$ represents its individual history and where $\Phi = \{\phi_1,\ldots,\phi_{T\text{-}1}\}$, is

$$L(\mathbf{u}_i;\Phi,\pi,\lambda) \propto \prod_{x=1}^{\omega_i-1}\left(\phi_x\pi^{u_{i,x}}(1-\pi)^{1-u_{i,x}}\right)\left[(1-\phi_{\omega_i})\lambda\right]^{\delta_i} \times \sum_{x=\omega_i}^{\upsilon_i}\left([(1-\phi_x)(1-\lambda]^{\min(1,\upsilon_i-x)} \times \left[(1-\pi)^{x-\omega_i}\prod_{m=\omega_i}^{x-1}\phi_m\right]^{\min(1,x-\omega_i)}\right)^{1-\delta_i} \qquad \text{eqn 8}$$

where δ_i is an indicator function for uncensored ($\delta_i = 1$) vs. censored ($\delta_i = 0$) individuals. ω_i is either (i) the age of a censored individual the last time it was detected ($l_i - b_i$) or (ii) the age at death for an uncensored individual X_i, thus $\omega_i = X_i^{\delta_i}(l_i - b_i)^{1-\delta_i}$, and υ_i is age at the end of the study ($\upsilon_i = t_T - b_i$) applied to censored individuals. The first factor on the right-hand side of eqn 8 corresponds to survival to age of last capture (for right-censored) or to last year before death (for uncensored), the second factor (second line) calculates mortality probability at ω_i for uncensored individuals, and the last factor (third line) is the probability of either dying without recovery or surviving without detection at every age after last detected for right-censored individuals. Maximum-likelihood estimates are obtained for the vector of age-specific survival probabilities $\hat{\Phi}$ and probabilities of detection $\hat{\pi}$ and recovery $\hat{\lambda}$ (see Catchpole *et al.* (1998) for a full description of the model and fitting method). For comparison with the estimates from our Bayesian model, we used the survivor function, which can be calculated as $S_x = \prod_{t=0}^{x}\phi_t$. Owing to the large number of samples (i.e. 160), we used a Metropolis algorithm to obtain mean and 95% confidence intervals for the parameters estimated. The acceptance criterion was simply the likelihood ratio for the previous and proposed parameters, namely $\frac{L(\mathbf{u}_i;\Phi',\pi',\lambda')}{L(\mathbf{u}_i;\Phi,\pi,\lambda)}$.

To test how accurately both models predicted the real survival patterns from each of the 160 study cases, we calculated predictive loss (Gelfand & Ghosh 1998) between the range of estimated survival probabilities and the real survival probability. This method is commonly used as a measure of predictive performance for model selection. We used the converged parameter chains to calculate survival probabilities at each age and calculated a measure of goodness-of-fit (G_m) as the error sum of squares between the average predicted survival probability and the real probability, and one of model dispersion or penalty (P_m) measured as the predictive variance. A deviance value is calculated as $D_m = G_m + P_m$. The model with the lowest D_m is considered to have the highest predictive ability.

We also tested the sensitivity of our models to the selection of priors for the mortality parameters. We ran the model on all populations with four sets of priors, each set describing a particular trend in survival. The Gompertz parameters for the priors were as follows: prior 1: $\alpha_p = 0{\cdot}001$, $\beta_p = 0{\cdot}001$; prior 2: $\alpha_p = 0{\cdot}001$, $\beta_p = 0{\cdot}15$; prior 3: $\alpha_p = 0{\cdot}1$, $\beta_p = 0{\cdot}001$ and prior 4: $\alpha_p = 0{\cdot}1$, $\beta_p = 0{\cdot}15$ (Fig. 1S in Appendix S2). The Beta priors for the detection probability π were $\rho_1 = 0{\cdot}1$ and $\rho_2 = 0{\cdot}1$, which yield a mean prior $\bar{\pi}_p = \rho_1\backslash(\rho_1 + \rho_2) = 0 \cdot 5$.

