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Correcting bias in survival probabilities for partially monitored populations via integrated models

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Abstract

We provide an integrated capture-recapture-recovery framework for partially monitored populations. In these studies live resightings are only observable at a set of monitored locations, so that if an individual leaves these specific locations they become unavailable for capture. Additional ring-recovery data reduces the corresponding bias obtained in the survival probability estimates from capture-recapture data due to the confounding with colony dispersal. We derive an explicit efficient likelihood expression for the integrated capture-recapture-recovery data, and state the associated sufficient statistics. We demonstrate the significant improvements in the estimation of the survival probabilities using the integrated approach for a colony of guillemots (*Uria aalge*), where we additionally specify a hierarchical approach to deal with low sample size over the early period of the study.

Keywords: Bias; Capture-recapture-recovery data; Hierarchical model; Partial monitoring.

1. Introduction

Capture-recapture studies are frequently used to study wild animal populations, often with a particular focus on estimating survival probabilities. These involve biologists going into the field at a series of capture occasions to observe live resightings of uniquely marked individuals. For an overview of capture-recapture studies and associated statistical models, see for example, King et al. (2010); McCrea and Morgan (2015); Seber and Schofield (2019). However, such studies are generally limited with mortality confounded with dispersal from the study area. The associated *apparent* survival estimates are negatively biased with regard to *true* survival probabilities. The greater the dispersal from the study area, the greater the level of bias.

We consider partially monitored populations where only a limited number of locations are monitored at the study site. The problem is motivated by a long-term study of common guillemots (*Uria aalge*). Individuals are marked as young at the monitored sites, but due to their life cycle they may disperse (at natal or breeding stage) to unmonitored sites where they subsequently become unavailable for capture. Due to this dispersal, standard capture-recapture models lead to biased survival estimates (Sarzo et al., 2019). Attempts to correct for the partial monitoring include the use of external estimates of the probability that individuals recruit to the monitored sites (Sanz-Aguilar et al., 2016). Alternatively, integrating capture-recapture data (of live resightings) with ring-recovery data (of dead recoveries) permits the disentangling of survival from dispersal, assuming that all individuals remain available to be recovered dead (irrespective of whether or not they are available for resighting). An integrated modelling approach, considering the joint analysis of live resightings and ring-recovery (MRR) data was first presented by Burnham (1993), allowing for time-dependent model parameters, and extended by Barker (1999) to include age-dependence. Catchpole et al. (1998) considered both time and age dependence, and derived a set of sufficient statistics (though these cannot be used for goodness-of-fit as the set of sufficient statistics are non-independent with the same data observations contributing to more than one sufficient statistic). Further developments include a state-space formulation (King, 2012), and incorporating time-varying individual covariates, which are either discrete (King and Brooks, 2003; McCrea et al., 2012; King and McCrea, 2014) or continuous (Catchpole et al., 2008; Bonner et al., 2010; Langrock and King, 2013).

Integrated population modelling approaches have been applied to a wide range of data combinations including (but far from limited to): ring-recovery data with productivity data (Abadi et al., 2010) and population count data (Besbeas et al., 2002; King et al., 2008); telemetry data with spatial mark-resight data (Sollmann et al., 2013) and distance sampling (Glennie et al., 2020); and occupancy models (using eDNA) and aural surveys (Guillera-Arroita et al., 2017). For a review of integrated population models, see for example Schaub and Abadi (2011). Integrated population models are attractive as they use all the available information within a single analysis, often leading to improved precision of the estimated parameters, and may permit the estimation of parameters that are unidentifiable when using the different datasets individually.

We consider integrated MRR data where all individuals are able to be recovered dead, but not all individuals are available to be resighted alive (i.e. if they move to an unmonitored site). We provide an efficient likelihood expression, and associated (independent) sufficient statistics in the presence of both age and time parameter dependence. We specify a hierarchical model formulation to permit additional borrowing of information over time leading to increased precision of the model parameters, particularly for early years of the study where sample size is small. We fit the model to the guillemot data using a Bayesian approach, permitting prior information to be specified on relative resighting probabilities over time given the study design.

In Section 2 we describe the data. Section 3 provides the integrated MRR model formulation and associated likelihood, including the efficient m-array formulation and summary statistics. In Section 4 we describe the hierarchical model for the guillemot data, comparing the results to the capture-recapture only case. We conclude with a discussion in Section 5.

2. Data

We consider data relating to the largest guillemot colony in the Baltic Sea, on the island of Stora Karlsö (Sweden), with a recorded breeding population of 15,700 pairs in 2014 (Olsson and Hentati-Sundberg, 2017). Over the study period 39,681 chicks were ringed between late June and early July. We consider resightings of individuals carried out at five different monitored locations: two clubs (aggregations of birds at rocks beneath the breeding ledges) and three breeding ledges. Long-ranged telescopes were used to record the unique ring identifiers (metallic and plastic rings) at the monitored locations to minimise disturbance. Recoveries of dead individuals took place at colony level and elsewhere (mainly in the Baltic Sea but also in the Atlantic Ocean). The capture-recapture data were collected over the period 2002 to 2016, while the ring-recovery database spanned 1992 to 2018. A total of 6,477 unique individuals were resighted within the study period with 937 individuals recovered dead. The data are provided (in form of summary m-arrays) in the public repository: `https://blancasarzo@bitbucket.org/blancasarzo/data_sarzo_et_al.git`.

[Figure 1 about here.]

Previous studies have shown that one and two year old birds are mainly resighted at rocks while individuals older than two years are primarily resighted at the monitored breeding ledges (≈89% of the >2 year olds observed; Kadin, 2007; Sarzo et al., 2019). These locations are related to their life cycle. Guillemots are philopatric to both breeding colony, and natal subcolony (Halley et al., 1995). Younger birds generally move around the colony and hence are observable, but as immature birds get older, they become increasingly present on breeding ledges, reflecting the prospecting behaviour in preparation for breeding (Oro and Pradel, 2000), and due to their philopatric behaviour remain at their chosen ledge. This latter behaviour leads to capture heterogeneity dependent on whether or not an individual settles at a monitored breeding ledge. Sarzo et al. (2019) showed that this behaviour, combined with the monitoring regime, leads to biased capture-recapture estimates for older ages, and in particular, reduced survival probabilities. Additional ring-recovery data of (dead) individuals are collected by the Bird Ringing Centre mainly at the colony level and in the Baltic Sea so that recoveries are not affected by the partial monitoring as for the live resightings.

