

Age-dependent mixture models for recovery data on animals marked at unknown age

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Summary. Data are often collected from wild animals that have been marked at unknown age. As a result, standard probability models, fitted by maximum likelihood, cannot incorporate age-dependence in probabilities of annual survival. We propose and fit new mixture models to ring-recovery data on birds ringed of unknown age, in which it is possible to incorporate age dependence in survival. It is shown that it is important to analyse simultaneously data on animals marked as young, and of known age, as otherwise the mixture model is parameter redundant. The potential of the approach is illustrated by a new analysis of data on mallards, *Anas platyrhynchos*, and the wider performance of the approach is demonstrated through simulation. The models provide a way of analysing correctly large numbers of historical data sets.

1. Introduction

Ring-recovery experiments require individuals to be ringed uniquely, so that rings recovered from dead individuals can be used for the estimation of mortality. The resulting data can be summarised by a triangular matrix, where the row index represents the year of ringing and the column index represents the year during which the ring was recovered. Additionally, individuals may be categorised by features such as sex, age, cause of mortality and geographical location when marked.

The motivating data for the work of this paper was ring-recovery information collected on male mallards, *Anas platyrhynchos*, and given in Table 1. The data are subdivided into two categories: birds ringed as young, and thus always of known age, and birds ringed nominally as ‘adults’. It is not possible to identify the age of adult mallards, and thus the individuals ringed as adults are of unknown age. This historical data set was collected between 1963 and 1971, and has been used extensively to demonstrate time-dependent and subsequently age-dependent ring-recovery models (Brownie et. al., 1985; Freeman and Morgan, 1992; Catchpole et. al., 2001).

Freeman and Morgan (1992) proposed a modelling strategy for ring-recovery data from birds of known age, however in many cases age is unknown. For example, this is true of long-term studies of sea birds which are marked as breeding adults of unknown age; see for example Reynolds et. al. (2009). In order to understand recent declines in populations of sea-birds it is vital to be able to include age-structure in probability models of survival. Failure to account for age-variation in demographic parameters can result in biased parameter estimators and may adversely affect model discrimination. One approach to the unknown-age problem is through the use of a beta distribution for the adult survival probability (see for example, Besbeas et. al. (2009)). This approach however does not naturally extend to modelling data of known and unknown age simultaneously. Robinson (2010) examined how knowledge of the proportion of individuals in a specific age class can be used to adapt esti-

mates of age-dependent survival probabilities, however he used an ad-hoc approach which ignored the effect of estimation error.

In the fisheries literature, age-dependence has also been found to be important. Fournier et al (1991, 1998) proposed a method for linking length of recovered individuals with age by using a von Bertalanffy growth curve.

More generally, a range of models with state uncertainty have been recently developed - see Pradel (2005), Pledger et. al. (2009) and Wright (2009). Stopover models (Pledger et. al., 2009), which incorporate the uncertain arrival time of individuals entering a study area, were the motivating approach for the model presented in this paper. The direct analogue to stopover models for ring-recovery data would require modelling the time from birth of individuals to the time of death; however this is in fact unnecessary for the modelling of individuals of unknown age and the approach we take conditions on the age and time of marking of the individuals within the study.

There is a pressing need for new methodology in this area. Our approach estimates the discrete age distribution of individuals marked at unknown age as a parameter of the model, and if we have an unbiased sample of the underlying population this age distribution has a valuable biological interpretation.

The construction of the likelihood for the model is presented in Section 2. We then apply the model to the mallard data set in Section 3. The performance of the model is investigated using simulation in Section 4 and the paper concludes with a general discussion. An appendix contains a detailed computation of the parameter redundancy of the models considered in the paper.

2. Likelihood construction and model notation

Suppose that annual cohorts of marked individuals are released during I years, that the recovery of dead individuals spans τ years, where $I \leq \tau$, and the population has $(J - J_0 + 1)$ age-classes of individuals, where J_0 denotes the minimum age of individuals within the population and J denotes the maximum age-class of the population, such that individuals can be categorised from age J_0 , up to $J - 1$, and then individuals of age greater than or equal to J are grouped in a category $J+$. Adopting the general notation of a subscript denoting time, and age-dependence being denoted in parentheses, we define the parameters:

$\phi_t(a)$: the probability an individual aged a at time t survives until time $t + 1$;

$\lambda_t(a)$: the probability of a mark being reported from an individual aged a when it died in the time interval $(t, t + 1)$;

$\beta_t(a)$: the proportion of individuals marked at time t that are age a .

Let $\nu_{i,t}(a)$ denote the probability an individual that is marked at time i at age a , is recovered dead between times t and $t + 1$. Let $\nu_{i,\infty}(a)$ denote the probability an individual that is marked at time i at age a , is never recovered dead during the study. We assume that a increments by integer values from age $J_0, \dots, J+$. We note that $\sum_{a=J_0}^{J+} \beta_t(a) = 1$ for each cohort of individuals marked at time t . Then, for $i = 1, \dots, I$ and $t = 1, \dots, \tau$,

$$\nu_{i,t}(a) = \begin{cases} 0 & \text{if } i > t \\ \{1 - \phi_t(a)\}\lambda_t(a) & \text{if } i = t \\ \{\prod_{k=i}^{t-1} \phi_k(a+k-i)\} \times \{1 - \phi_t(a+t-i)\}\lambda_t(a+t-i) & \text{if } i < t \end{cases}$$

and

$$\nu_{i,\infty}(a) = 1 - \sum_{t=1}^{\tau} \nu_{i,t}(a),$$

for $a = J_0, \dots, J-1, J+$.