To test for convergence and to find how many initial steps had to be discarded (i.e. burn-in sequence), we ran 10 parallel MCMC sequences with different starting parameter values on the poorest data set. From the resulting MCMC chains, we computed potential scale reduction for each parameter (Gelman *et al.* 2004). This diagnostic is calculated as $\hat{R} = \sqrt{\hat{v}^{+}/W}$, where W is a measure of the within-sequence variance and $\hat{v}^{+}$ is a weighted average of the between-sequence variance (B) and W. Convergence is attained when $\hat{R}$ is close to 1. Our tests showed that R is closest to 1 after

an initial sequence of 5000 iterations ($\hat{R}_\alpha = 1 \cdot 00067$; $\hat{R}_\beta = 1 \cdot 00068$; $\hat{R}_\pi = 1 \cdot 00006$). The dependence between consecutive observations was reduced to values lower than $R^2 = 0{\cdot}05$ after a lag of 50 estimates. We set the number of iterations to 55 000 steps with a burn-in of 5001 initial steps.

We calculated credible intervals for all parameters for each subpopulation from the estimates in the MCMC chains after burn-in. Finally, we tested the bias and dispersion in the estimation of ages at death for truncated and censored records for all populations and scenarios as the difference between the estimated age and the real age: $e_x = x_{est} - x_{real}$, for each individual with unknown time of birth or of death (truncated, censored or both) at each estimated value per MCMC step after burn-in. With these results, we calculated predictive intervals for e_x for each subpopulation.

APPLICATION

We obtained CRR data from a free-ranging population of Soay sheep (*O. aries*) from Hirta, St Kilda's archipelago, Scotland (57°49′N, 08°34′W) studied since 1985 (for details on data collection, see Clutton-Brock & Pemberton (2004)). The data set consists of over 7000 individual histories that include times of birth and death and capture histories. Because the aim of this analysis was to illustrate the performance of our model and not to implement an in-depth analysis of Soay sheep demography (for extensive examples, see Coulson *et al.* 2001; King *et al.* 2006; Pelletier *et al.* 2007; Coulson *et al.* 2008), we only used a subsample of individuals detected between 1995 and 2005 for a total of 2577 capture histories. We assumed that individuals born before the study were left-truncated while those dying beyond the study were right-censored, for a total of 944 records with missing data. For 648 of these records, we had the real times of birth and death, and thus, we were able to use them to calculate errors in age estimation. We conditioned our analysis on survival after the first year of life to avoid the complexities of juvenile mortality (Jones *et al.* 2005). After a visual exploration of the data, we decided to use a Siler mortality rate function (Siler 1979), which allows the exploration of 'bathtub' patterns in mortality. The Siler hazard rate is calculated as

$$\mu(x) = \alpha_1 e^{-\beta_1 x} + c + \alpha_2 e^{\beta_2 x} \qquad \text{eqn 9a}$$

with survival probability

$$S(x) = \exp\left[\frac{\alpha_1}{\beta_1}(e^{-\beta_1 x} - 1) + cx + \frac{\alpha_2}{\beta_2}(1 - e^{\beta_2 x})\right] \qquad \text{eqn 9b}$$

The pdf for ages at death is calculated as depicted in eqn 1c. To illustrate how to incorporate covariates, we tested whether males and females differed in mortality rates (see Appendix S1 for model description and implementation in R). We tested the difference in parameter estimates between both sexes by calculating Kullback–Liebler (K–L) discrepancy, D_{fm}, (Burnham & Anderson 2001) on the resulting parameter posterior densities. This metric calculates the distance between the distribution of a given parameter θ for females $[P_f(\theta)]$ and males $[P_m(\theta)]$ as

$$D_{fm} = \int_{-\infty}^{\infty} P_f(\theta) \log\left(\frac{P_f(\theta)}{P_m(\theta)}\right) d\theta$$

If both distributions are similar, D_{fm} should be close to 0.