3. Methods

We initially describe the notation and model parameters before providing a description of the associated m-array summary statistics for MRR data and (efficient) likelihood function.

3.1 Notation

MRR data are typically displayed in the form of individual capture histories for each individual observed within the study period. We let $i = 1, \dots, N$ denote the individuals in the study and $t = 1, \dots, T$ the capture occasions. We let $\boldsymbol{y}$ denote the $N \times T$ observed data matrix such that,

$$y_{i,t} = \begin{cases} 0 & \text{individual } i \text{ is not resighted at time } t; \\ 1 & \text{individual } i \text{ is resighted alive at time } t; \\ 2 & \text{individual } i \text{ is recovered dead in the interval } (t-1, t]. \end{cases}$$

The ith row of $\boldsymbol{y}$, denoted $\boldsymbol{y}_i = \{y_{i,t} : t = 1, \dots, T\}$, corresponds to the capture history of individual i. An individual recovered dead in $(t-1, t]$ is recorded as recovered at time t. For example, consider: $\boldsymbol{y}_1 = \{1\,0\,0\,1\,0\,2\}$ and $\boldsymbol{y}_2 = \{0\,1\,1\,0\,1\,0\}$. Capture history $\boldsymbol{y}_1$ represents an individual marked at occasion 1, next observed at occasion 4 before being recorded dead at occasion 6 (i.e. recovered dead in the interval $(5, 6]$); $\boldsymbol{y}_2$ to an individual marked at time 2, and subsequently observed at occasions 3 and 5, only. For our case study, individuals can only be resighted if they are in the monitored areas; however, all individuals may be recovered dead (if they die) irrespective of whether or not they are in the monitored areas.

3.2 Model parameters

We initially describe the parameters associated with the individual capture-recapture and ring-recovery models, before considering the integrated case. We assume that the parameters are age and time dependent. More generally, the parameters may be written as a function of many different factors, including environmental and/or individual-level covariates. See for example McCrea and Morgan (2015) for further discussion. For the capture-recapture data we define:

$$\begin{aligned}
\phi_{a,t} &= \mathbb{P}(\text{an individual aged } a \text{ at time } t \text{ is alive and available for capture at time } t+1 \mid \\
&\qquad\qquad \text{alive and available for capture at time } t); \\
p_{a,t+1} &= \mathbb{P}(\text{an individual aged } a \text{ at time } t+1 \text{ is observed} \mid \text{alive and available for} \\
&\qquad\qquad \text{capture at time } t+1),
\end{aligned}$$

for $t = 1, \dots, T-1$ and $a = 1, \dots, A$. Available for capture equates to the individual being present at the monitored colony sites. The term $\phi_{a,t}$ is often referred to as the survival probability; however this is *apparent* survival (death and non-availability/dispersal are confounded).

For ring-recovery data, we define the associated model parameters:

$$
\begin{aligned}
S_{a,t} &= \mathbb{P}(\text{an individual aged } a \text{ at time } t \text{ is alive and at the colony at time } t+1 \mid \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{alive and at the colony at time } t); \\
\lambda_{a,t+1} &= \mathbb{P}(\text{an individual aged } a \text{ is recovered dead in the interval } (t, t+1] \mid \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{dies in the interval } (t, t+1]),
\end{aligned}
$$

for $t = 1, \dots, T-1$ and $a = 1, \dots, A$. Again $S_{a,t}$ is often referred to as the survival probability, but in this case recovered individuals are known to be dead (rather than unavailable, which may include dispersal), and so this corresponds to the *true* survival probability.

Combining the capture-recapture and ring-recovery data we note the difference in interpretation between $\phi_{a,t}$ and $S_{a,t}$ of *apparent* and *true* survival, respectively. This directly permits the estimation of the dispersal probability, i.e. the probability an individual moves permanently from a monitored site to an unmonitored site (where they are unavailable for resighting but available for recovery, if they die). In particular we have $\phi_{a,t} = S_{a,t}(1 - \gamma_{a,t})$, such that,

$$
\begin{aligned}
\gamma_{a,t} &= \mathbb{P}(\text{an individual is at an unmonitored site at time } t+1 \mid \text{alive at time } t+1 \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{and in a monitored site aged } a \text{ at time } t),
\end{aligned}
$$

for $t = 1, \dots, T-1$ and $a = 1, \dots, A$. For notational convenience we let $\boldsymbol{S} = \{S_{a,t} : a = 1, \dots, A; t = 1, \dots, T-1\}$, and analogously for $\boldsymbol{p}$, $\boldsymbol{\lambda}$ and $\boldsymbol{\gamma}$. The set of parameters is denoted by $\boldsymbol{\theta} = \{\boldsymbol{S}, \boldsymbol{p}, \boldsymbol{\lambda}, \boldsymbol{\gamma}\}$. The ability to estimate additional, previously confounded, parameters from integrated models (in our case $\boldsymbol{\gamma}$), has been noted many times within the literature for different types of data (see for example, Burnham, 1993; Reynolds et al., 2009; McCrea et al., 2010; King and McCrea, 2014; McCrea and Morgan, 2015). We note that a full age and time dependence on the model parameters may lead to parameter redundancy (Hubbard et al., 2014). We discuss in Section 4.1 the particular dependence structure we impose on the model parameters for our case study, based on biological knowledge, for which no such issues were identified.

3.3 Sufficient statistics

The likelihood function is the product over each observed individual of their corresponding capture history probability (McCrea and Morgan, 2015). Each capture history can be expressed in the form of a hidden Markov model (HMM), with latent states corresponding to being available to be resighted or recovered (King, 2014; McClintock et al., 2021). See Supplementary material Appendix A for further discussion of the latent states and HMM-type formulation. Equivalently, the likelihood can be usefully and efficiently expressed via the form of sufficient statistics in the form of an extended m-array.

Capture-recapture and ring-recovery data can each be usefully summarised in terms of individual *m*-arrays (Lebreton et al., 1992; McCrea and Morgan, 2015). The *m*-arrays summarise the number of individuals released at occasion $j = 1, \dots, T-1$ and subsequently next observed alive (for capture-recapture data), or recovered dead (for ring-recovery data) at capture occasion $t = 2, \dots, T$. Often, instead of recording the number of individuals released in a given year, the m-arrays are given with the (equivalent) number of individuals never observed again. We use this latter approach in the presentation of the m-arrays. We present the extended m-array formulation for the combined MRR data before providing the efficient likelihood specification. The additional age dependence extends the data to a three-dimensional m-array, or alternatively, a separate extended m-array for each age that an individual may be released.