Suppose the age of an individual is unknown at the time of marking; we let $\nu_{i,t}(u)$ denote the probability an individual of unknown age is marked at time i and recovered dead at time t . Then,

$$\nu_{i,t}(u) = \sum_{a=J_0}^{J+} \beta_i(a) \nu_{i,t}(a),$$

where $\sum_{a=J_0}^{J+} \beta_i(a) = 1, \forall i$, and

$$\nu_{i,\infty}(u) = 1 - \sum_{t=1}^{\tau} \nu_{i,t}(u).$$

The likelihood is then simply a product of multinomial likelihoods, with the i th multinomial index corresponding to the number of released individuals at time i , given by

$$L \propto \prod_{\alpha=a \cup u} \prod_{i=1}^I \left[\left\{ \prod_{t=1}^{\tau} \nu_{i,t}(\alpha)^{m_{i,t}(\alpha)} \right\} \times \nu_{i,\infty}(\alpha)^{m_{i,\infty}(\alpha)} \right],$$

where $a \cup u$ denotes that the product is taken over all known and unknown aged individuals, $m_{i,t}(\alpha)$ denotes the number of individuals released at time i at age α and recovered between times t and $t+1$ and the number of individuals released at time i at age α and never recovered dead is denoted by $m_{i,\infty}(\alpha)$.

A quasi-Newton optimisation function was used to maximise the likelihood functions considered in this paper. Within simulations, where parameter values were known, informed initial values were used whilst for applications to the data multiple random starts were used to avoid local optima. Convergence was checked to ensure global optima were reached.

2.1. Model notation

To simplify consideration of parameter dependencies, we introduce an extension to the notation for Freeman-Morgan ring-recovery models introduced by Catchpole and Morgan (1996). Thus a model is defined by $X/Y/Z/W$ where X, Y, Z and W denote the assumptions made regarding the parameters denoting first year survival probability, $\phi(0)$, adult survival probability, $\phi(1+)$ (recalling that this denotes the survival probability for individuals aged greater than or equal to 1), recovery probability λ and the age-distribution, β respectively. The possible parameter dependencies considered will vary by parameter, however a general list of possible dependencies is:

C: constant;

T: time dependence: i.e. a separate parameter for each year;

$A_{j:k}$: age-dependence from age j to age $k+$: i.e. a separate parameter for ages $j, \dots, k-1$ and $\geq k$;

Interactions of these dependencies may also be considered; such interactions are denoted by the above notation separated by a comma and additive models may also be considered which are denoted by $+$; these models represent constrained models where age and time-effects are additive on the logistic scale. If the data do not contain any first-year individuals we denote the model by $-/Y/Z/W$. For simplicity of notation we let $A_{j:j} = A_j$.

We note that due to the structure of the models we consider, if survival or recovery probabilities are age-dependent, $A_{j_1:k}$ then β will similarly need to be age-dependent $A_{j_2:k-1}$ with $\beta(k) = 1 - \sum_{i=j_2}^{k-1} \beta(i)$, where $j_2 \leq j_1$.

We further note that if a model is constrained so that all marked individuals belong to a single age-class, this can be denoted by $X/Y/Z/-$. For the applications in this paper it is assumed that this means that all individuals are assigned to the category of ‘age greater than or equal to 1’, i.e. $\beta(1) = 1$.

Although not necessary for the applications within this paper, the age-dependent notation can be extended to incorporate grouped age classes, for example $A_{1-j:j+1-k}$ for adult survival would denote a constraint on survival probabilities such that $\phi(1) = \dots = \phi(j) = a$ and $\phi(j+1) = \dots = \phi(k-1) = \phi(k+) = b$ where $a \neq b$.

2.2. Parameter redundancy

Complex models for ring-recovery data may be parameter redundant, which occurs when not all parameters can be estimated by classical inference. Parameter-redundant models are non-identifiable and can be re-parameterised in terms of a smaller parameter set; see Catchpole and Morgan (1997) and Cole et. al. (2010).

A parameter redundant model has deficiency $d > 0$, which is the difference between the number of parameters in the model and the number of parameters that can be estimated. If a model is not parameter redundant it is in theory possible to estimate all the parameters. Such models are termed full-rank and have deficiency $d = 0$.

It is possible to examine whether a model is parameter redundant using symbolic computation. Furthermore, if the model is parameter redundant, symbolic computation can then be used to determine which parameters may be estimated; see Catchpole and Morgan (1997), Catchpole et. al. (1998b) and Cole et. al. (2010). It is possible to determine the deficiency of additive or covariate models using the theorem of Cole and Morgan (2010a). The utility of this symbolic approach is demonstrated in Cole and Morgan (2010b) and Cole (2010).

Several of the mixture models that we propose possess large numbers of parameters, as it is important to model nuisance parameters, such as the reporting probabilities correctly, to avoid biases in parameters of interest. Therefore before attempting to fit models to data, we used symbolic computation to determine whether the models of this paper are parameter redundant. The appendix contains details of the parameter redundancy for the class of mixture models of interest.

3. Mallard ring-recoveries

Model selection was conducted on the data of Table 1(a) by Freeman and Morgan (1992) using likelihood-ratio tests, and they identified a best model with time-dependent first-year

Table 2. Maximum-likelihood estimates and corresponding standard errors from fitting model $T/C/T/-$ to the separate ‘young’ mallard data only and model $-/C/T/-$ to the ‘adult’ mallard data only. SE denotes standard error, obtained from inverting the hessian at the maximum likelihood estimates.