We performed all our analyses on the free software R (R development Core Team 2010). We used the R library snowfall (Knaus 2010) for parallel computing.

Results

SIMULATION STUDY

Using simulated data to test model performance has the advantage that parameters and latent states are known, allowing for accurate model evaluations. We simulated 10 different populations, each of which was subsampled for 16 different scenarios, covering a wide range of sample sizes, the smallest of which had only 51 records for the short study, low proportion of known ages and low recapture and recovery probabilities, and the largest had up to 4720 for the best scenario. After calculating predictive loss on the estimation of age-specific survival probabilities on all models, we found that the CRR model (Catchpole *et al.* 1998) was considerably more sensitive to sample sizes than our model (Figs 1 and 2). Also, of all the variables tested, both models were most sensitive to recapture probability followed by study span. With high recapture probability, all the Bayesian models tested converged to the same predictive loss values irrespective of sample size, while the effect of sample size on the CRR model was only noticeable for the smallest samples (Fig. 1). As expected, the most important effect of sample size on our Bayesian model was that the credible intervals were wider for small samples than for larger samples (Fig. 2).

The choice of priors affected the performance of our model, particularly when recapture probability was low. The model constructed with priors 4 strongly under-predicted survival. To a lesser extent, priors 3 affected inference similarly, while models constructed with priors 1 and 2 performed consistently better (Fig. 1). Low recapture probabilities result in individual histories that are considerably short. When such short histories are combined with priors that under-predict survival, the estimation of ages at death is driven towards younger ages. Still, in most cases, models constructed with priors 1, 2 and 3 performed better than the reference model (CRR).

Overall, parameter estimation was better with higher recapture probability and longer studies (Fig. 3 and Figs S2 and S3 in Appendix S2). Also, with a low proportion of known-age individuals, the estimation of the Gompertz baseline mortality, α, was biased towards slightly lower values than the real parameter (Fig. S2 of Appendix S2), while the estimation of the shape β parameter was biased towards higher values (Fig. 3). Nonetheless, in most cases, the value of the real β fell within the 95% credible intervals.

In general, our model estimated ages at death without bias (Fig. 4). The two exceptions included a slight overestimation when all variables were at their lowest levels and a noticeable underestimation with high recovery probability, low recapture probability and low proportion of known-age individuals. This last was also evident in the estimation of the Gompertz baseline mortality parameter, α (Fig. S2 of Appendix S2). Presumably, this was because we only allowed recoveries to happen within the study span, which resulted in a large proportion of early death records.