We define an $A \times (T-1) \times (2T-1)$ extended (or integrated) m-array with cell entries denoted by $m_{a,j,t}$ such that the cells are indexed by $a = 1, \dots, A$, $j = 1, \dots, T-1$ and $t = 2, \dots, 2T$. For simplicity we condition on age, a, and consider the associated $(T-1) \times (2T-1)$ array. The first $T-1$ columns (labelled $t = 2, \dots, T$) correspond to the capture-recapture components (i.e. live resightings), with cell entries, $m_{a,j,t}$, equal to the number of individuals that are observed at time $j = 1, \ldots, T-1$ (aged a) that are *next* observed alive at time $t = 2, \ldots, T$. The following $T-1$ columns (labelled $t = T+1, \ldots, 2T-1$) correspond to the ring-recovery components (i.e. dead recoveries) with cell entries, $m_{a,j,t}$, equal to the number of individuals that are observed at the time $j = 1, \ldots, T-1$ (aged a) that are *next* observed as a dead recovery at time $t^* = t - (T-1)$, for $t = T+1, \ldots, 2T-1$ (so that $t^* = 2, \ldots, T$). The final column (labelled $t = 2T$) has cell entries, $m_{a,j,2T}$, corresponding to the number of individuals last observed at time $j = 1, \ldots, T-1$ (aged a) that are never observed again within the study (either alive or dead). Finally, we let $q_{a,j,t}$ denote the associated cell probabilities of the integrated *m*-array, for $a = 1, \ldots, A$, $j = 1, \ldots, T-1$ and $t = 2, \ldots, 2T$. For notational purposes we let the set of sufficient statistics be denoted by $\boldsymbol{m} = \{m_{a,j,t} : a = 1, \ldots, A; j = 1, \ldots, T; t = 2, \ldots, 2T\}$, and similarly for $\boldsymbol{q}$ (the set of cell probabilities).

For illustration, we provide a toy numerical example where $T = 5$ and there is a single age for all individuals (e.g. all individuals are ringed and observed as adults), so that $A = 1$. Table 1 provides the capture histories of a set of individuals; while Table 2 the corresponding set of m-arrays associated with only capture-recapture data (no dead recoveries); only ring-recovery data (no live resightings); and the combined MRR data.

[Table 1 about here.]

[Table 2 about here.]

We note that the observed m-array cell entries associated with the resighting of individuals do not change between the capture-recapture only m-array and the integrated MRR m-array (i.e. columns $t = 2, \ldots, T$). However, for the m-array cells corresponding to the recovery of individuals, these do differ between the ring-recovery only data and the integrated MRR data (i.e. columns $t = T+1, \ldots, 2T-1$), as this is dependent on whether an individual *is* resighted prior to recovery. If a bird is resighted prior to recovery, then the year of release for the individual will differ between the ring-recovery only m-array and integrated m-array; alternatively if the individual is not resighted alive within the study the contribution to the ring-recovery component of the integrated m-arrays remains the same. Similarly the number of individuals not observed again (i.e. column $2T$) will differ in the integrated MMR m-array to the individual m-arrays to take into account the additional resightings or recoveries not observed within the individual ring-recovery and capture-recapture only m-arrays, respectively. Finally we also note that the number of individuals released each year (equal to the row sums) differs between the capture-recapture only m-array and the ring-recovery only m-array as birds that are resighted in year t, say, are then counted within the number of birds released in year t. However, for the ring-recovery only m-array there are no resightings, and so all releases correspond to initial captures. The row sums for the capture-recapture only and integrated m-arrays are however equal, with the difference between these m-arrays corresponding to what happens following release in terms of whether dead recoveries are recorded or not.

3.4 Likelihood

The likelihood is calculated as a product over multinomial terms. Each row, $j = 1, \ldots, T-1$, of the integrated m-array (for a given age, $a = 1, \ldots, A$) follows a multinomial distribution, with sample size equal to the number of individuals released at time j, denoted $R_{a,j}$, and associated cell probabilities $\boldsymbol{q}_{a,j} = \{q_{a,j,t} : t = 2, \ldots, 2T\}$. We note that $R_{a,j} = \sum_{t=2}^{2T} m_{a,j,t}$. Thus, the likelihood can be expressed in the form:

$$f(\boldsymbol{m}; \boldsymbol{\theta}) = \prod_{a=1}^{A} \prod_{j=1}^{T-1} \frac{R_{a,j}!}{\left(\prod_{t=2}^{2T} m_{a,j,t}!\right)} \left(\prod_{t=j+1}^{2T-1} q_{a,j,t}^{m_{a,j,t}} \right) \chi_{a,j}^{m_{a,j,2T}}, \tag{1}$$

where $\chi_{a,j}$ denotes the probability an individual released at time j aged a is not observed again.

To specify the non-zero cell probabilities we initially consider two separate cases corresponding to the resightings and recoveries, before we consider the final column corresponding to those individuals not observed again following their release (the final term in Equation (1)). We note that an alternative specification of the cell probabilities is provided in Supplementary material Appendix A via an HMM-type matrix formulation.

Case I: Columns $t = 2, \dots, T$ (live resightings)

We initially consider the probability an individual released at time $j = 1, \dots, T-1$, aged $a = 1, \dots, A$ is next observed alive again at time $t = j+1, \dots, T$, denoted by $q_{a,j,t}$. In this case the individual must survive each time between release to resighting, remain available for capture, not be observed at times $j+1, \dots, t-1$, before being resighted at time t, so that,

$$q_{a,j,t} = \prod_{k=j}^{t-1} \{S_{a+k-j,k}(1-\gamma_{a+k-j,k})\} \times \prod_{k=j}^{t-2} (1 - p_{a+k-j+1,k+1}) \times p_{a+t-j,t},$$

where we use the convention throughout that the null product $\prod_{k=j}^{j-1} \equiv 1$. The first product corresponds to individuals surviving and remaining available for capture within the monitored areas from time j to t; the second product corresponds to the observation process (not being observed between times $j+1$ to $t-1$ before being observed at time t). Recall that, *apparent* survival, $\phi_{a,t}$, can be expressed as a simple function of the *true* survival probability, $S_{a,t}$, and dispersal probability, $\gamma_{a,t}$, such that $\phi_{a,t} = S_{a,t}(1-\gamma_{a,t})$. Substituting this relationship into the expression for $q_{a,j,t}$ gives the "standard" capture-recapture only m-array cell probability. Finally, we note that as is common in capture-recapture studies, we assume there is no temporary dispersal, so that once an individual leaves the monitored sites (monitored rocks or breeding ledges) they are not able to return. This seems reasonable for the given case study with the philopatric nature of individuals once they settle at a given location within their life cycle.