Parameter	Young Only		Adults Only	
	MLE	SE	MLE	SE
$\phi_1(0)$	0.44	0.049		
$\phi_2(0)$	0.48	0.055		
$\phi_3(0)$	0.59	0.046		
$\phi_4(0)$	0.46	0.042		
$\phi_5(0)$	0.43	0.042		
$\phi_6(0)$	0.60	0.044		
$\phi_7(0)$	0.59	0.045		
$\phi_8(0)$	0.56	0.055		
$\phi_9(0)$	0.29	0.135		
$\phi(1+)$	0.69	0.020	0.64	0.015
λ_1	0.15	0.020	0.13	0.037
λ_2	0.28	0.033	0.25	0.029
λ_3	0.18	0.022	0.16	0.018
λ_4	0.22	0.019	0.19	0.019
λ_5	0.17	0.015	0.17	0.016
λ_6	0.24	0.022	0.19	0.015
λ_7	0.27	0.023	0.20	0.014
λ_8	0.24	0.021	0.23	0.015
λ_9	0.15	0.017	0.16	0.014

survival, constant adult survival and time-dependent recovery probability as being the most appropriate for the data set, denoted by $T/C/T/-$. In order to model all the data of Table 1 simultaneously, we have to be sure that the data sets are compatible. We present in Table 2 the maximum-likelihood estimates (MLEs) from the known-age data with the MLEs from the unknown-age data, where we fit model $-/C/T/-$. We observe that the estimate of adult survival probability from the known-age data, denoted by $\phi(1+)$, is noticeably higher than that from the unknown-age data. Performing a likelihood-ratio test of the $\phi(1+)$ parameter being equal between the two data sets results in a significant test statistic (p-value of 0.029). We further observe that the ring-recovery probabilities are also lower for the individuals marked as adults. This suggests that ring-recovery probabilities may be age-dependent and we test the significance of this effect later in the paper. In an earlier analysis of the data, Freeman and Morgan (1992) also found that the recovery probability for juveniles is greater than that for adults. They surmise that this might be due to juveniles being more vulnerable than adults to hunting (and as a result easier to recover).

Freeman and Morgan (1992) considered the joint model $T/C/T/-$, and we shall compare the fit of this model with that of the mixture models proposed earlier. The mixture models fitted to the mallard data will enable estimation of the proportions of individuals marked as adults assigned to specific age-classes. We first considered models with $J_0 \geq 1$, and therefore assumed $\beta(0) = 0$. Estimates from the model with 2 age classes, $\beta(1)$ and $\beta(2+) = 1 - \beta(1)$ resulted in a boundary estimate of $\beta(1) = 1$. We therefore also considered models with

Table 3. Mixture models fitted to the mallard data sets and ranked by AIC. Here n denotes the number of estimable parameters and model notation is provided in the text. The AIC of model $T/C/T + A_{0:1}/A_0$ is 20720.88.

Model	n	ΔAIC
$T/C/T + A_{0:1}/A_0$	21	0.00
$T/C/T/A_0$	20	2.82
$T/A_{1:2}/T + A_{0:1}/A_{0:1}$	23	3.65
$T/C/T, A_{0:1}/A_0$	29	5.43
$T/A_{1:2}/T + A_{0:1}/A_1$	22	7.11
$T/C/T + A_{0:1}/-$	20	8.50
$T/A_{1:2}/T/A_1$	21	8.56
$T/C/T/-$	19	11.23

$J_0 = 0$.

Table 3 displays the models fitted to the young and adult data ranked in increasing order of AIC. From the results of Table 6 we deduce that all the models presented in Table 3 are full rank.

The models containing no mixtures are ranked very low: $\Delta AIC > 8$ when compared to the best model. The model with the smallest AIC, $T/C/T + A_{0:1}/A_0$, has identified the need for one mixture parameter, $\beta(0)$, which means that some ‘adult’ individuals have been assigned to the first-year age class. It was also examined whether more age classes were needed, however the model, $T/A_{1:2}/T + A_{0:1}/A_{0:1}$, with two estimated mixture probabilities, $(\beta(0), \beta(1), \beta(2) = 1 - \beta(0) - \beta(1))$ had the larger AIC.

We note further that an additive age effect as well as time dependence was found to be significant for the ring-recovery probabilities. The MLEs for the model with the smallest AIC are displayed in Table 4. For this model a Pearson chi-squared test results in a p-value of 0.358 indicating no evidence of lack of fit. We have examined the assumption of the population having a stable age structure by fitting a time-dependent β model: $T/C/T + A_{0:1}/T, A_0$. This model has an AIC of 20725.99, showing that the stable-age structure assumption is valid for this data set.

As with all ring-recovery models, the need to allocate individuals to discrete annual cohorts means that any individuals born within a 12 month period are assigned to a single cohort. However, the complication of multiple broods (Olsen et. al., 2003) and/or difficulties with age-identification of mallards may mean that individuals aged less than 12 months are assigned to the ‘adult’ category.

The model selection of Table 3 has in fact chosen a model which suggests that some of the ‘adult’ individuals are within their first year of life and we conclude that 30% of the ‘adult’ individuals of unknown age are in fact in their first year of life. The survival probability of individuals aged 1 or more is higher than first-year survival, and the recovery probability of adult individuals is lower than for individuals in their first year of life.

