A state-space modelling approach to population size estimation

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Abstract

We consider populations of wild animals that are closely monitored over time, by being recaptured on multiple occasions, until finally recovered dead or lost to follow up. We propose a state-space formulation that enables us to estimate, simultaneously: time-varying size, demographic composition and geographical dispersal of an open population. Simulations show that our method is robust to low proportions of monitored individuals. Parameters are estimated with MCMC methods within a fully Bayesian approach and our model is applied to a real population for which we are able to provide new results.

Keywords: Bayesian estimation; MCMC; Population ecology; Recapture; Recovery; Seasonality; Soay sheep; Spatio-Temporal; State-Space.

1 Introduction

Consider a population of wild animals where some individuals are marked when first captured and after being released they may be either recaptured or simply resighted from a distance on multiple occasions, within each year, until finally recovered dead within the study period or not seen again. Live recaptures and distant resightings are often carried out at different times, independently of one another, with a different design, implementation scheme and typically with a different effect on the behaviour of the monitored individuals. The scientific interest lies in understanding changes in key

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demographic parameters, such as survival and fertility, and in relating these changes to both individual and environmental factors. Closely monitored populations provide access to extensive and detailed individual data and we propose a method to use such information efficiently in order to estimate different aspects of the population dynamics. We consider a discrete time framework which is often appropriate in ecological applications because important demographic events, such as reproduction and survival, may be modelled on a seasonal basis rather than on an individual one. This also influences the study design, as researchers will prefer to capture or observe individuals during specific time periods. Thus we adopt a seasonal temporal scale, as opposed to an annual one which is often used for long-term mark-recapture-recovery (MRR) studies, to allow for heterogeneity in the behaviour of individuals and in the data collection process, within each year. We propose a novel state-space modelling formulation that combines the two independent observation processes, live recaptures and distant resightings (RES), with a latent system process describing the demographic structure of the population. Our model allows us to estimate simultaneously: time-varying size, demographic composition and geographical dispersal of an open population. In Section 2 we first describe the general modelling framework and then develop a specific model for each of the processes considered. In Section 3 we illustrate the role of the system process as an informative prior structure for the population size and some possible uses of the estimated time-varying dispersal. Section 4 provides implementation details while Section 5 contains a simulation study to asses the robustness of the population size estimation to varying the proportion of individuals resighted. In Section 6 we apply our model to a well-known population that has been studied for over twenty years and we obtain new interesting results.

2 A State-space modelling framework

State-space models consider the simultaneous evolution over time, (here indexed by j), of an observable process, $\mathbf{C}_j$, and of a non-observable one, $\mathbf{N}_j$, called the system process. The system process represents the underlying mechanism that explains the temporal dynamics of $\mathbf{C}_j$, while the latter is also the result of a potentially complicated structure of sampling variability. The aim is to estimate the underlying process $\mathbf{N}_j$, given these noisy observations, and one of the main advantages of this formulation is that sampling variability and changes in the underlying system are modelled separately (West & Harrison, 1997). In population ecology state-space models may be used to model noisy counts of individuals from a population and to explain the temporal dynamics with an underlying species-specific demographic structure. Within this application area, three main approaches have been used to estimate parameters: Kalman Filtering (Besbeas et al., 2002), Sequential Importance Sampling (SIS) (Thomas et al., 2005) and MCMC (Brooks et al., 2004). Other applications include estimating the order of density dependence by means of Reversible Jump MCMC (Jamieson & Brooks, 2004), a relationship between the system variance and the amount of smoothing induced on a population index (Mazzetta et al., 2007), and a comparison of the performance of SIS and MCMC (Newman et al., 2009). In this article we consider non-linear and non-normal processes, both for the system and for the observations, and we adopt a fully Bayesian parameteric approach where the estimation is performed by using MCMC methods.

2.1 System Process: seasonal demographic structure

The system process is used to model changes over time in the demographic structure of the population, thus its corresponding parameters are of direct interest because of their ecological interpretation. Here we assume that individuals become adults, able to give birth, at the beginning of their second year of life and that births always occur during Spring, but this may be modified to accommodate different species. Let the index $j = 1, \ldots, J$ denote the season, here defined as {Mar-May, Jun-Aug, Sep-Nov, Dec-Feb} = {Sp, Su, Au, Wi}, and let $a = 1, \ldots, A+$ denote the age group, with $a = 1$ corresponding to the first year of life and $a = A+$ to individuals in their A^{th} year of life or older. The size of the population aged a at the beginning of season j is denoted by N_j^a and the number of offspring, $N^1_{Sp_j}$, is modelled with a discrete-valued distribution that depends on the particular species. In our application we may observe only $0, 1$ or 2 offspring per adult female and we decided to describe such a number with a binomial distribution, $\mathrm{Bin}(2, \rho_{Sp_j})$. We assumed that individuals reproduce independently of one another according to a common ρ_{Sp_j} each Spring, so that the total number of individuals born each Spring is described with $\mathrm{Bin}(2N^{2+}_{Sp_j}, \rho_{Sp_j})$. An extension may account for individual-specific reproduction parameters ρ_{iSp_j}. We also use binomial distributions to describe the number of individuals surviving from one season to the next. In particular, we denote by ϕ^a_j the probability that an individual aged a survives the interval $(j, j+1)$; thus for appropriate nonnegative integers x we have that for individuals in their first year of life:

$$P(N^1_j = x) = \begin{array}{ll} \binom{2N^{2+}_j}{x}[\rho_j]^x[1-\rho_j]^{2N^{2+}_j - x} & j = \mathrm{Sp} \\ \binom{N^1_{j-1}}{x}[\phi^1_{j-1}]^x[1-\phi^1_{j-1}]^{N^1_{j-1}-x} & j \neq \mathrm{Sp}. \end{array} \qquad (1)$$

When modelling adult survival we need to account for all changes in age groups ccurring each Spring and for $1 < a < A$ we have that:

$$P(N^a_j = x) = \begin{array}{ll} \binom{N^{a-1}_{j-1}}{x}[\phi^{a-1}_{j-1}]^x[1-\phi^{a-1}_{j-1}]^{N^{a-1}_{j-1}-x} & j = \mathrm{Sp} \\ \binom{N^a_{j-1}}{x}[\phi^a_{j-1}]^x[1-\phi^a_{j-1}]^{N^a_{j-1}-x} & j \neq \mathrm{Sp}. \end{array} \qquad (2)$$

The distribution of the number of individuals aged $A+$ at the beginning of each Spring requires the convolution of two binomials because $N^{A+}_{j_{Sp}}$ is equal to the number of surviving individuals that were aged $A-1$ the previous Winter plus the number of surviving individuals that were already in $A+$, so that $P(N^{A+}_j = x)$:

$$\begin{array}{ll} \sum_{k_j=\mathrm{L}_j}^{\mathrm{U}_j} \binom{N^{A+}_{j-1}}{k_j}[\phi^{A+}_{j-1}]^{k_j}[1-\phi^{A+}_{j-1}]^{N^{A+}_{j-1}-k_j} \binom{N^{A-1}_{j-1}}{x-k_j}[\phi^{A-1}_{j-1}]^{x-k_j}[1-\phi^{A-1}_{j-1}]^{N^{A-1}_{j-1}-x+k_j} & j = \mathrm{Sp} \\ \binom{N^{A+}_{j-1}}{x}[\phi^{A+}_{j-1}]^x[1-\phi^{A+}_{j-1}]^{N^{A+}_{j-1}-x} & j \neq \mathrm{Sp} \end{array} \qquad (3)$$

where the extremes for the summation are defined as $\mathrm{L}_j = \max\{0, x - N^{A-1}_{j-1}\}$ and $\mathrm{U}_j = \min\{x, N^{A+}_{j-1}\}$. The system (1)-(3) is defined by using standard distributions and its ecological interpretation is clear, but its implementation can be challenging. For a Bayesian approach, the posteriors for the population parameters are non-standard and the series of binomials requires a set of constraints that need to be satisfied when estimating parameters N_j^a for $j = 1, \ldots, J$ and $a = 1, \ldots, A+$, for example with an MCMC algorithm. More details regarding the estimation are provided in Appendix A.