Case II: Columns $t = T+1, \dots, 2T-1$ (dead recoveries)

We now consider the dead recovery component. We note that the column labels $t = T + 1, \dots, 2T-1$ correspond to the capture occasions $2, \dots, T$. Thus, we define t^* to be the capture occasion associated with column label t, such that $t^* = t - T + 1$, for $t = T+1, \ldots, 2T-1$. Now, consider the probability an individual observed at time $j = 1, \ldots, T-1$ at age $a = 1, \ldots, A$ is unseen until recovered dead in the interval $(t^* - 1, t^*]$. This means that an individual survives between times j to $t^* - 1$ before dying within the interval $(t^* - 1, t^*]$ and is recovered at this time (we make the standard ring-recovery assumption that an animal that dies in the interval $(t^* - 1, t^*]$ can only be recovered in the same interval, due to mark loss after this period). To account for not observing the individual at times $j+1, \ldots, t^* - 1$ we also need to take into account that an individual may move away from the monitored locations, where they are not observable via the capture-recapture study, but still available to be recovered dead if they die. Accounting for these different processes, the cell probabilities can be expressed in the form,

$$\begin{aligned} q_{a,j,t} &= (1 - S_{a+t^*-1-j,t^*-1})\lambda_{a+t^*-j,t^*} \times \left(\prod_{k=j}^{t^*-2} S_{a+k-j,k} \right) \\ &\quad \times \left\{ \sum_{k=j}^{t^*-2} \left((\gamma_{a+k-j,k}) \prod_{n=j}^{k-1} (1 - \gamma_{a+n-j,n})(1 - p_{a+n-j+1,n+1}) \right) \right. \\ &\quad \left. + \left(\prod_{n=j}^{t^*-2} (1 - \gamma_{a+n-j,n})(1 - p_{a+n-j+1,n+1}) \right) \right\}, \end{aligned}$$

where $t^* = j - T + 1$. The first line corresponds to the probability an individual released at time j, aged a, survives until time $t^* - 1$, before dying in the interval $(t^* - 1, t^*]$ and being recovered. The second and third lines correspond to the probability an individual released at time j aged a is not observed alive prior to being recovered dead at time t^*. However, for such an individual that is not resighted we need to account for the partial monitoring - an individual may move to an unmonitored site at each capture occasion. While they remain at the monitored sites they are available for capture (but are not observed); once they disperse to an unmonitored site they are no longer available for capture. The associated probability of the resighting process is calculated by summing over all possible times an individual may disperse to an unmonitored site following release (line 2), or remain throughout at the monitored site (line 3), until its death.

Case III: Columns $t = 2T$ (not observed again)

We first note that the lower triangular elements of the resighting and recovery components are structural zeros (an individual cannot be resighted or recovered again prior to its time of release). Thus for $j = 2, \dots, T-1$, and $t = 2, \dots, j$; $t = T+1, \dots, T-1+j$, we have that, $q_{a,j,t} = 0$. Then, since an individual released at time j must either be observed again (either alive or dead), or not observed, the row cell probabilities must sum to unity. The probability an individual released at time j, aged a, is not observed again can be expressed as,

$$\chi_{a,j} = 1 - \sum_{t=2}^{2T-1} q_{a,j,t}.$$

Substituting the $q_{a,j,t}$ and $\chi_{a,j}$ terms into Equation (1) provides an explicit expression for the likelihood function. We note that setting $\gamma_{a,j,t} = 0$ for all $a = 1, \dots, A$, $j = 1, \dots, T-1$ and $t = 2, \dots, T$ reduces the likelihood to the standard (non partial monitoring) MRR likelihood where the survival probabilities are assumed to be equal for the capture-recapture and ring-recovery components (see for example, Catchpole et al., 1998, though the likelihood specified is not expressed using the multinomial form).

4. Case Study

We consider the data relating to guillemots described in Section 2. The MRR data were collected from 1992-2018 (so that $T = 27$), where the live resightings only occur within the period 2002-2016; and dead recoveries are available throughout the whole study duration, 1993-2018.

4.1 Model

We initially consider the dependence of the model parameters on age and time, based on biological knowledge and study protocols. Due to the life cycle of guillemots we consider the maximum set of distinct ages, $1, 2, 3, 4, 5+$, where age corresponds to “year of life”, so that age 1 corresponds to birds in their first year of life; age 2 to one year old birds, etc; and 5+ corresponds to (adult) individuals of at least age 5.

The capture-recapture database only includes resighting occasions from 2002-2016. For years where there were no resightings possible, we set the resighting probability equal to 0, i.e. $p_{a,t} = 0$ for $t = 2, \dots, 10, 26, 27$, (corresponding to years $1993, \dots, 2001; 2017, 2018$), for $a = 2, \dots, 5+$. During the capture-recapture study period resightings occurred during the breeding season (May to July) but under two different intensity regimes of low and high effort. The low effort regime was from 2002-6 (mean resighting effort of 35.80 hours per year); while from 2007-16 a higher effort was used (mean resighting effort of 82.8 hours per year). Thus we consider two distinct resighting probabilities relating to the different effort periods. Further, the behaviour of individuals is such that most juveniles (one and two year olds, i.e. those aged 2 and 3) are generally observed on rocks (48$\%$ of resightings), while older birds (aged 4+) are increasingly present on the breeding ledges, first to learn competencies for breeding and when they reach sexual maturity, to breed. Therefore, to allow for the differing proportions of individuals who may use the rocks/ledges in early adulthood, the resighting probabilities are assumed to be fully age dependent. Hence we specify the capture probabilities such that $p_{a,t} = p^*_a$ for $t = 11, \dots, 15$ (i.e. years 2002-6) and $p_{a,t} = p_a$ for $t = 16, \dots, 25$ (i.e. years 2007-16); for $a = 2, \dots, 5+$. In contrast, the recovery effort was constant throughout the period, and with no rationale to suggest the age of the death of an individual would influence whether or not they were recovered, we assume a constant recovery probability across all ages and time, such that $\lambda_{a,t} = \lambda$ for all a and t. For the survival probabilities, it is well understood that these typically vary inter-annually due to variation in food availability and environmental conditions (Votier et al., 2008). Similarly, age is generally a very important factor affecting survival (see for example, Crespin et al., 2006; Harris et al., 2007). We assume the presence of both age and time effects, where they are additive (on the logit scale) and set $\text{logit}(S_{a,t}) = \alpha_a + \beta_t$ for $a = 1, \dots, 5+$ and $t = 1, \dots, T - 1$. However, we note that sexual maturity of guillemots occurs at ages 4-6 (Birkhead and Hudson, 1977), and so we consider the reduced age structure and set $\alpha_4 = \alpha_{5+}$, which we denote by α_{4+}.