We have fitted a two-age-class model to the adult data alone, and we estimate $\phi(J+)$ to be 0.68 (0.022), which lies between the adult survival probability MLE from the non-mixture model for unknown-age data alone (0.64 (0.015)) and the mixture model for combined known and unknown-age data (0.69 (0.015)). Although we are unable to estimate the proportions of animals marked in each age class due to parameter redundancy (see Table 5), the ability

Table 4. Maximum likelihood estimates and corresponding standard errors (SE) from the model selected for the mallard data: $T/C/T + A_{0.1}/A_0$.

Parameter	MLE	SE	Parameter	MLE	SE
$\beta(0) = 1 - \beta(1)$	0.30	0.083			
$\phi_1(0)$	0.49	0.058			
$\phi_2(0)$	0.54	0.061			
$\phi_3(0)$	0.67	0.053			
$\phi_4(0)$	0.51	0.053			
$\phi_5(0)$	0.52	0.053			
$\phi_6(0)$	0.66	0.047			
$\phi_7(0)$	0.61	0.051			
$\phi_8(0)$	0.59	0.057			
$\phi_9(0)$	0.44	0.112			
$\phi(1+)$	0.69	0.015			
$\lambda_1(0)$	0.17	0.024	$\lambda_1(1+)$	0.12	0.074
$\lambda_2(0)$	0.31	0.038	$\lambda_2(1+)$	0.24	0.097
$\lambda_3(0)$	0.22	0.032	$\lambda_3(1+)$	0.17	0.081
$\lambda_4(0)$	0.25	0.027	$\lambda_4(1+)$	0.19	0.076
$\lambda_5(0)$	0.21	0.023	$\lambda_5(1+)$	0.16	0.068
$\lambda_6(0)$	0.27	0.030	$\lambda_6(1+)$	0.21	0.079
$\lambda_7(0)$	0.28	0.031	$\lambda_7(1+)$	0.22	0.079
$\lambda_8(0)$	0.28	0.031	$\lambda_8(1+)$	0.22	0.079
$\lambda_9(0)$	0.19	0.025	$\lambda_9(1+)$	0.15	0.067

to estimate the adult survival probability of 0.68, supports the hypothesis of the occurrence of individuals in their first-year of life within the adult data.

4. Simulation study

4.1. Ring-recovery models

We ran a total of 250 simulations from model $C/C/C/C$, for each of which we have simulated 1000 ring-recovery encounter histories spanning 8 encounter occasions for individuals of unknown age (proportion $\beta(0) = 0.3$ are in their first year of life, whilst proportion $1 - \beta(0)$ are classified as adults). Also, we have simulated 800 ring-recovery encounter histories for individuals marked in their first year of life. The parameter values used for both components of the simulation are: $\phi(0) = 0.4$, $\phi(1+) = 0.8$, $\lambda = 0.3$. Generally, with this type of data it would be usual to fit a model $C/C/C/-$ to the data for individuals of known age, and a model $-/C/C/-$ to the data of individuals of unknown age. We compare the MLEs from this modelling approach with the approach of fitting the $C/C/C/C$ model applied to combined data on individuals of known and unknown age, where we estimate the proportion of first-year individuals in the unknown age sample and also to data on individuals of unknown age only. Boxplots of the MLEs from the two modelling approaches are displayed in Figure 1. For the mixture model applied to individuals of unknown age only, the model is parameter redundant (see Table 5): we are able to estimate $\phi(1+)$ and λ , but we are unable to estimate $\beta(0)$ and $\phi(0)$ separately.

We observe that by not accounting for the heterogenous population in the sample of unknown age, we obtain biased estimates of adult survival and recovery probability, as would be expected, since we would incorrectly be assuming that the individuals of unknown

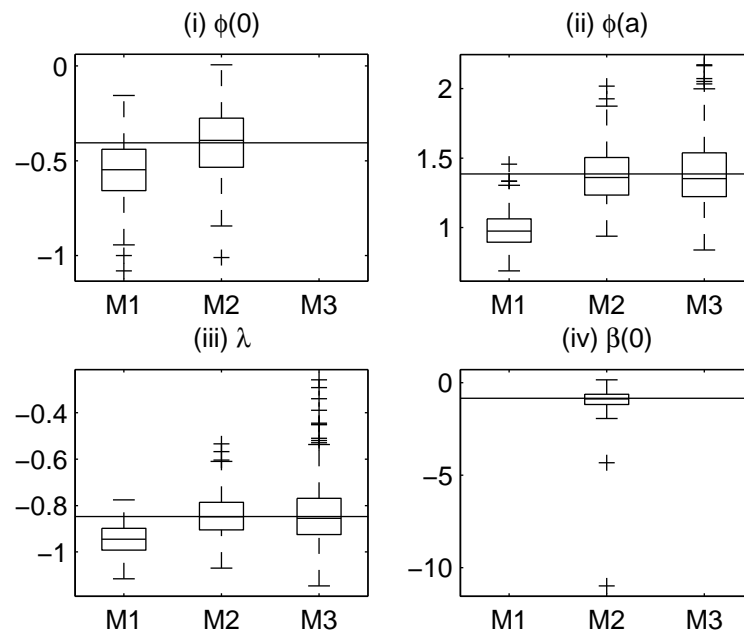


Fig. 1. Maximum-likelihood estimates (on the logistic scale) from model M1: $C/C/C/-$ for the known-age individuals and $-/C/C/-$ for the unknown-age individuals, model M2: $C/C/C/A_0$ and model M3: $C/C/C/A_0$ for the unknown-age individuals only, for parameters: (i) $\phi(0)$, (ii) $\phi(1+)$, (iii) λ , and (iv) $\beta(0)$. The horizontal lines represent the true value of each parameter.

age all fall within the adult category. We also observe that we are able to estimate parameter $\beta(0)$ from the data available. We note that from the 250 simulations, we obtained two outlier boundary estimates of $\beta(0)$ represented by the crosses in Figure 1(iv).