2.2 Observation process 1: population size and dispersal

The first observation process that we model concerns the resightings (RES) of animals where we assume that individuals may be seen in a study area partitioned in S locations that are all easily accessible (no barriers or geographical constraints). The survival and reproduction of the resighted individuals should not differ from that of the non-resighted ones and births or deaths may occur during the observation period. The data should be in the form of individual resighting histories as we assume that, each season, researchers are able to identify individuals uniquely. From this observation process we aim to estimate the size of the population accessing the study area and to understand how its geographical dispersal changes with time. Let N be the unknown size of a population, S the number of samples taken sequentially and for each sampling occasion $l = 1, \ldots, S$ let π_l be the probability of resighting an individual, c_l the number of individuals sampled, m_l the number of marked individuals in the sample and M_l the corresponding number in the population just before the l^{th} sample. Then, assuming that: (i) the population remains constant throughout the study; (ii) there are initially no marked animals; and (iii) in a given sample all animals have the same propensity of being caught, it is possible to show (see for example Casteldine (1981)) that the likelihood takes the following form:

$$L_{RES}(\mathbf{c}, n \mid N, \boldsymbol{\pi}) \propto \frac{N!}{(N-n)!} \prod_{l=1}^{S} [\pi_l]^{c_l} [1-\pi_l]^{N-c_l} \tag{4}$$

where $n = \sum_l (c_l - m_l)$ is the number of distinct individuals. Now, if we refer to the sequential resighting of individuals in S locations during a specific season j we may write:

$$L_{RES}(\mathbf{c}_j, n_j \mid N_j, \boldsymbol{\pi}) \propto \frac{N_j!}{(N_j-n_j)!} \prod_{l=1}^{S} [\pi_{lj}]^{c_{lj}} [1-\pi_{lj}]^{N_j-c_{lj}} \tag{5}$$

but since we are considering observation periods of three months, assumption (i) cannot be satisfied, and we need to account explicitly for seasonal survival. We do so by exploiting the autoregressive structure of the system process and by relating the resightings during the period $(j, j+1)$ to the population available at the beginning of the next season, i.e. the N_{j+1} that survived with probability ϕ_j:

$$L_{RES}(\mathbf{c}_j, n_j \mid N_{j+1}, \boldsymbol{\pi}) \propto \frac{N_{j+1}!}{(N_{j+1} - n_j)!} \prod_{l=1}^{S} [\pi_{lj}]^{c_{lj}} [1 - \pi_{lj}]^{N_{j+1} - c_{lj}}. \tag{6}$$

Assumption (iii) is not compatible with our interest in the long term population dynamics, thus here we allow the resighting probabilities to vary with time. We also wish to incorporate heterogeneity of resighting across different age groups but rather than allowing for age-specific resighting probabilities, π_{lj}^a, we exploit the information we already have on the age-specific structure of the population and we construct a likelihood that is consistent with the system process:

$$L_{RES}(\mathbf{c}, \mathbf{n} \mid \mathbf{N}, \boldsymbol{\pi}) \propto \prod_{a=1}^{A+} \prod_{j=1}^{J-1} \frac{N_{j+1}^*!}{(N_{j+1}^* - n_j^*)!} \prod_{l=1}^{S} [\pi_{lj}]^{c_{lj}} [1 - \pi_{lj}]^{N_{j+1}^* - c_{lj}} \tag{7}$$

where the number of distinct individuals, n_j^*, and the population size, N_{j+1}^*, take values:

$$\begin{cases} n_j^* = n_j^{a-1} & N_{j+1}^* = N_{j+1}^a, \quad \text{j} = \text{Wi and } 1 < a < A+ \\ n_j^* = n_j^{A-1} + n_j^{A+} & N_{j+1}^* = N_{j+1}^{A+}, \quad \text{j} = \text{Wi and } a = A+ \\ n_j^* = n_j^a & N_{j+1}^* = N_{j+1}^a, \quad \text{j} \neq \text{Wi and } 1 \leq a \leq A+ \end{cases}$$

The introduction of an autoregressive structure to account explicitly for deaths during the observation period is particularly important for a correct estimation of the population size, as the latent survival may act as a censoring mechanism on the resighting process, inducing an underestimation of the resighting probabilities and a consequent overestimation of the population size. In order to be able to use this relatively complex structure, the use of different sources of information to estimate different groups of parameters becomes very important. In the next section we describe how we estimate the survival parameters ϕ_j^a, for $j = 1, \ldots, J$ and $a = 1, \ldots, A+$, appearing in the system from a second observation process.

2.3 Observation process 2: survival, recapture and recovery

The estimation of survival parameters appearing in (1)-(3) relies on a second observation process where we combine live recaptures and dead recoveries, as in Catchpole et al. (1998), Besbeas et al. (2002) and King et al. (2006). The data consist of individual histories indicating for each season whether a marked animal was physically recaptured, found dead or not seen. The main challenge posed by this type of data is the potential presence of *blank* periods between the last live recapture and the dead recovery (or the end of the study) where we need to model all the possible survival patterns. For an individual i, let X_{ij} be an indicator function taking value 1 if recaptured alive at j, f_i and l_i the times of the first and last live recapture, respectively, and r_i the eventual recovery time. As for individual parameters, let $\phi_{ij}^{'}$ denote the probability of surviving the time interval $(j, j+1)$; $p_{ij+1}^{'}$ the probability of recapture at $j+1$; and $\lambda_{ij}^{'}$ the probability of being recovered in $(j-1, j)$ given death in (l_i, j). The contribution of each recaptured individual to the estimation of age- and season-specific MRR parameters, (ϕ_j^a, p_j^a and λ_j^a), can be obtained from the season of birth, say b_i, by setting $\theta_{ij} = \theta_j^a$ whenever $(j - b_i)/4 = a$, for $\theta_{ij} \in \{\phi_{ij}^{'}, \lambda_{ij}^{'}, p_{ij}^{'}\}$. From the individual capture histories it is possible to write down explicitly the MRR likelihood describing all live captures, all possible survival histories between l_i and r_i, and all possible survival histories between l_i and J for individuals who are never seen again. However, our *blank* intervals are similar to those we would encounter with delayed recoveries and, in particular, our likelihood would correspond to the case $\kappa = 1$ described in Catchpole et al. (2001). Thus we denote by χ_{il_i} the probability of not being recaptured between l_i and the end of the study J and by $\lambda_{il_ir_i}^{*}$ the probability of being recovered in $(r_i - 1, r_i)$ given last resighting was l_i, where $r_i = l_i + 1, \ldots J$. Note that we need the first index i because two individuals may have the same l_i (or r_i) but be of different age. The following recursions simplify the explicit likelihood expression and speed up the computation:

$$\begin{cases} \lambda^{*}_{il_ir_i} = & [1-\phi^{'}_{il_i}]\prod_{k=l_i+1}^{r_i-1}[1-\lambda^{'}_{ik}]\lambda^{'}_{ir_i} + \phi^{'}_{il_i}[1-p^{'}_{il_i+1}]\lambda^{*}_{il_i+1r_i} \\ \lambda^{*}_{ir_i-1r_i} = & [1-\phi^{'}_{ir_i-1}]\lambda^{'}_{ir_i} \\ \chi_{il_i} = & [1-\phi^{'}_{il_i}]\prod_{k=l_i+1}^{J}[1-\lambda^{'}_{ik}] + \phi^{'}_{il_i}[1-p^{'}_{il_i+1}]\chi_{il_i+1} \\ \chi_{iJ} = 1 & \end{cases} \tag{8}$$

so that the MRR likelihood may be written as:

$$L_{MRR}(\mathbf{X} \mid \boldsymbol{\phi}', \boldsymbol{\lambda}', \mathbf{p}^{'}) = \prod_{i=1}^{n}\Big[\prod_{j=f_i}^{l_i-1}\phi^{'}_{ij}(p^{'}_{ij+1})^{X_{ij+1}}(1-p^{'}_{ij+1})^{1-X_{ij+1}}\Big]\Big[\lambda^{*}_{il_ir_i}\Big]^{I_{[l_i<r_i\leq J]}}\Big[\chi_{il_i}\Big]^{I_{[r_i>J]}}. \tag{9}$$

The probabilities $p^{'}$ could be extended to include the effects of covariates (King & Brooks, 2008), individual random effects (Barry et al., 2003) or a behavioural response to recapture (Chao et al., 2000), for example by using a logistic link as in Catchpole et al. (2000). The use of covariates would reduce the number of parameters and facilitate the implementation, but we preferred to keep results more general when estimating, for the first time for our species, seasonal patterns of survival, recapture and recovery.

3 Model interpretation

The following sections further highlight the advantages of our method in terms of interpretability of the structure and possible uses of the estimates.

3.1 Priors for the population size

In general, when trying to estimate the size N of a population from capture-recapture data with a Bayesian approach the choice of the prior $\pi(N)$ is very important. When there is little information about the population under study a common choice is Jeffrey's non-informative prior $\pi(N) \propto N^{-1}$, see for example George & Robert (1992); when more information is available other priors may be used, for example a Negative Binomial (Madigan & York, 1997) or a Discrete Uniform (Basu & Ebrahimi, 2001).

Our problem is to estimate $N_j^a \ \forall(a, j)$ and a single prior common to all these parameters would not be efficient. Another complication would be to decide, in an ecologically meaningful way, how to choose the large number of parameters in the hyperpriors. We prefer instead to provide more information on the structure, which is interpretable, and less on the hyperpriors parameters. We obtain age and seasonal-specific priors, $\pi(N_j^a)$, as products of the distributions described in (1)-(3) that are adjacent in time and/or age, as described in Appendix A. The magnitude of the N_j^as depends on the resightings while the shape of the estimated time series of N_j^a (i.e. the population dynamics) depends on the survival parameters ϕ_j^a that are estimated from the recapture/recovery data.

3.2 Resighting probabilities

The catchability of individuals influences the estimation of the population size and there are typically three aspects that are studied: time effects, trap response and heterogeneity across individuals. One of the first papers to discuss these aspects is Otis et al. (1978) and both classical approaches (Pledger (2000), Dorazio & Royle (2003), Morgan & Ridout (2008)) and Bayesian approaches (Basu & Ebrahimi (2001), Tardella (2002), King & Brooks (2008)) have been used to incorporate these effects when estimating the size of a closed population. In (7) we do not incorporate trap response because we assume that individuals are observed from a distance; we account for heterogeneity across different age-groups by considering an age-varying parameter N_{j+1}^a, and we are interested in how the species uses the study area in different seasons. We choose a logistic link to regress resighting probabilities on location and time: $\pi_{lj} = \exp[\mu + \alpha_l + \beta_j]/(1 + \exp[\mu + \alpha_l + \beta_j])$, for $l = 1, \ldots, S$ and $j = 1, \ldots, J-1$, where, for example, we can set α_1 and β_1 equal to zero to ensure identifiability. We then specify the following hyperpriors:

$$\begin{array}{lll} \pi(\mu) = \exp(\mu)/[1 + \exp(\mu)]^2 & \alpha_l \sim N(0, \sigma_\alpha^2) & \beta_j \sim N(0, \sigma_\beta^2) \\ & \sigma_\alpha^2 \sim IG(\nu_\alpha, \lambda_\alpha) & \sigma_\beta^2 \sim IG(\nu_\beta, \lambda_\beta) \end{array} \qquad (10)$$

where $\pi(\mu)$, already described in King & Brooks (2008), is obtained by starting from a Uniform[0,1] prior on the overall RES probability, for $\alpha_l = \beta_j = 0$, and by then considering the transformation $\mu = \text{logit}(\pi_{lj})$. The hyperparameters for the variance terms should reflect the information available a priori and even with little or no information their choice should be consistent with the particular application and with the observation process chosen to model the data. We believe they should not be arbitrarily fixed to commonly chosen values if these imply unrealistic patterns for the time series.

3.3 Time-varying geographical dispersal

The probabilities, $\{\pi_{lj}, l = 1, \ldots, S; j = 1, \ldots, J-1\}$, help us to understand how the preferences for locations change with time. They may also be used to investigate whether the geographical dispersal changes with increasing/decreasing demographic pressure or simply with the behaviour of the two sexes in different seasons. If the locations differ from one another in terms of vegetation then these probabilities may be related to the feeding behaviour in different seasons or to changes in the quality of the environment for long term studies.

4 Implementation

We assign uniform priors on $[0,1]$ to the probabilities ϕ_j^a, λ_j^a and p_j^a and use a Metropolis-Hastings (M-H) algorithm where new values are proposed with a normal distribution truncated on the interval $[0,1]$. The computations remain slow, with an iteration taking about half a second with the specifications reported at the end of this section, despite the recursions introduced in §2.3, but the parameters stabilise rapidly around their posterior means. Note that posteriors for λ_j^a and p_j^a are built from MRR likelihood while those for ϕ_j^a are also related to the system process. For parameters N_j^a we use again M-H but with asymmetric discrete uniform proposals over intervals that change at each iteration to ensure consistency with both the system and the observation process (details are provided in Appendix B). Parameters (μ, α_l, β_j) are simply proposed with normals centered on the current values and since we are using a logistic regression the computations required for the RES probabilities are very fast. Finally we use Gibbs sampling for parameters σ_α^2, σ_β^2 that have standard gamma posteriors and for the ρ_js that have standard beta posteriors. We may need to estimate thousands of parameters (see §6) so we consider a pilot adaptive phase of m iterations, (before the burn in), in which we start with a proposal variance equal for all parameters and then every k iterations we measure the average acceptance rates (AR) over the last $m/2$ generated values. We require values between 0.25 and 0.45, so if a parameter has an AR below 0.25 (above 0.45) then the variance of its proposal is increased (decreased) by 10%. These m iterations are then discarded as the only aim is to find a better proposal; the method is based on a paper by Gelman et al. (1996). In Section 6 we ran simultaneously 5 independent chains of length 10^5 and assessed convergence with the method proposed by Gelman & Rubin (1992); see also Brooks & Gelman (1998). We discarded the first 2×10^4 iterations as a burn-in and then retained the second half of each chain obtaining a sample of 2×10^5 iterations. This procedure took 7 hours to run on a multiple core 3.4 GHz server.