Finally, for the dispersal probabilities it is expected that the majority of these will occur as individuals begin to increase their use of breeding ledges (i.e. breeding dispersal), although there will also be some additional natal dispersal in younger birds. For the given colony, individuals predominantly visit breeding ledges by the time they are 3 years old, so that for the dispersal probabilities we consider the age structure, $1, 2, 3+$ (where ages 1 and 2 we refer to as natal dispersal, and for age 3+ as breeding dispersal). We note that we assume dispersal from the monitored locations is permanent, as individuals once settled are philopatric.

Thus, the full set of model parameters in the proposed integrated model is: $\boldsymbol{\alpha} = \{\alpha_1, \dots, \alpha_{4+}\}$, $\boldsymbol{\beta} = \{\beta_1, \dots, \beta_{T-1}\}$, $\boldsymbol{p} = \{p_2^*, \dots, p_{5+}^*, p_2, \dots, p_{5+}\}$, $\boldsymbol{\gamma} = \{\gamma_1, \gamma_2, \gamma_{3+}\}$ and λ. Note that we comment further on the given dependence structure in Section 4.4.

4.2 Bayesian modeling

We consider a Bayesian modelling approach, which permits the formal incorporation of some (weak) prior information on the structure of the capture probabilities. We have no prior information on the resighting probabilities for the period 2007-16, or the recovery probabilities so that we specify $p_a \sim \text{U}(0, 1)$ for $a = 2, \dots, 5+$ and $\lambda \sim \text{U}(0, 1)$, respectively. However, for the earlier period 2002-6, with the significantly lower number of resighting hours, we expect the associated resighting probabilities to be less than the later study years, and so specify the conditional prior distribution, $p_a^* | p_a \sim \text{U}(0, p_a)$, for $a = 2, \dots, 5+$.

For the survival parameters, there are several years with relatively limited amount of data.

For birds ringed prior to 2006, there are very few individuals resighted (a total of 986 individuals, corresponding to an average of 66 individuals per year), and few recoveries in future years. Thus, we consider a hierarchical structure to model the time effects, so that information can be borrowed across the whole study period and specify, $\beta_t \sim$N(μ, σ^2), where $\mu \sim$N$(0, 10)$ and $\sigma^2 \sim \Gamma^{-1}(0.001, 0.001)$. For the age effects, for identifiability, we set $\alpha_1 = 0$, and specify non-informative priors on the remaining terms, such that $\alpha_a \sim$N$(0, 5)$ for $a = 2, \dots, 4+$. Thus we note that α_a is interpreted as the age effect relative to age 1, for $a = 2, \dots, 4+$.

4.3 Simulation study

To compare the performance of the integrated MRR model with the capture-recapture only model we conducted a simulation study, using 50 simulated datasets. For these data, using the capture-recapture only model (i.e. omitting dead recoveries), consistently led to substantially biased survival probability estimates; whereas the MRR model provided reliable estimates. For further details and simulation results see the Supplementary material Appendix B.

4.4 Results

The `jags` software (Plummer, 2003) was used to fit the model to the data. The Markov chain Monte Carlo simulations were run for 400,000 iterations for each of three chains. A conservative burn-in of 40,000 iterations was discarded in each case and no convergence issues were identified via the Brooks-Gelman-Rubin (BGR) statistic (Gelman et al., 2013). We also conducted a prior sensitivity analysis. The corresponding results were robust to different uninformative priors, with the biological interpretation remaining consistent throughout.

We fitted both the integrated MRR data and the capture-recapture only data for comparison. Figure 2 provides the posterior mean and associated 95% symmetric credible intervals for the survival probabilities, $S_{a,t}$, for $a = 1, \dots, 4+$ and $t = 1, \dots, T-1$. Table 3 provides the associated posterior mean and 95% symmetric credible intervals for the α_a (for $a = 2, \dots, 4+$) and β_t (for $t = 1, \dots, T-1$) parameters. We note that for the capture-recapture analysis we only use the data from 2006-16, due to very few individuals were released prior to 2006. Further the estimates for the capture-recapture only data refer to *apparent* survival, whereas for the integrated data these correspond to *true* survival. We observe that the survival probabilities are very similar for ages 3 and 4+ for the integrated analysis. Further, the difference between the *apparent* and *true* survival estimates are most marked for ages 3+. This is unsurprising as this is the age where the partial monitoring has most impact, when individuals are more likely to move to breeding ledges away from the monitored locations (i.e. move from the resighting monitored sites). We note that for the capture-recapture only analysis the *apparent* survival probabilities for age 2 individuals are unrealistically high (and higher than the *true* survival probability estimates in the integrated analysis). For the capture-recapture data relatively few individuals were observed aged 2 (i.e. when one year old); while a significantly greater number of individuals were observed aged 3. This leads to a reduced (*apparent*) first-year survival probability (and hence reduced expected number of birds at age 2), which to then account for the large number of birds observed at age 3 leads to the very large (and unrealistic) second-year survival probabilities. Including the additional dead recoveries provides additional information in relation to the survival probabilities, leading to an increased first-year survival probability which in turn leads to more realistic age 2 survival probabilities to fit the large number of observed individuals at age 3. Further we note that for the integrated analysis, as would be expected biologically, $\mathbb{E}_\pi(\alpha_i) < \mathbb{E}_\pi(\alpha_j)$ for $i < j$, so that survival is increasing with age for younger birds until adulthood. Finally, we observe that all the survival probabilities are significantly reduced in 1999. A local oil spill occurred in 1999, that may have led to the increased mortality rates of the birds in that given year (J. Hentati pers.com.). The general temporal variability may also be related to other factors such as prey availability and/or environmental conditions.