4.2. *Extension to joint recapture and recovery models*

The model presented in Section 2 is for ring-recovery data only. However, it is straightforward to adapt this mixture modelling approach to the case of joint recapture and recovery data measured on the same animals (Catchpole et. al., 1998). Due to the need to account for individuals being marked at all possible ages, it is not possible to construct a closed-form likelihood as for the ring-recovery likelihood, however the likelihood function can be constructed through the formation of probabilistic statements for each observed encounter history. Thus suppose the probability of observed encounter history x_i is denoted by $\Pr(x_i)$, then the likelihood function for the individuals of unknown age at time of marking is given by:

$$L = \prod_i \Pr(x_i) = \prod_i \left\{ \sum_a \beta(a) \times \Pr(x_i|a) \right\}$$

where $\Pr(x_i|a)$ is a function of model parameters $\phi_t(a)$ and $\lambda_t(a)$ as well as the additional parameters $p_t(a)$, which denotes the probability that an individual aged a and alive at time t is recaptured at that occasion. Although computationally slower than a sufficient-statistic approach for likelihood construction (Catchpole et al, 1998), the approach is not prohibitively slow for model discrimination.

In Figure 2 we display the MLEs from simulated joint recapture and recovery data and from the same data set with the recaptures removed, which results in simple ring-recovery data. As expected, estimates of survival probability and recovery probability are more precise for joint recapture and recovery data than for ring-recovery data alone. We also observe that the estimate of $\beta(0)$ is better for the joint data than for ring-recovery data alone.

4.3. *Effect of senescence*

Senescence describes the change in demographic parameters of ageing individuals. For animal populations it is usual for survival probabilities in their first-year of life to be lower than in older years. Further, in some populations it is possible to detect a decline of survival probabilities for older individuals. We have run a simulation to examine whether the existence of low survival probabilities of old individuals may incorrectly allocate individuals to each of the age classes and bias estimates of the β parameter.

We simulated data from model $\{\phi(0) = 0.4, \phi(1+) = 0.8, \lambda = 0.3, \beta(0) = 0.3\}$ and also model $\{\phi(0) = 0.4, \phi(1) = \dots = \phi(4) = 0.6, \phi(5) = 0.4, \phi(6+) = 0.2\}$. To each data set we fit model $C/C/C/A_0$ and Figure 3 displays boxplots of the MLEs of $\beta(0)$.

As expected from earlier simulations, $\beta(0)$ is estimated well for the case where no senescence exists in the data. However, for the simulations exhibiting senescence, $\beta(0)$ is shown to be underestimated. This underestimation is due to the wrong age-structured survival probability being fitted to the model: the parameters $\phi(0)$ and $\phi(1+)$ do not adequately describe the age-dependent variation in the second simulation.

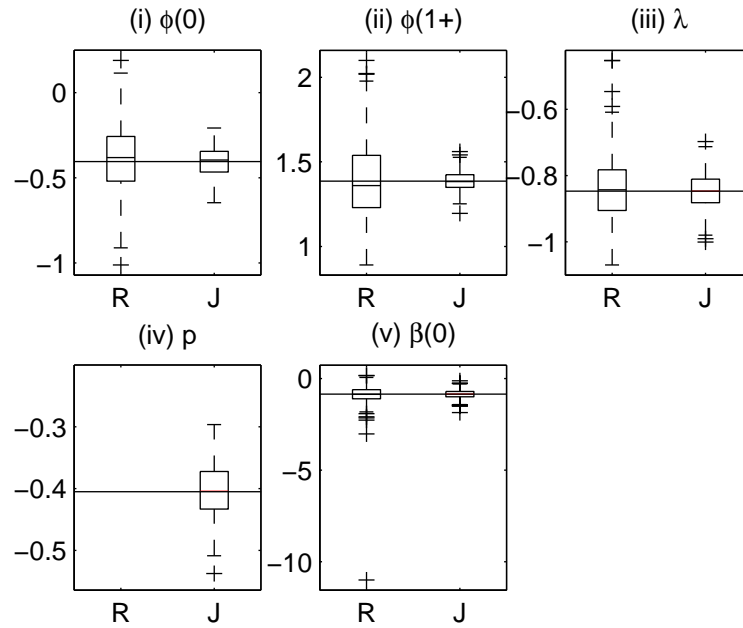


Fig. 2. Maximum likelihood estimates (on the logistic scale) from R: ring-recovery data and J: joint recapture and recovery data for parameters: (i) $\phi(0)$, (ii) $\phi(1+)$, (iii) λ , (iv) p and (v) $\beta(0)$.