5 Simulation Study

We conducted a simulation study to investigate the robustness of the population size estimation with respect to a changing proportion of resighted individuals and we chose $A = 8$, $S = 30$ and $J = 79$ to match the dimensions we had in the real data set analysed in Section 6. Algorithm 1 ($A1$) below describes one way to generate parameters and Algorithm 2 ($A2$) may be used either to generate data or to appropriately format raw data. We considered a few values for μ to have different magnitudes for the proportions of distinct individuals resighted over the J seasons. For example, if we use $A2$ to generate a data set 100 times then, on average when $J = 79$: for $\mu = -4.5$ the mean (across seasons) proportion of distinct individuals resighted is 40% (min=12%, max=83%); for $\mu = -5.0$ the mean proportion is 28% (7%, 66%); for $\mu = -5.5$ it is 19%

(min=5%, max=49%); and for $\mu = -6.0$ ii is 12% (min=3%, max=33%). Note that for a given μ these proportions also increase with J. Figure 1 shows the posterior means with 95% HPDIs, (after one run of the algorithm): despite uncertainty increases as the percentage if individuals resighted decreases, the estimation of the overall population size is very good in all four scenarios.

[Figure 1 about here.]

5.1 Algorithm 1: generation of parameters

1. *Dimensions*: J=79, S=30, A=8; let: $j = 1, \dots, J$; $l = 1, \dots, S$; $a = 1, \dots, A$
2. *Births*: $\rho_j \sim \text{Unif}(0.1, 0.6)$ if $j = \text{Sp}$ and $\rho_j = 0$ if $j \neq \text{Sp}$
3. *Survival*: $\phi_j^1 \sim \text{Unif}(0.3, 0.7)$ for $(j = \text{Sp})$; $\phi_j^1 \sim \text{Unif}(0.8, 1.0)$ for $(j \neq \text{Sp})$; $\phi_j^{2:4}, \phi_j^{5:7} \sim \text{Unif}(0.9, 1.0)\ \forall j$; $\phi_j^{8+} \sim \text{Unif}(0.7, 1.0)\ \forall j$
4. *Beginning of series*: set initial values for N_j^a
5. *Population size*: generate $N_j^a, \forall(a, j)$ according to the system process
6. *Resighting*: choose $\mu_k \in \{-2.5, -3, -3.5, -4\}$; set $\sigma_\alpha^2 = 2.0$ and $\sigma_\beta^2 = 0.4$; generate $\alpha_1, \dots, \alpha_S \sim N(0, \sigma_\alpha^2)$ and $\beta_1, \dots, \beta_{J-1} \sim N(0, \sigma_\beta^2)$; calculate $\pi_{lj(k)} = \exp(\mu_k + \alpha_l + \beta_j)/[1 + \exp(\mu_k + \alpha_l + \beta_j)]$, $\forall(l, j)$

5.2 Algorithm 2: generation/format of resighting data

Given a value μ_k, for $a = 1, \dots, A$ and for $j = 1, \dots, J-1$, if $(N_{j+1}^a > 0)$:

1. Generate $X_{i_j l}^a \sim \text{Bin}(1, \pi_{lj(k)})$ for $i_j = 1, \dots, N_{j+1}^a$ and $l = 1, \dots, S$ and store values in a matrix, say X, of dimension $N_{j+1}^a \times S$
2. Build a matrix Y, same dimensions as X, for the already marked individuals: $Y_{i_j l} = 1$, if $\sum_{h=1}^{l-1} X_{i_j, h]} > 0$ and $Y_{i_j l} = 0$ otherwise
3. *Numbers recaptured*: $(c_{1j}^a, \dots, c_{Sj}^a) = (\sum_{i_j} X_{i_j 1}^a, \dots, \sum_{i_j} X_{i_j S}^a)$

4. *Numbers marked*: $(m^a_{1j}, \ldots, m^a_{Sj}) = (\sum_{i_j} Y_{i_j 1}, \ldots, \sum_{i_j} Y_{i_j S})$

5. *Distinct individuals*: $n^a_j = \sum_l (c^a_{lj} - m^a_{lj})$

Note that for Winter resightings n^a_j and c^a_{lj} will refer to N^{a+1}_{j+1} and that in particular from N^{A+}_{Sp} we are actually generating $(n^{A-1}_{Wi} + n^{A+}_{Wi})$ and $(c^{A-1}_{lWi} + c^{A+}_{lWi})$. When using real data, step 1 is replaced by the calculation of the matrix X from the raw data.

6 Application

We analyse data for the Soay sheep population on the island of Hirta, 200 Km west of Scotland in the archipelago of St Kilda, a species similar to the neolithic sheep introduced in Britain around 5000BC (Clutton-Brock & Pemberton, 2004). The total population has been counted annually since the 1950s and MRR data are available since 1985. A recent Bayesian analysis for this species is for example in King et al. (2006). The majority of dead recoveries take place during Winter and the majority of live recaptures during Summer. The population level has an interesting trend over time as it periodically increases to a level higher than the island can support and then it suddenly falls (Coulson et al., 2001). The age structure of this population has been studied in many papers and, since we specifically consider the female population, we refer to the extensive work of King et al. (2006) who considered $a = 1, \ldots, 8+$ and then identified the most probable age class groupings for the MRR parameters by means of Reversible Jump MCMC. In this article we build for the first time a season-specific data set, from Spring 1986 to Autumn 2005 ($J = 79$), where MRR data are available for 1185 female individuals while RES data are available for 1501 individuals.

6.1 Survival, recapture and recovery

We follow King et al. (2006) and for survival we consider four age groups, $a = 1$, $1 < a < 5$, $4 < a < 8$ and 8+ but we consider a seasonal rather than an annual scale. The estimates are reported in Figure 2 and highlight a higher seasonal variability for younger and older individuals. The uncertainty for parameter ϕ^1_{Sp} in 2001 is due to the fact that there are no recapture data in that season and such data is the only source of information that allows us to estimate survival in the first season of life. Differently from other seasons and ages, the required information cannot be inferred from adjacent (in time or age) parameters, thus the posterior for ϕ^1_{Sp} has essentially the same variability as the prior and this produces a higher uncertainty also on ρ_{Sp} and N^1_{Sp} in the same year.

[Figure 2 about here.]

For recovery probabilities we separate recovery of lambs, λ^1_j, from that of adults, λ^{2+}_j, and obtain results similar to King et al. (2006), with peak recovery corresponding to the years of population reduction ('88, '91, '94, '98, '01, '04) plus some additional information on seasonality: the peaks are completely determined by winter recoveries; adult recovery probabilities can be estimated well in each season; lamb recoveries can only be estimated reliably during Winter. Results are not shown but available on request. Our probabilities p^a_j have a different interpretation from King et al. (2006) as they specifically refer to physical recaptures, thus we report results for each age group. Figure 3 shows the posterior means and corresponding 95% HPDIs characterised by a strong seasonal component which is related to the study design: researchers prefer to recapture individuals during the Summer when the weather conditions make it easier to reach the island.