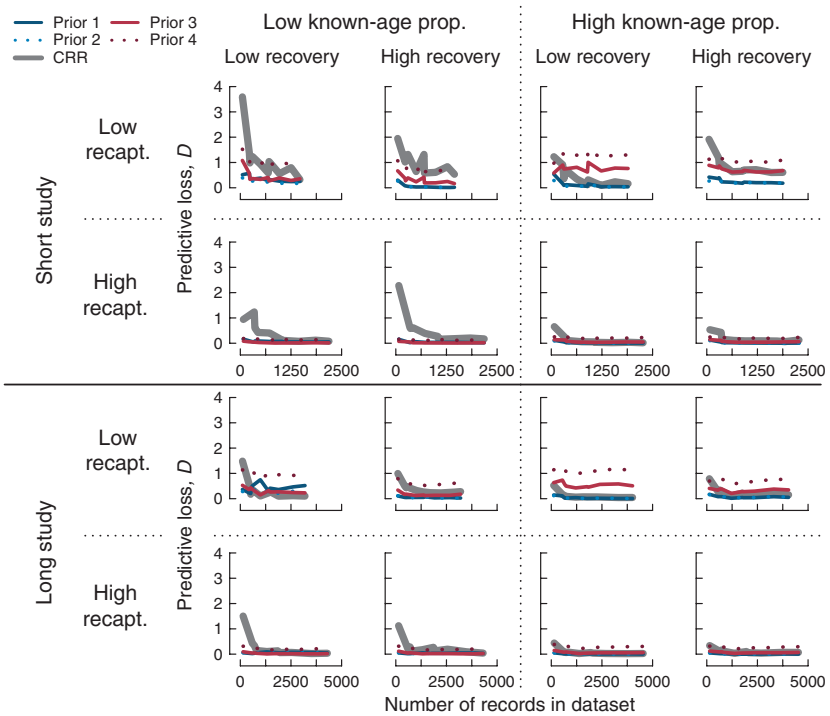

Fig. 1. Predictive loss, *D*, (i.e. sum of goodness-of-fit and model dispersion) in the estimation of the real (simulated) survival probability as a function of sample size for the capture–recapture/recovery (grey line) model and for the Bayesian model (BAYES; blue and red lines). The Bayesian model was implemented with four sets of prior parameters for the survival function.

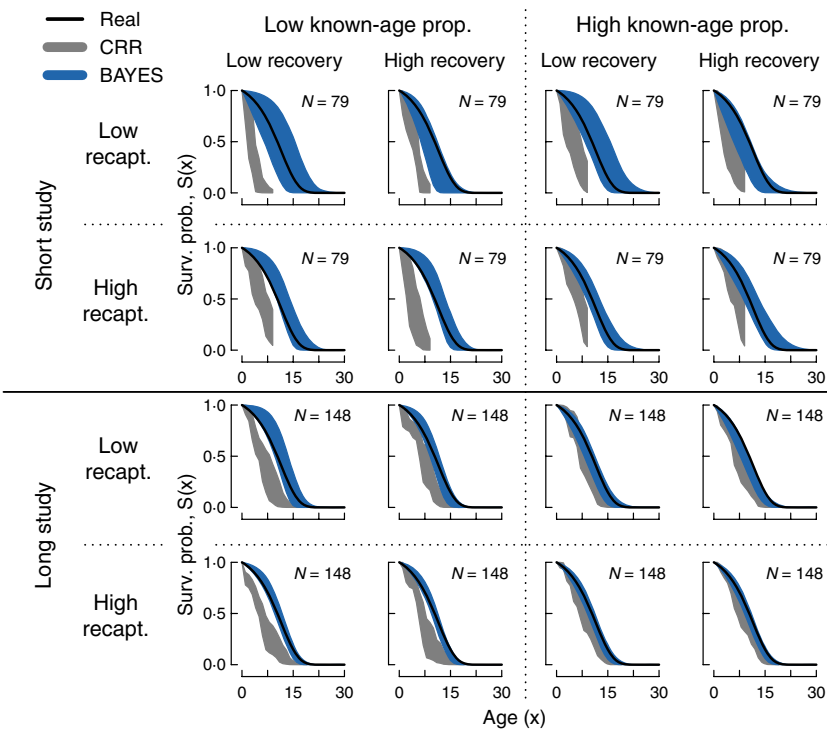

Fig. 2. Predicted survival probability for the capture–recapture/recovery (CRR; red polygons) model and for the Bayesian model (BAYES; blue polygons) for the smallest simulated population implemented with prior 2 compared to the real survival (black line). The width of the polygons along the survival axis corresponds to the 95% confidence (CRR) and credible (BAYES) intervals. *N* corresponds to the sample size for each subsample.

APPLICATION

Convergence on the analysis of the Soay sheep data set was achieved satisfactorily, with a maximum potential scale reduction of $\hat{R}_{\text{c.male}} = 1 \cdot 0096$for the Siler *c* parameter for males (see Fig. S4 of Appendix S2 for one set of trace plots). Our results on the survival analysis for Soay sheep showed that age-specific mortality in this species follows a clear 'bath-tub' shape for both sexes, with decreasing mortality after the first year of age until the 4th or 5th years, and then a steeper increase in mortality at older ages (Fig. 5), consistent with previous findings (Catchpole *et al.* 2000; Tavecchia *et al.* 2005). We also show that male and female mortality differ considerably, where female mortality declines more steeply