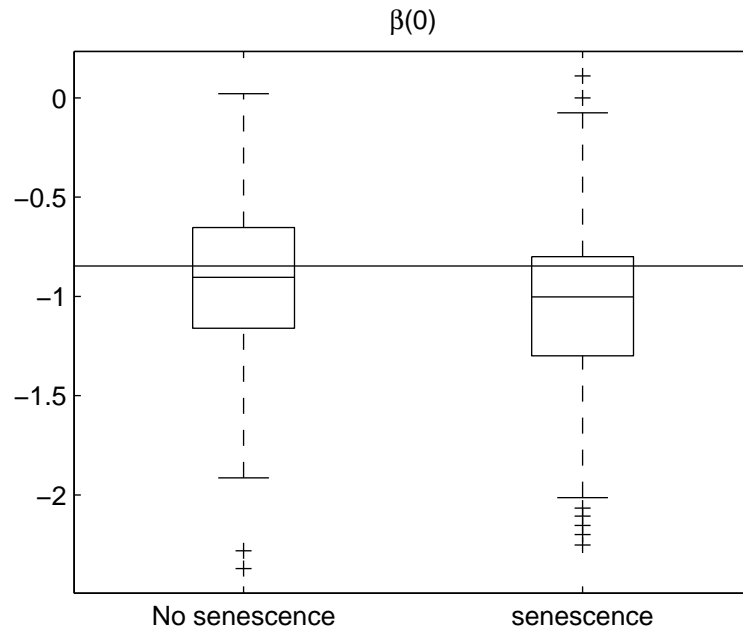


Fig. 3. Maximum-likelihood estimates of $\beta(0)$ from simulations with no senescence and senescence.

Within this simulation, the estimate of adult survival is an underestimate of the true adult survival probability before the senescent decline commences as it is a compromise estimate of the survival probabilities for all individuals aged greater than or equal to 1. Therefore the individuals are incorrectly being allocated to the adult age class rather than the juvenile age class as the adult age class has a correspondingly low survival probability.

Therefore if this mixture model is used for individuals of unknown age, it is necessary to take care selecting the age-structure of the population for individuals of known-age, before modelling individuals of unknown-age. One approach would be to use a step-wise score-test procedure to detect age-dependence within the data of individuals of known age as proposed in Catchpole and Morgan (1996) and McCrea and Morgan (2011).

5. Discussion

The mixture model of this paper has conditioned on the time of marking of individuals of unknown age. This differs from stopover-type mixture models (Pledger et. al., 2009) which extrapolate the possible encounter histories back to the time of birth. The primary difference however is that for our proposed model there exists a subset of non-ringed individuals, and since for ring-recovery experiments live animals are only captured at the time of marking, we would need an additional parameter to model the probability of this initial capture, thus unnecessarily complicating the model.

The mixture model has the ability to estimate the age distribution of individuals marked at unknown age, rather than needing to obtain this information from other sources. Through the application to the mallard data, we have identified that in fact the population of ‘adult’ mallards consists of a mixture of mature birds and mallards in their first-year of life. In general this feature has important biological implications, such as determining the stability or growth rate of species (Caswell, 2001).

It would be possible to adapt the proposed model if more was known regarding the months of ringing and recovery, and this monthly information could be directly incorporated into the model.

Through simulation we have determined that the model provides unbiased estimators of survival, recovery and age-proportion parameters. We have further extended the theory to apply to the joint analysis of capture-recapture and recovery data, and have verified that the parameters are better estimated from the greater information available from such integrated studies.

Without additional information from individuals of known age, we have demonstrated that the mixture models would be parameter redundant, and therefore the additional information from studies of individuals of known age is necessary for all parameters to be estimable. This is similar to a particular finding of Brownie et. al. (1985). However, we have further seen that we are able to estimate the highest age-class survival probabilities from only data from individuals of unknown age. This could be of considerable use in practice, for instance with regard to providing new analyses of historical data sets, which is now possible using the models of this paper.

Table 5. Parameter redundancy results for models of unknown-age individuals. For each model the number of parameters, q , and the deficiency of the model, d , are given. Model notation is described in the text. The estimable parameter combinations are presented and expressions for ω_i and $q_{A,t}$ are given below the table.

Model	q	d	Estimable Parameters
$-/A_{J_0:J}/C/A_{J_0:J-1}$	$2J - 2J_0 + 2$	$J - J_0$	$\phi(J+), \lambda, \omega_1$
$-/A_{J_0:J}/T/A_{J_0:J-1}$	$\tau + 2J - 2J_0 + 1$	$J - J_0$	$\phi(J+), \{\lambda_t\}, \omega_1$
$-/A_{J_0:J}/A_{J_0:J}/A_{J_0:J-1}$	$3J - 3J_0 + 2$	$2J - 2J_0$	$\phi(J+), \omega_2, \omega_3$
$-/A_{J_0:J}/T, A_{J_0:J}/A_{J_0:J-1}$	$q_{A,t}$	$\frac{1}{2}(J - J_0)^2 + \frac{5}{2}(J - J_0)$	$\phi(J+), \omega_4, \omega_5, \omega_6$
$\omega_1 = \left\{ \sum_{j=J_0}^i \beta(j)(\phi(J+) - \phi(j - i - 1 + J)) \prod_{k=J_0}^{J-i-J_0} \phi(k) \right\}_{i=J_0, \dots, J+}$ $\omega_2 = \nu_{1, J-J_0+1} / \{1 - \phi(J+)\}$ $\omega_3 = \left\{ \nu_{1, J-J_0+1}(u) - \phi(J+) \prod_{k=J_0}^{J-J_0-k+1} \nu_{1, k}(u) \right\}_{k=J_0, \dots, J+}$ $\omega_4 = \left\{ \frac{\lambda_{J+t}(J+)}{\lambda_J(J+)} \right\}_{t=J+1, \dots, \tau}$ $\omega_5 = \frac{\nu_{1, J-J_0+1}(u)}{1 - \phi(J+)}$ $\omega_6 = \left\{ \nu_{i, j}(u) \right\}_{j=i, \dots, J-J_0, i=1, \dots, I}$			
$q_{A,T} = \begin{cases} I\tau - \frac{1}{2}I^2 + \frac{1}{2}I + (J - J_0)(\tau + 2) - \frac{1}{2}\tau^2 + \frac{1}{2}\tau + 1 & \tau - I \leq J - J_0 \\ I(J - J_0) + \tau + \frac{1}{2}(J - J_0)^2 + \frac{3}{2}(J - J_0) + 1 & \tau - I > J - J_0 \end{cases}$			