[Figure 3 about here.]

6.2 Geographical dispersal

The study area on Hirta is divided into 30 distinct locations and each individual may be seen on more than one location within a season. In Figure 4, the estimated π_{lj}s for 9 of the 30 locations show the preference for some specific locations and a seasonal trend in their use, here evident for 'WESF', 'WESM' and 'OLDV'. The estimated effect for each location and its associated uncertainty is reported in Table 1. Here, apart from a few locations (ANLA, CEME, GEAR, GYM and HELI) where individuals are rarely resighted, the estimates are quite precise and highlight a marked preference for some specific locations, probably attributable to the quality of the vegetation.

[Figure 4 about here.]

[Table 1 about here.]

6.3 Population size

The study area on Hirta represents about one third of the island and is regularly accessed by a proportion of the island population that varies with season. A formal estimation of the geographical dispersal through the probabilities π_{lj} has never been done before and the population has never been estimated specifically by age and season. Each Summer all individuals on the island are counted, thus we compared our estimated dynamics with these raw data that we have only for the Summer season. In Figure 5 we plotted the estimated female population (all age groups) accessing the study area together with the number of distinct individuals resighted, the raw Summer counts in the study area and the raw Summer counts in the whole island. Although this population is very well monitored, counting all the individuals present in the study area in one specific season would underestimate the size of the population accessing the study area, if individuals are free to enter and exit the study area and their presence varies from one season to the next. It appears that our system process, which describes age and seasonal specific survival and reproduction, models with enough detail the demographic structure to be able to estimate the population dynamics over a long period of time. Interestingly, the population accessing the study area appears to have a more stable dynamic, fluctuating less than the population in the whole island.

[Figure 5 about here.]

7 Conclusions

The state-space formulation that we propose accounts for survival when estimating the geographical dispersal, and the combination of these two pieces of information is typically difficult. Thus a common assumption is that the population is demographically closed during the period of observation as, for example, in Borchers & Efford (2008) and Dorazio et al. (2008). The use of a seasonal time scale is particularly important as seasonality characterises survival and reproduction, but may also characterise recaptures for logistical reasons and geographical dispersal through changes in behaviour. Here we preferred to assign a major role to the demographic structure, as opposed to environmental covariates, as the increased complexity is balanced by a better ecological interpretation of the population dynamics. Moreover we can make better use of the available information and avoid strong assumptions on the homogeneity of the data and of their collection, within a year. We showed how by understanding the seasonality of mortality and reproduction we can estimate the varying size of an open population over a long period of time. Our method assumes that the population is homogeneously mixing, thus it is able to estimate only the population that has access to the study area. The Soay sheep population has been studied extensively so we had the opportunity to check the consistency of our results with previous work while providing substantial new information. In our application locations are close to one another and individuals are able to move quickly between them, but this assumption may not always be appropriate. Thus, an interesting extension would be the introduction of a structure of dependency between locations while preserving an easy interpretation of the corresponding parameters.

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Appendix A

Full conditional distributions for the population size $\pi(N_j^a \mid \dots)$

The system process describing the age and seasonal specific demographic structure requires a number of constraints for the corresponding parameters such that $L_j^a \leq N_j^a \leq U_j^a$. These constraints are reported in the following table where: $L_j^{A-1} = N_{j+1}^{A+} - N_j^{A+}$, $L_j^{A+} = N_{j+1}^{A+} - N_j^{A-1}$ and $U_j^{A+} = N_{j-1}^{A+} + N_{j-1}^{A-1}$:

j = Spring	j = Summer	j = Autumn	j = Winter
$N_{j+1}^1 \leq N_j^1 \leq 2N_j^{2+}$	$N_{j+1}^1 \leq N_j^1 \leq N_{j-1}^1$	$N_{j+1}^1 \leq N_j^1 \leq N_{j-1}^1$	$N_{j+1}^2 \leq N_j^1 \leq N_{j-1}^1$
$N_{j+1}^a \leq N_j^a \leq N_{j-1}^{a-1}$	$N_{j+1}^a \leq N_j^a \leq N_{j-1}^a$	$N_{j+1}^a \leq N_j^a \leq N_{j-1}^a$	$N_{j+1}^{a+1} \leq N_j^a \leq N_{j-1}^a$
$N_{j+1}^{A-1} \leq N_j^{A-1} \leq N_{j-1}^{A-2}$	$N_{j+1}^{A-1} \leq N_j^{A-1} \leq N_{j-1}^{A-1}$	$N_{j+1}^{A-1} \leq N_j^{A-1} \leq N_{j-1}^{A-1}$	$L_j^{A-1} \leq N_j^{A-1} \leq N_{j-1}^{A-1}$
$N_{j+1}^{A+} \leq N_j^{A+} \leq U_j^{A+}$	$N_{j+1}^{A+} \leq N_j^{A+} \leq N_{j-1}^{A+}$	$N_{j+1}^{A+} \leq N_j^{A+} \leq N_{j-1}^{A+}$	$L_j^{A+} \leq N_j^{A+} \leq N_{j-1}^{A+}$

The posteriors for the population size parameters are obtained by substituting the distributions used in (1)-(3) in the following equations:

If $a = 1$ then $\pi(N_j^1 \mid \dots)$ is obtained from:

$$\begin{array}{ll}
\pi(N_j^1 \mid N_j^{2+}, \rho_j)\pi(N_{j+1}^1 \mid N_j^1, \phi_j^1)L(\mathbf{C}_{j-1}^1 \mid N_j^1, \boldsymbol{\pi}_{j-1}) & \text{j=Sp} \\
\pi(N_j^1 \mid N_{j-1}^1, \phi_{j-1}^1)\pi(N_{j+1}^1 \mid N_j^1, \phi_j^1)L(\mathbf{C}_{j-1}^1 \mid N_j^1, \boldsymbol{\pi}_{j-1}) & \text{j=Su,Au} \\
\pi(N_j^1 \mid N_{j-1}^1, \phi_{j-1}^1)\pi(N_{j+1}^2 \mid N_j^1, \phi_j^1)L(\mathbf{C}_{j-1}^1 \mid N_j^1, \boldsymbol{\pi}_{j-1}) & \text{j=Wi}
\end{array}$$

If $1 < a < A-1$ then $\pi(N_j^a \mid \dots)$ is obtained from:

$$\begin{aligned}
&\pi(N_j^a \mid N_{j-1}^{a-1}, \phi_{j-1}^{a-1})\pi(N_{j+1}^a \mid N_j^a, \phi_j^a)L(\mathbf{C}_{j-1}^{a-1} \mid N_j^a, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Sp}\\
&\pi(N_j^a \mid N_{j-1}^{a}, \phi_{j-1}^{a})\pi(N_{j+1}^a \mid N_j^a, \phi_j^a)L(\mathbf{C}_{j-1}^{a} \mid N_j^a, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Su,Au}\\
&\pi(N_j^a \mid N_{j-1}^{a}, \phi_{j-1}^{a})\pi(N_{j+1}^{a+1} \mid N_j^a, \phi_j^a)L(\mathbf{C}_{j-1}^{a} \mid N_j^a, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Wi}
\end{aligned}$$