[Table 3 about here.]

We note that we can compare the estimated adult (*true*) survival probabilities with previous estimates for guillemot colonies where *true* survival probabilities were also estimated. For example, for this colony, Österblom et al. (2004) suggested high adult survival estimates, of 0.937 (0.91, 0.96). Alternatively, for the Isle of May guillemot colony, adult (age 4+) survival probabilities were estimated to have a posterior mean of 0.912 with 95% posterior credible interval (0.872, 0.941) (Reynolds et al., 2009). Thus, the survival estimates obtained from this integrated MRR study are comparable; however, as expected (and noted above), the capture-recapture only estimates are significantly lower (except for age 2 individuals) as these are *apparent* survival probabilities and are confounded with dispersal.

[Figure 2 about here.]

The posterior mean and 95% posterior credible intervals for the resighting, recovery and dispersal parameters are given in Table 4. The resighting probabilities for the early years of the study (with low resighting effort) are all estimated to be very small, as expected. For the later years (with increased resighting effort) there is clear, strong, age dependence across the resighting probabilities. Age 2 individuals are significantly less likely to be resighted within the study. The resighting probability increases for age 3 birds and again for individuals of ages 4 onwards, for the integrated analysis. There is very little difference in the resighting probabilities for those aged 4 and 5+, suggesting that individuals are equally observable from age 4, if they remain in the monitored locations. This is most likely due to young guillemots (namely one and two years old, i.e. ages 2 and 3) spending time at sea so that the proportion of individuals resighted at these ages is commonly low (particularly for one year old individuals, Harris et al., 2007). Comparing the resighting probabilities between the integrated model and capture-recapture only model it is noticeable that the estimates are generally smaller in the capture-recapture only model (the exception is for p_2). In particular, we note that the largest difference is for adult birds (aged 5+), where the credible intervals between the integrated analysis, and capture-recapture only analysis, are non-overlapping. For capture-recapture(-recovery) studies the survival probabilities are negatively correlated with the resighting probabilities: lower resighting probabilities lead to higher survival probabilities (if the probability of seeing an individual is lower, this means that more individuals are alive in the study area but not seen, hence leading to an increased survival probability). Conversely, higher resighting probabilities (as for the capture-recapture only analysis) generally leads to lower survival estimates. Finally we note that the recovery probability is relatively small, as is often the case with ring-recovery studies.

[Table 4 about here.]

As noted previously, one common advantage of integrated models is that they permit the estimation of parameters not otherwise estimable. In our case, combining the capture-recapture data with the ring-recovery data permits the estimation of the dispersal probabilities, γ_a, to unmonitored areas. Harris et al. (2007) and Crespin et al. (2006) suggested that prospecting for breeding sites is biased towards the natal colony; and prebreeders who decide to disperse do so if conditions are poor at their natal site or if they are unable to secure a site. From Table 4 it is clear that dispersal is most pronounced for individuals aged 3+, as expected, given their general behaviour. In general, individuals aged 2 and 3 (i.e. one and two years old) temporarily visit rocks; individuals aged 3 and 4 (i.e. two and three years old) will start to visit breeding ledges; while individuals aged 4 or more (i.e. 3+ years old individuals) are more likely to be at breeding ledges and start pair-bonding after which they are philopatric to the given ledge.

While individuals at the monitored rocks are more likely to be observable, not all breeding ledges are monitored, and so if an individual settles at one of these they are no longer available for resighting (but are available for recovery if they die). Extending the model with separate age-dependent dispersal probabilities (3, 4+) led to similar probabilities for the specific ages.

5. Discussion

Reliable estimates of demographic parameters are essential to understand dynamics of wildlife populations. Capture-recapture (and/or ring-recovery) are commonly used across a wide range of species to study populations, often with the aim of estimating survival probabilities, which can be important for conservation and/or management. Within such studies there can be many different practical issues within the data collection process. We focus on the particular issue of partial monitoring populations, where live resightings are only observed for a small subset of the given colony. The approach developed is motivated by a colony of guillemots on the island of Stora Karlsö, the largest colony in the Baltic Sea (Olsson and Hentati-Sundberg, 2017). For this colony, the birds are ringed as chicks and are highly philopatric to their ledges, once they reach maturity. Thus, individuals may permanently move to locations that are outside the monitored locations, at which point they are no longer able to be observed. This typically leads to biased estimates of survival (Sanz-Aguilar et al., 2016; Sarzo et al., 2019), with *true* survival and movement away from the monitored locations confounded.

To address the issue, we used additional ring-recovery data within an integrated modelling framework to permit the estimation of both dispersal and *true* survival probabilities, where the majority of dispersal is assumed to be within-colony with few birds recovered long-distances from the colony. We derive the associated efficient integrated MMR m-array likelihood expression in the presence of dispersal, corresponding to a product of multinomial distributions where the model parameters are both age and time dependent. This likelihood formulation also permits the use of standard goodness-of-fit tests, such as a Pearson χ^2 test, to be applied within classical analyses (McCrea et al., 2010).

Further, for these data, additional modelling considerations were specified, due to the particular structure of the guillemot study and resulting small sample size of the data within time periods of the study. In particular, for the early years of the study (1993-2001) there were no live resightings, and the number of birds released (and recovered) are generally low. Thus, we use a hierarchical structure for the year effects for the survival probabilities which permits the borrowing of information across years. We note that fitting an alternative non-hierarchical fixed effects model leads to significantly lower precision in the year effects (and corresponding survival estimates), particularly for the ring-recovery only years (1993-2001, 2017, 2018) and years with the low intensity capture regime (2002-6). The corresponding adult survival estimates for the integrated MRR analysis are significantly higher than for the capture-recapture only data, reflecting the difference between *true* survival and *apparent* survival, correcting for the additional dispersal from the monitored locations. In addition, the integrated analysis led to biologically plausible survival estimates for age 2 individuals, whose estimates are unrealistically high for the capture-recapture only data (as discussed in Section 4.4). The newly derived *true* survival estimates are comparable to other studies of guillemot colonies (for example, Reynolds et al., 2009; Österblom et al., 2004). The survival probabilities appear to vary substantially over time (as evidenced by Figure 2), with many non-overlapping credible intervals across years). Further, we note that the age-specific dispersal probabilities of interest which largely distinguishes between natal and breeding dispersal, has the largest dispersal estimated to be for ages 3+ corresponding to when individuals start to reach maturity (breeding dispersal).