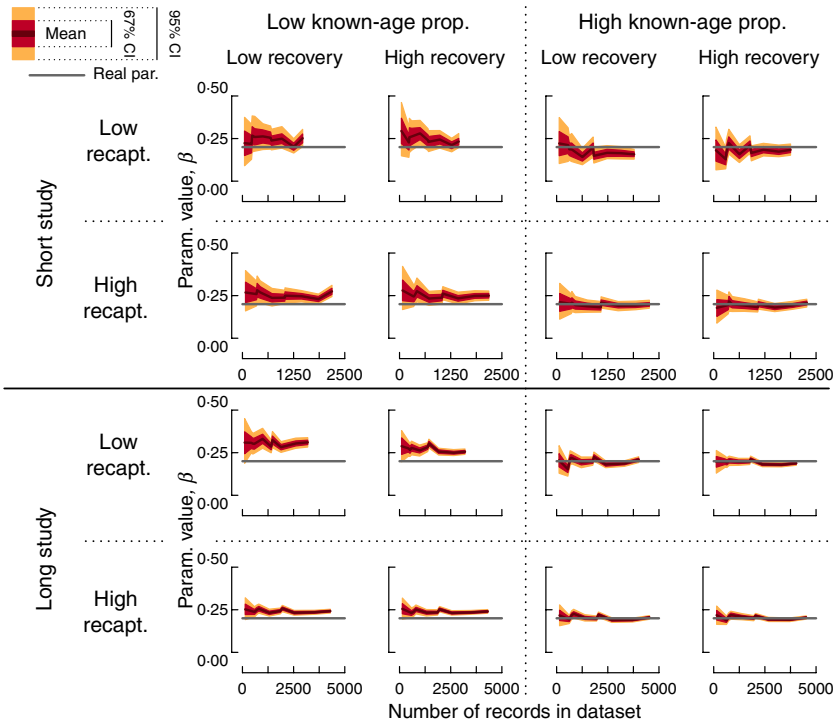

Fig. 3. Estimation of Gompertz parameter β (rate parameter) implemented with prior 2 compared to the parameter used to simulate the data (dotted grey line) as a function of sample size. The 67% and 95% credible intervals were calculated from the Markov Chain Monte Carlo chains after burn-in. The results for parameters α and π are shown in Appendix S2.