If $a = A-1$ then $\pi(N_j^{A-1} \mid \dots)$ is obtained from:

$$\begin{aligned}
&\pi(N_j^{A-1} \mid N_{j-1}^{A-2}, \phi_{j-1}^{A-2})\pi(N_{j+1}^{A-1} \mid N_j^{A-1}, \phi_j^{A-1})L(\mathbf{C}_{j-1}^{A-1} \mid N_j^{A-1}, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Sp}\\
&\pi(N_j^{A-1} \mid N_{j-1}^{A-1}, \phi_{j-1}^{A-1})\pi(N_{j+1}^{A-1} \mid N_j^{A-1}, \phi_j^{A-1})L(\mathbf{C}_{j-1}^{A-1} \mid N_j^{A-1}, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Su,Au}\\
&\pi(N_j^{A-1} \mid N_{j-1}^{A-1}, \phi_{j-1}^{A-1})\pi(N_{j+1}^{A+} \mid N_j^{A-1}, N_j^{A+}, \phi_j^{A-1}, \phi_j^{A+})L(\mathbf{C}_{j-1}^{A-1} \mid N_j^{A-1}, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Wi}
\end{aligned}$$

Finally, if $a = A+$ then $\pi(N_j^{A+} \mid \dots)$ is obtained from:

$$\begin{aligned}
&\pi(N_j^{A+} \mid N_{j-1}^{A-1}, N_{j-1}^{A+}, \phi_{j-1}^{A-1}, \phi_{j-1}^{A+})\pi(N_{j+1}^{A+} \mid N_j^{A+}, \phi_j^{A+})L(\mathbf{C}_{j-1}^{A-1} + C_{j-1}^{A+} \mid N_j^{A+}, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Sp}\\
&\pi(N_j^{A+} \mid N_{j-1}^{A+}, \phi_{j-1}^{A+})\pi(N_{j+1}^{A+} \mid N_j^{A+}, \phi_j^{A+})L(\mathbf{C}_{j-1}^{A+} \mid N_j^{A+}, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Su,Au}\\
&\pi(N_j^{A+} \mid N_{j-1}^{A+}, \phi_{j-1}^{A+})\pi(N_{j+1}^{A+} \mid N_j^{A-1}, N_j^{A+}, \phi_j^{A-1}, \phi_j^{A+})L(\mathbf{C}_{j-1}^{A+} \mid N_j^{A+}, \boldsymbol{\pi}_{j-1}) \quad && \text{j=Wi}
\end{aligned}$$

Appendix B

Discrete Uniform asymmetric proposals used to estimate the population size with the Metropolis-Hastings algorithm

Let q(.) be a proposal distribution to move from the current value $N_j^{a(C)}$ to the proposed value $N_j^{a(P)}$. Since the constraints in the system process limit the range of values to be explored, we use a discrete Uniform proposal because it is simple and provides a good mixing. Without any constraints such a proposal would be: $q(N_j^{a(C)}, N_j^{a(P)}) = \text{DUnif}(\text{au}_j^a, \text{bu}_j^a)$ where $\text{au}_j^a = N_j^{a(C)} - \epsilon_j^a$, $\text{bu}_j^a = N_j^{a(C)} + \epsilon_j^a$ and ϵ_j^a may be either fixed or (more efficiently) used to tune the proposal every k iterations (Section 4). However, the binomial coefficients in the system process and the autoregressive structure in the resightings require that we choose:

$$\begin{aligned}
\text{au}_j^a &= \max\{L_j^a, n_j^a, N_j^a - \epsilon_j^a\} \qquad && j \neq \text{Sp}\\
\text{au}_j^a &= \max\{L_j^a, n_j^{a-1}, N_j^a - \epsilon_j^a\} && j = \text{Sp}\\
\text{bu}_j^a &= \min\{L_j^a, N_j^a + \epsilon_j^a\}
\end{aligned}$$

where L_j^a and U_j^a are defined in Appendix A. Note that since the proposals are not symmetric their corresponding normalising constants do not cancel out in the acceptance ratio, so that we also need to calculate values, say auN_j^a and buN_j^a, for the reverse move $q(N_j^{a(P)}, N_j^{a(C)})$.

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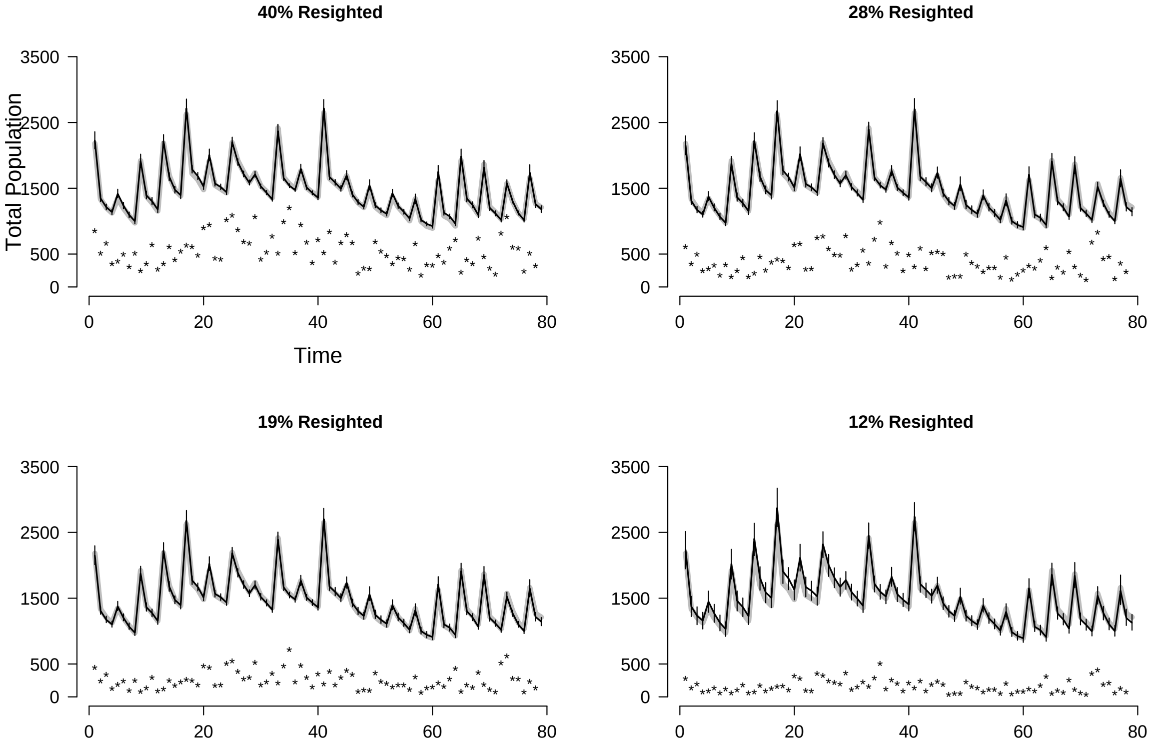


Figure 1: Simulation study: estimates from one run of the algorithm with 4×10^6 iterations after an adaptive phase of 10^5 iterations. The grey line is the true population size; the black line is the posterior mean with 95% HPDIs, and the stars are the number of distinct individuals used for the estimation.