Finally, we investigated the goodness of fit of the fitted model to the data by considering

Bayesian p-values at the m-array level. In particular we considered three different discrepancy statistics: corresponding to the deviance, Pearson's χ^2 statistic and the Freeman-Tukey statistic (Conn et al., 2018). For all discrepancy functions an overall lack of fit of the model to the data was identified across the different age m-arrays, with the strongest discrepancy for the age 1 m-array associated with the capture-recapture component. Further investigation suggested that the time invariant dispersal probabilities may be a significant factor in the lack of fit. However, adding in time dependence to the dispersal parameters led to estimation issues. Thus identifying potential covariates to explain the temporal variability in the model parameters, such as prey availability and/or environmental conditions is the focus of current research. Finally we note that additional unobserved individual heterogeneity may also be present, and incorporating such heterogeneity is also an active area of research.

Long-term studies are essential for assessing trends over time and/or permitting the identification of relationships with possible factors. Combining studies of differing lengths can extend the possible inferences, and a hierarchical modelling structure permits borrowing of information to improve the precision of the estimates over these periods of time. We use a hierarchical structure to model year effects due to the variability in the amount of information contained in the data over the years with periods of low sample effort. Individual heterogeneity can also be an important biological modelling component, and hierarchical structures are often implemented to model these. However, for these data (with approximately 30,000 individuals), fitting these individual heterogeneity models using standard techniques, such as Bayesian data augmentation (often referred to as a complete data likelihood approach), leads to significant, and potentially infeasible, computational expense. Consequently, further computational techniques are needed for such analyses, which is an area of current focus.

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Figure 1: Location of the Stora Karlsö guillemot colony in the Baltic Sea (left). Map of the island (right) shows the location of the main breeding ledges used by guillemots (areas A, B and C) and monitored areas (indicated with asterisks). Chicks were captured and banded in area A. Recoveries take place over the whole colony and elsewhere (mainly in Baltic Sea but also in the Atlantic Ocean).

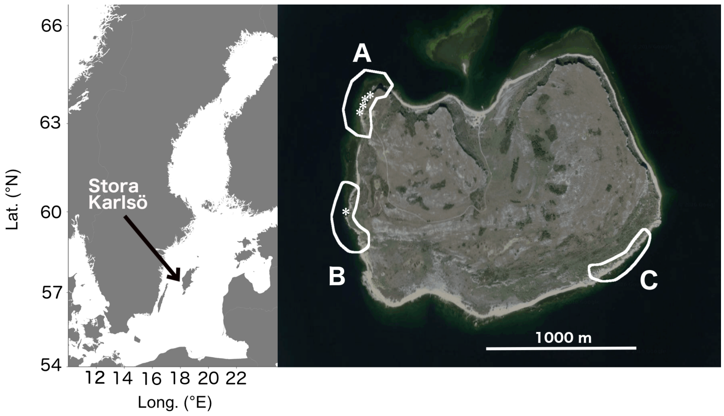

Figure 2: Posterior mean and 95% symmetric credible intervals (CIs) for the survival probabilities by age classes ($a = 1, \ldots, 4+$) for the study period, obtained through capture-recapture (CR) data only (grey); and integrated MRR data (black). We note that the capture-recapture data are only able to estimate *apparent* survival (survival confounded with availability); while the MRR data provide estimates of *true* survival.

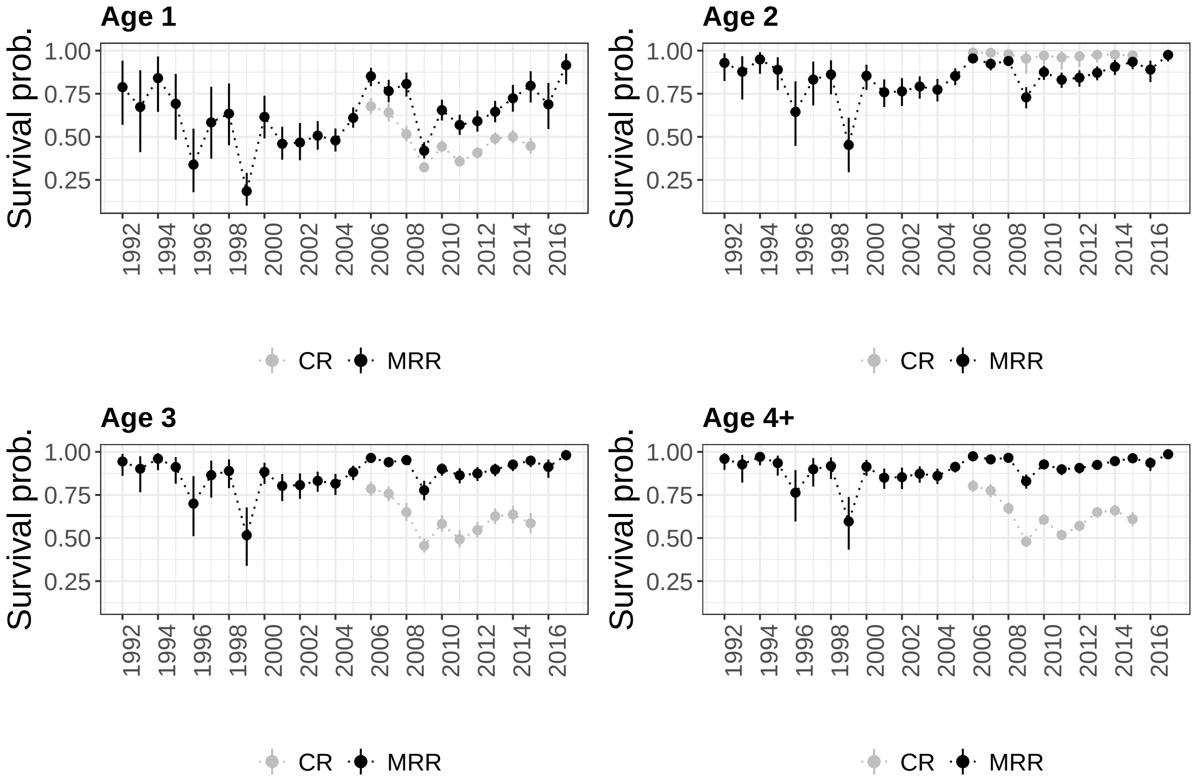

Table 1: Toy example capture histories, where 0 denotes unobserved; 1 observed alive; and 2 recovered dead; and associated number of individuals with given history.