Appendix

Parameter redundancy results for the class of models considered in the paper

The results of this appendix are obtained using the tools described in Cole et. al. (2010), in particular extension theorems, which provide general results, without reference to the duration of field studies. Attention is restricted here to the class of models fitted to the mallard data set. A computer package is available which allows the parameter redundancy of the full family of models described in this paper to be checked, and details are given at the end of the paper.

First we consider models for individuals of unknown age only. In the models we consider, the probability of annual survival, ϕ , and the proportion of individuals marked of age a , β , are both age dependent but not time-dependent. The parameter set is completed by the reporting probability, λ , which is either constant, time dependent, age dependent or age and time dependent. Results are given in Table 5.

If only unknown-age data are considered then we see from Table 5 that models are always parameter redundant. It is never possible to separate the proportions of animals marked at age a , $\{\beta(a)\}_{a=0, \dots, J-1}$, from the survival probabilities, $\{\phi(a)\}_{a=0, \dots, J-1}$. However an important finding is that it is always possible to estimate the adult survival probability, $\phi(J+)$.

We next consider combining unknown-age data with data on individuals marked as young, for which the full age dependence is known. Frequently we would take $J_0 > 0$, however if birds in their first year of life are present in a data set with older birds then we would take $J_0 = 0$. In cases of adult birds being marked at a breeding site then we might take $J_0 > 1$; for example this would be appropriate for sea birds, that do not breed as early as the second year of life. In Tables 6(a) and 6(b) the known-age data are assumed to have

Table 6. Parameter redundancy results for two combined data sets: recoveries from individuals ringed as young (all data of known age) and recoveries from individuals of unknown age. (a) $J_0 = 0$ and (b) $J_0 > 0$. For each model the number of parameters, q , and the deficiency of the model, d are given. Model notation is described in the text. Here $[\cdot]$ stands for ‘round to the nearest integer’. The results with \dagger are only valid if $\tau - I \leq J - J_0$. Expressions for $q_{A,t}$ can be found in Table 5.

(a) $J_0 = 0$		
	q	d
$C/A_{1:J}/C/A_{0:J-1}$	$2J + 2$	0
$T/A_{1:J}/C/A_{0:J-1}$	$2J + I + 1$	0
$C/A_{1:J}/T/A_{0:J-1}$	$\tau + 2J + 1$	0
$T/A_{1:J}/T/A_{0:J-1}$	$\tau + I + 2J$	0
$C/A_{1:J}/A_{0:J}/A_{0:J-1}$	$3J + 2$	$J - 1$
$T/A_{1:J}/A_{0:J}/A_{0:J-1}$	$3J + I + 1$	$\min(0, J - 2)$
$C/A_{1:J}/T, A_{0:J}/A_{0:J-1}$	$q_{A,t}$	$2J - 2$
$T/A_{1:J}/T, A_{0:J}/A_{0:J-1}$	$q_{A,t} + \tau - 1$	$[\frac{1}{4}J^2 + J]^\dagger$
(b) $J_0 > 0$		
	q	d
$C/A_{1:J}/C/A_{J_0:J-1}$	$2J - J_0 + 2$	0
$T/A_{1:J}/C/A_{J_0:J-1}$	$2J - J_0 + I + 1$	0
$C/A_{1:J}/T/A_{J_0:J-1}$	$\tau + 2J - J_0 + 1$	0
$T/A_{1:J}/T/A_{J_0:J-1}$	$\tau + I + 2J - J_0$	0
$C/A_{1:J}/A_{0:J}/A_{J_0:J-1}$	$3J - J_0 + 2$	$J - J_0$
$T/A_{1:J}/A_{0:J}/A_{J_0:J-1}$	$3J - J_0 + I + 1$	$J - J_0$
$C/A_{1:J}/T, A_{0:J}/A_{J_0:J-1}$	$q_{A,t} + J_0\tau - \frac{1}{2}J_0^2 + \frac{3}{2}J_0$	$[J + \frac{1}{4}J^2 - \frac{1}{2}J_0^2 + \frac{1}{2}J_0 - 1]^\dagger$ $J \geq 2J_0$
		$\frac{3}{2}J + \frac{1}{2}J^2 - JJ_0 + \frac{1}{2}J_0^2 - \frac{1}{2}J_0 - 1^\dagger$ $J < 2J_0$
$T/A_{1:J}/T, A_{0:J}/A_{J_0:J-1}$	$q_{A,T} + I + J_0\tau - \frac{1}{2}J_0^2 + \frac{3}{2}J_0 + 1$	$[J + \frac{1}{4}J^2 - \frac{1}{2}J_0^2 + \frac{3}{2}J_0 - 1]^\dagger$ $J \geq 2J_0$
		$\frac{3}{2}J + \frac{1}{2}J^2 - JJ_0 + \frac{1}{2}J_0^2 + \frac{1}{2}J_0 - 1^\dagger$ $J < 2J_0$

the same parameters as the unknown-age data, when appropriate.