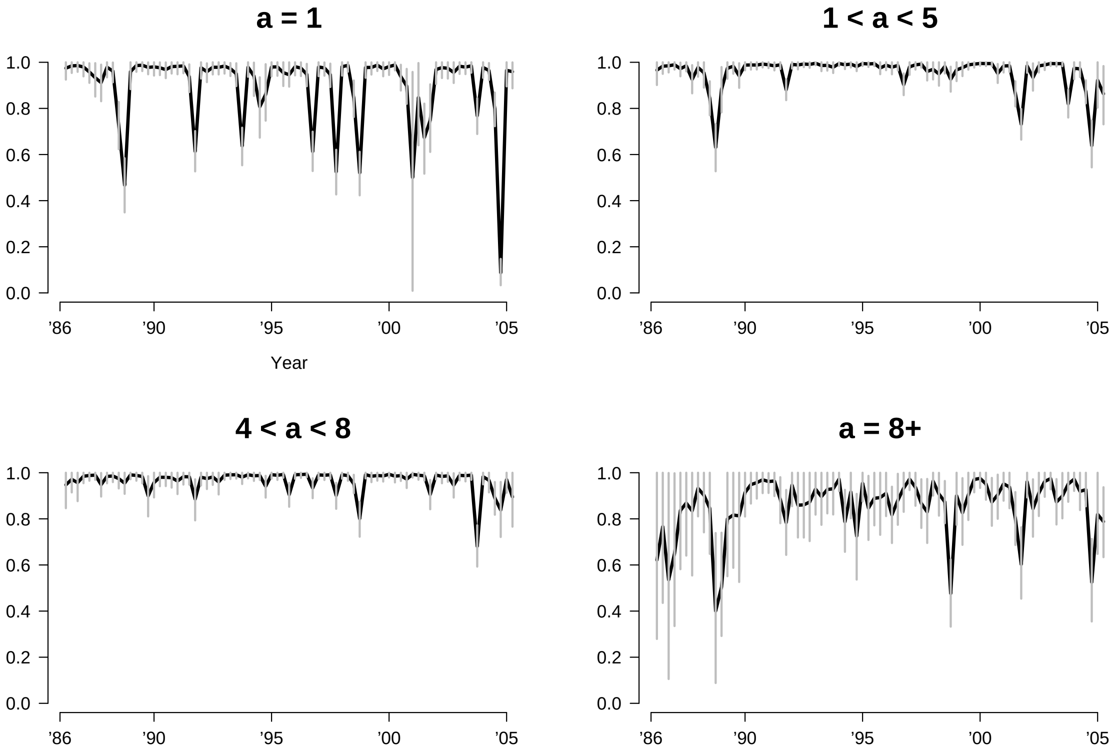
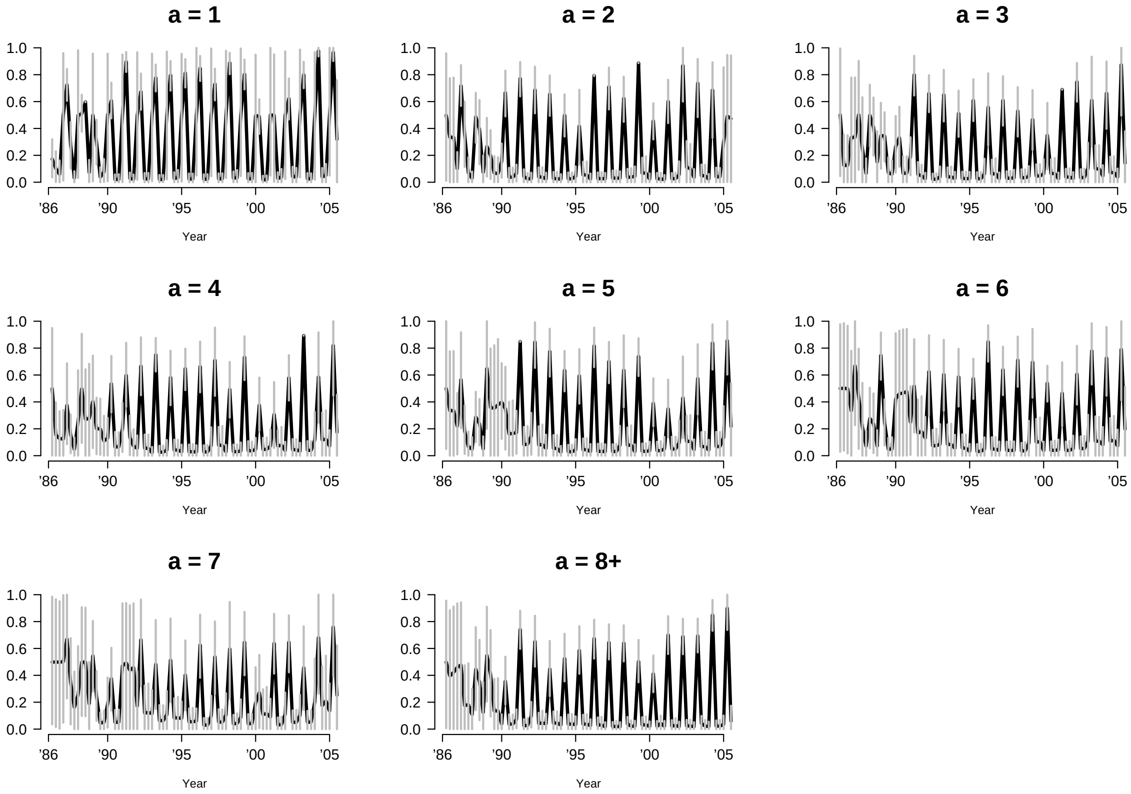


Figure 2: Female Soay sheep: series of posterior means and 95% HPDIs for seasonal survival probabilities, by age group. The plots highlight the increased sensitivity to Winter for lamb survival, especially in the years of population decline, and a higher seasonal variability for the group $a = 8+$ where mortality is not only confined to Winter. Note that ϕ^1_{61} has the same variability as the prior because there are no captures in Spring 2001



a = 1

a = 2

a = 3

a = 4

a = 5

a = 6

a = 7

a = 8+

Figure 3: Female Soay sheep: series of posterior means and 95% HPDIs for seasonal recapture probabilities, by age group. The strong seasonal pattern highlights the preference of researchers for the Summer season to recapture individuals