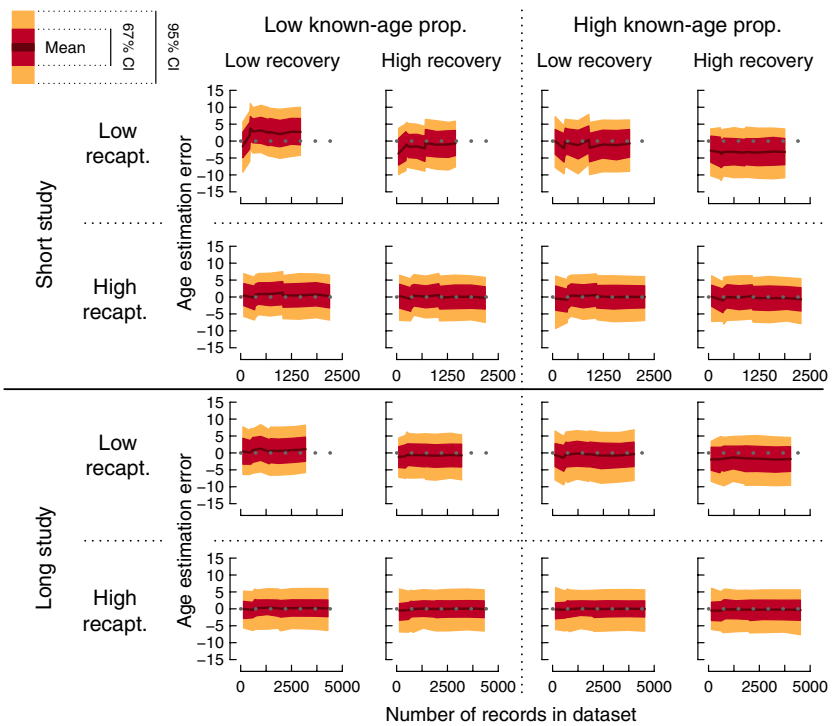

Fig. 4. Error (in years) in estimation of ages at death as a function of sample size, calculated as the difference between the estimated age and the real age at death ($e_x = x_{est} - x_{real}$) for those records for which either the time of birth (b_i) or death (d_i) was unknown. The 67% and 95% credible intervals were obtained by calculating the difference from all estimates on the Markov Chain Monte Carlo chains after burn-in.

after age 1, reaching considerably lower mortality rate values than males. The age at lowest mortality is 5·59 years (±0·37) for females, and 4·57 years (±1·33) for males. Life expectancy at age 1 for males is $E[X] = 1{\cdot}54$ years (±0·9), and for females $E[X] = 3{\cdot}43$ years (±0·27). The only parameter with K–L discrepancy close to 0 was β_2 ($D_{mf} = 0{\cdot}34$). Although slightly skewed, the estimation of ages at death for censored and truncated records had little bias with mean error $\bar{e}_x = 0{\cdot}94$ years (±2·11).

Discussion

Our results stress the existence of important problems in the estimation of age-specific survival from CRR data sets, most

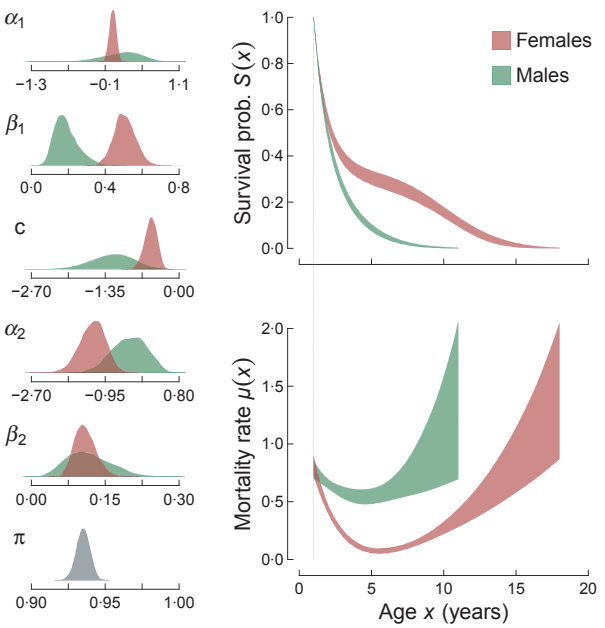

Fig. 5. Posterior distributions of Siler parameter estimates for female and male Soay sheep, and resulting age-specific survival probabilities, $S(x)$ (top row), and mortality rates, $\mu(x)$ (bottom row) for both sexes. The analysis was conditioned on individuals that survived to the first year of life (vertical dotted lines). The width of the survival probability and mortality rate polygons represents the 95% credible intervals.

of which are associated with data collection. Traditional methods to estimate age-specific survival from CRR data can be inaccurate when the population studied has a low recapture probability and small sample sizes, or when the duration of the study only spans a fraction of the life span of the species. Here, we demonstrate that it is possible to reduce these inaccuracies by adopting a hierarchical structure within a Bayesian framework that draws inference from censored records to estimate survival parameters, recapture probabilities and the latent (unknown) times of birth and death. Although the inclusion of these latent variables incorporates additional sources of uncertainty into the inferential process, the magnitude of the resulting credible intervals is negligible in comparison to the accuracy of the estimates (Fig. 2). Thus, the risk of higher uncertainty is counterbalanced by the increased sample size associated with admitting truncated data. This brings us back to the original problem of having a small number of older individuals in most data sets, which limits the estimation of age-specific survival under a traditional framework (Nisbet 2001). Once again, here, we have shown that our method has the power to overcome this otherwise unavoidable limitation.