Capture occasion						Capture occasion					
1	2	3	4	5	Number	1	2	3	4	5	Number
1	0	0	0	0	1466	0	1	1	1	0	25
1	1	0	0	0	101	0	1	1	1	2	2
1	2	0	0	0	13	0	1	0	1	0	43
1	1	1	0	0	15	0	1	0	2	0	10
1	1	2	0	0	1	0	1	0	0	1	5
1	1	0	1	0	13	0	0	1	0	0	1251
1	1	0	0	2	1	0	0	1	1	0	98
1	0	1	0	0	76	0	0	1	2	0	17
1	0	2	0	0	9	0	0	1	1	1	23
1	0	1	1	0	8	0	0	1	1	2	2
1	0	0	1	0	42	0	0	1	0	1	15
1	0	0	0	1	12	0	0	1	0	2	5
0	1	0	0	0	1001	0	0	0	1	0	1235
0	1	1	0	0	94	0	0	0	1	1	68
0	1	2	0	0	18	0	0	0	1	2	10

Table 2: Example of *m*-arrays for capture-recapture (top left), ring-recovery (top right) data and the resulting integrated *m*-array (bottom) with the observed individuals and cell probabilities (parenthesis) for $T = 5$ and a single adult age category. A '$-$' denotes a structural zero entry (and hence cell probability is equal to 0).

Capture-recapture only m-array

	Capture occasion				
	2	**3**	**4**	**5**	**Never seen**
1	131	84	42	12	1488
2	–	136	56	5	1132
3	–	–	158	15	1458
4	–	–	–	91	1478

Ring recovery only m-array

	Capture occasion				
	2	**3**	**4**	**5**	**Never seen**
1	13	10	0	1	1733
2	–	18	10	2	1168
3	–	–	17	7	1387
4	–	–	–	10	1303

Integrated m-array

	Capture-recapture component				**Ring recovery component**				
	Capture occasion								
	2	**3**	**4**	**5**	**2**	**3**	**4**	**5**	**Never seen**
1	131 $(q_{1,1,2})$	84 $(q_{1,1,3})$	42 $(q_{1,1,4})$	12 $(q_{1,1,5})$	13 $(q_{1,1,6})$	9 $(q_{1,1,7})$	0 $(q_{1,1,8})$	0 $(q_{1,1,9})$	1466 $(\chi_{1,1})$
2	–	136 $(q_{1,2,3})$	56 $(q_{1,2,4})$	5 $(q_{1,2,5})$	–	19 $(q_{1,2,7})$	10 $(q_{1,2,8})$	1 $(q_{1,2,9})$	1102 $(\chi_{1,2})$
3	–	–	158 $(q_{1,3,4})$	15 $(q_{1,3,5})$	–	–	17 $(q_{1,3,8})$	5 $(q_{1,3,9})$	1436 $(\chi_{1,3})$
4	–	–	–	91 $(q_{1,4,5})$	–	–	–	12 $(q_{1,4,9})$	1464 $(\chi_{1,4})$
	Column label (t)								
	2	3	4	5	6	7	8	9	10

Table 3: Mean and 95% symmetric credible intervals (CIs) for α_a ($a = 2, \ldots, 4+$; $\alpha_1 = 0$) and β_t ($t = 1, \ldots, T-1$) parameters obtained through the integrated model.

Parameters	**Mean**	**95% CI**
α_2	1.32	[1.02, 1.63]
α_3	1.59	[1.27, 1.92]
α_{4+}	1.92	[1.64, 2.20]
β_1	1.43	[0.28, 2.78]
β_2	0.78	[-0.36, 2.05]
β_3	1.82	[0.60, 3.36]
β_4	0.85	[-0.07, 1.86]
β_5	-0.70	[-1.53, 0.19]
β_6	0.36	[-0.52, 1.33]
β_7	0.58	[-0.20, 1.45]
β_8	-1.52	[-2.19, -0.89]
β_9	0.48	[-0.04, 1.04]
β_{10}	-0.16	[-0.54, 0.24]
β_{11}	-0.13	[-0.56, 0.32]
β_{12}	0.03	[-0.30, 0.37]
β_{13}	-0.09	[-0.34, 0.19]
β_{14}	0.45	[0.21, 0.71]
β_{15}	1.76	[1.35, 2.20]
β_{16}	1.20	[0.85, 1.59]
β_{17}	1.45	[1.02, 1.93]
β_{18}	-0.33	[-0.52, -0.12]
β_{19}	0.64	[0.38, 0.92]
β_{20}	0.28	[0.05, 0.53]
β_{21}	0.37	[0.12, 0.63]
β_{22}	0.60	[0.34, 0.89]
β_{23}	0.97	[0.60, 1.40]
β_{24}	1.39	[0.84, 1.76]
β_{25}	0.81	[0.18, 2.00]
β_{26}	2.56	[1.42, 4.01]

Table 4: Posterior mean and 95% symmetric credible intervals (CIs) for the resighting probabilities (p_a^* and p_a, for $a = 2, \ldots, 5+$), recovery probability (λ) and dispersal probabilities (γ_a, for $a = 1, \ldots, 3+$) for the integrated model; and capture-recapture only model.

	Integrated		**Capture-recapture only**	
Parameter	Mean	95% CI	Mean	95% CI
p_2^*	0.02	[0.01, 0.03]	–	–
p_3^*	0.03	[0.03, 0.04]	–	–
p_4^*	0.03	[0.02, 0.04]	–	–
p_{5+}^*	0.02	[0.01, 0.03]	–	–
p_2	0.06	[0.06, 0.07]	0.07	[0.07, 0.08]
p_3	0.27	[0.26, 0.28]	0.25	[0.23, 0.26]
p_4	0.38	[0.36, 0.40]	0.35	[0.33, 0.37]
p_{5+}	0.37	[0.35, 0.38]	0.41	[0.38, 0.43]
λ	0.02	[0.01, 0.02]	–	–
γ_1	0.20	[0.11, 0.27]	–	–
γ_2	0.07	[0.01, 0.15]	–	–
γ_{3+}	0.32	[0.30, 0.34]	–	–