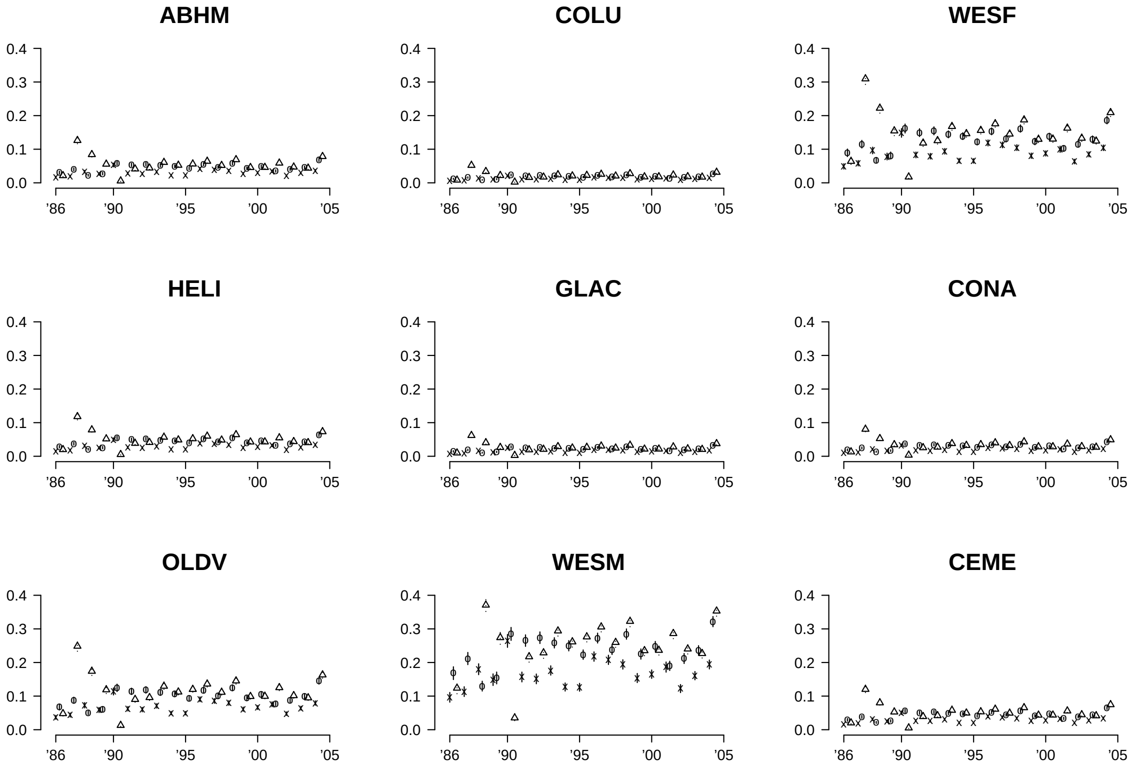


Figure 4: Female Soay sheep: posterior means and 95% HPDIs for the probability of being resighted in 9 of the 30 locations in different seasons. The crosses are for Spring, circles for Summer and triangles for Autumn. No resightings are available in Winter due to difficult weather conditions. Each individual may be resighted at more than one location during a season.

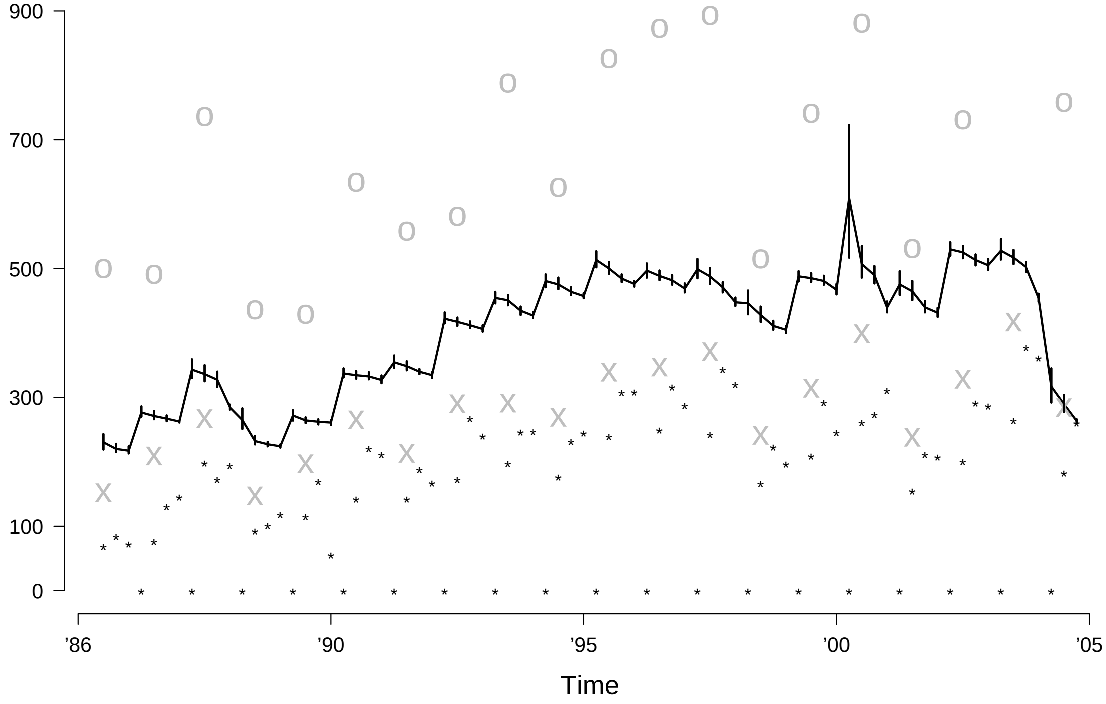


Figure 5: Female Soay sheep: estimated posterior means and 95% HPDIs for the population accessing the study area. The stars are the number of distinct individuals resighted in each season and used for the estimation. The higher uncertainty in Spring 2001 comes from the first age group, N_{61}^{1}, (see §6.1). The grey crosses are the raw counts of the population in the study area each Summer. The grey circles are the raw counts of the population in the whole island each Summer. These raw counts were not used for the estimation and are reported here in order to compare the overall island dynamics to that in the study area and to check the consistency of our method.

Table 1: Female Soay sheep: posterior means (SD) and [95% HDPI] for location coefficients of the logistic model described in §3.2

Effect	Mean(SD)	95%HPDI	Effect	Mean(SD)	95%HPDI
ABHM	0		HELI	-0.07 (0.04)	[-0.16, 0.01]
ANLA	0.01 (0.05)	[-0.08, 0.09]	LAGA	-0.36 (0.05)	[-0.45, -0.26]
BASE	0.09 (0.04)	[0.00, 0.17]	MIDF	1.28 (0.04)	[1.21, 1.35]
CEME	-0.05 (0.04)	[-0.14 , 0.03]	MMOR	-2.18 (0.10)	[-2.37, -1.99]
CHIM	-0.41 (0.05)	[-0.50 , -0.31]	OISE	0.44 (0.04)	[0.36, 0.52]
COLU	-0.97 (0.06)	[-1.08 , -0.85]	OLDV	0.83 (0.04)	[0.76, 0.91]
CONA	-0.50 (0.05)	[-0.60, -0.40]	QUAR	-0.32 (0.05)	[-0.41, -0.22]
FACF	0.35 (0.04)	[0.27, 0.43]	RUAI	-3.26 (0.16)	[-3.56,-2.85]
GAP	-2.25 (0.10)	[-2.45 ,-2.06]	SGAR	0.46 (0.04)	[0.37,0.54]
GEAL	-0.36 (0.05)	[-0.45, -0.26]	SHOR	-1.78 (0.08)	[-1.94, -1.62]
GEAR	-0.01 (0.04)	[0.27, 0.43]	SIGM	1.64 (0.04)	[1.57, 1.71]
GLAC	-0.78 (0.06)	[-0.89, -0.67]	SINK	-0.72 (0.06)	[-0.83 , -0.61]
GLEB	-0.19 (0.05)	[-0.28, -0.10]	STBR	0.39 (0.04)	[0.31, 0.47]
GUNM	-0.32 (0.05)	[-0.41, -0.22]	WESF	1.13 (0.04)	[1.06, 1.21]
GYM	-0.01 (0.04)	[-0.10, 0.07]	WESM	1.86 (0.04)	[1.80, 1.93]

[2] Parameters α_1 (Abhainn Mhor) and β_1 (Spring '86) were set to 0 for identifiability.