Despite the advantages outlined above, it is important to stress that our model was sensitive to the selection of priors when recapture probabilities were low (Fig. 1). We found that priors that result in low survival probability tend to penalize the estimation of ages at death towards younger ages when recapture probabilities are low. We improved inference by selecting priors that overestimated survival probability (see Fig. 1S of Appendix S2). Specifically, the best combination of priors had a relatively low baseline mortality parameter (Gompertz α) with the shape parameter (Gompertz β) being slightly smaller than the real value.

Importantly, our results reveal that many of the limitations in the estimation of vital rates and their parameters can be reduced through a more efficient field-sampling scheme. For instance, a common problem for the two models we tested is that estimation of survival parameters and latent states becomes less accurate when recapture probability is low. For many species, recapture probabilities can be increased by focusing the sampling effort on a subset of the population, instead of attempting to capture–recapture individuals across the entire population. This can further be combined with population surveys, independent from the capture–recapture effort, to estimate population sizes (Besbeas *et al.* 2002; Schofield & Barker 2008). Another important problem is the bias in the estimation of age-specific survival probabilities when recoveries are restricted to the study span and the recapture probability is low. In this case, there are a disproportionate number of known deaths for younger individuals, while most individual capture histories tend to be shorter because of the low recapture probability, forcing the model to underestimate ages at death. A solution to this problem is to either increase recapture probabilities by focalizing the effort or to extend the study so that it approximates the duration of the species life span.

Analyses of age-specific patterns of mortality and survival in ungulates have suggested that mortality changes with age (Loison *et al.* 1999; Catchpole *et al.* 2000; Tavecchia *et al.* 2005). As noted by Catchpole *et al.* (2000) and Tavecchia *et al.* (2005), Soay sheep survival (or mortality) is strongly age-dependent. In agreement with these previous results, our analysis of a subset of the Hirta Soay sheep data set shows clearly a 'bathtub' shape in mortality rate with age (Fig. 5). Moreover, our results stress differences in mortality between males and females, with females having longer life expectancy than males and reaching the age of lower mortality 1 year later than males. Still, the similarity in K–L discrepancy in the Siler parameter β_2 suggests that, after reaching the age of minimum mortality, the rate of ageing for both sexes is similar. We want to stress that other covariates have been shown to strongly influence mortality in Soay sheep (Catchpole *et al.* 2000; Coulson *et al.* 2001; Tavecchia *et al.* 2005; King *et al.* 2006; Pelletier *et al.* 2007). However, the purpose of this exercise was not to perform an in-depth study of mortality drivers in Soay sheep, but to illustrate the use of the model and how covariates could be included, as well as the accuracy in the estimation of ages at death (mean error of only 0·94 years) despite the short duration of the study (T = 10 years, with maximum life span of 16 years).

There are important trade-offs between using traditional models, for which powerful software packages are easily available (e.g. MARK; White & Burnham 1999), and applying more complex models that require larger conceptual and computational investments. In that sense, the purpose of this analysis was to assess under which circumstances that extra

effort becomes advisable, or even necessary. From our analyses, we believe that the investment is worthwhile at least when the detection probability and sample size are low. However, for those willing to explore these models, we stress that the advantages of this hierarchical Bayesian framework are considerable, irrespective of the quality of the data sets. In that sense, to facilitate the implementation of this approach and to make it accessible to a wider audience, we are incorporating these methods into an upcoming R package (BaSTA-Bayesian Survival Trajectory Analysis; F. Colchero, O. R. Jones & M. Rebke, unpublished data).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R code for Bayesian hierarchical model.

Appendix S2. Figure S1 survival probabilities, mortality rates and cdf's of ages at death from the four sets of priors tested. Figures S2 and S3 that show the results of the estimation of the Gompertz baseline mortality parameter, α and the recapture probability, π. Figure S4 shows trace plots for Gompertz parameters for the Soay sheep analysis.

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