In many cases combining the two data sets results in models that are not parameter redundant, unlike the results from unknown-age data alone. In general it can be shown that if the model for the known-age data is full rank then combining with an age-dependent mixture model will also result in a full-rank model. The proof of this follows the extension theorem of Catchpole and Morgan (1997) and is not given here. The results presented in Table 6 for models with age- and time-dependent recovery probabilities hold only for the case of $\tau - I \leq J - J_0$, which the mallard data set satisfies. If $\tau - I > J - J_0$ the deficiency of the models can still be determined, but it is more complex than the forms of Table 6.

We note finally that the parameter-redundancy results presented assume that there are no missing data. For the mallard data only two cells have zero recoveries, and these are in different rows of the recovery tables. In such a case the zeros have no effect on the parameter redundancy. In general if there are more zeros in recovery tables then this may affect model deficiency and can be dealt with as explained by Cole et. al. (2010).

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Computer software

A symbolic computation package has been written to allow the parameter redundancy of any members of the family of models described in this paper to be checked. It is available from www.kent.ac.uk/ims/personal/djc24. MATLAB code for fitting the new mixture model is available from RSM.

References

- Besbeas, P., Borysiewicz, R.S. and Morgan, B.J.T. (2009) Completing the ecological jigsaw. pp 513-539 in *Modeling Demographic processes in marked populations*, Eds., Thomson, D. L., Cooch, E.G. and Conroy, M.J. Springer.
- Brownie, C., Anderson, D.R., Burnham, K.P. and Robson, D.S. (1985) *Statistical inference from band recovery data - A handbook*. 2nd Ed. U.S. Fish and Wildlife Service, Resource Publication 156. Washington, D.C., USA. 305pp.
- Caswell, H. (2001) *Matrix population models*, Sinauer, Massachusetts.
- Catchpole, E.A. and Morgan, B.J.T. (1996) Model selection in ring-recovery models using score tests. *Biometrics* **52**, 664-672.
- Catchpole, E.A. and Morgan, B.J.T. (1997) Detecting parameter redundancy. *Biometrika* **84**, 187-196.
- Catchpole, E.A., Morgan, B.J.T. and Freeman, S.N.(1998b) Estimation in parameter redundant models. *Biometrika* **85**, 462-468.
- Catchpole, E.A., Morgan, B.J.T., Freeman, S.N. and Harris, M.P. (1998) Integrated recovery/recapture data analysis. *Biometrics* **54**, 33-46.

- Catchpole, E.A., Kgosi, P.M. and Morgan, B.J.T. (2001) On the near-singularity of models for animal recovery data. *Biometrics* **57**, 720–726.
- Cole, D.J. (2010) Determining parameter redundancy of multi-state mark-recapture models for sea birds. *Journal of Ornithology* In press.
- Cole, D.J. and Morgan, B.J.T. (2010a) Parameter redundancy with covariates. *Biometrika* **97**, 1002–1005.
- Cole, D.J. and Morgan, B.J.T. (2010b) A note on determining parameter redundancy in age-dependent tag-return models for estimating fishing mortality, natural mortality and selectivity. *JABES* **15**, 431–434.
- Cole, D.J., Morgan, B.J.T. and Titterton, D.M. (2010) Determining the parametric structure of models. *Mathematical Biosciences* **228**, 16–30.
- Fournier, D.A., Sibert, J.R. and Terceiro, M. (1991) Analysis of length frequency samples with relative abundance data for the gulf of maine northern shrimp, *Pandalus borealis*, by the MULTIFAN method. *Can. J. Fish. Aquat. Sci.* **48**, 591–598.
- Fournier, D.A., Hampton, J. and Sibert, J.R. (1998) AMULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Can. J. Fish. Aquat. Sci.* **55**, 2105–2116.
- Freeman, S.N. and Morgan, B.J.T. (1992) A modelling strategy for recovery data from birds ringed as nestlings. *Biometrics* **48**, 217–235.
- McCrea, R.S. and Morgan, B.J.T. (2011) Multistate mark-recapture-recovery model selection using score tests. *Biometrics* **67**, 234–241.
- Olsen, R.E., Yerkesi, T. and Simpson, J.W. (2003) Occurrence of second broods in mallards in the midwest.. *The American Midland Naturalist* **150**, 302–307.
- Pledger, S., Efford, M., Pollock, K., Collazo, J. and Lynons, J. (2009) Stopover duration analysis with departure probability dependent on unknown time since arrival. pp 349–364 in *Modeling Demographic processes in marked populations*, Eds., Thomson, D. L., Cooch, E.G. and Conroy, M.J. Springer.
- Pradel, R. (2005) Multievent: an extension of multi-state capture-recapture models to uncertain states. *Biometrics* **61**, 442–447.
- Reynolds, T. J., King, R., Harwood, J., Frederiksen, M., Harris, M.P. and Wanless, S. (2009) Integrated data analysis in the presence of emigration and mark loss. *JABES* **14**, 411–431.
- Robinson, R.A. (2010) Estimating age-specific survival rates from historical ringing data. *Ibis* **152**, 651–653.
- Wright, J.A., Barker, R.J., Schofield, M.R., Frantz, A.C., Byrom, A.E. and Gleeson, D.M. (2009) Incorporating genotype uncertainty into mark-recapture-type models for estimating abundance using DNA samples. *Biometrics* **65**, 833–840.