

Stopover Duration Analysis with Departure Probability Dependent on Unknown Time Since Arrival

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Abstract In stopover duration analysis for migratory birds, models with the probability of departure dependent upon time since arrival are useful if the birds are stopping over to replenish body fat. In capture–recapture studies, the exact time of arrival is not generally known, as a bird may not be captured soon after arrival, or it may not be captured at all. We present models which allow for the uncertain knowledge of arrival time, while providing estimates of the total number of birds stopping over, and the distribution and mean of true stopover times for the population.

Keywords Age-related survival · Capture–recapture · Jolly–Seber model · Mark-recapture · migratory birds · residence time · Schwarz–Arnason model · Stopover duration · Survival curve

1 Introduction

Many migratory bird populations stop over at predictable sites en route, replenishing body reserves before flying on. The total number of birds using the staging site is important when studying the population (see e.g. Routledge et al. 1999; Fredericksen et al. 2001; Ydenberg et al. 2004), and detection of trends in population size uses comparisons of these totals over the years. Individual residence time at stopover sites is also an important variable in the biology of migratory birds for at least three reasons. First, if there is turnover of the population during staging, with some birds leaving before others have arrived, a snapshot estimate of the number of birds will underestimate the total throughput. Second, individual residence times, together with rate of refueling, shape overall migration strategies (Ålerstam and Lindström 1990). Migrating birds typically spend more time and energy at stopover sites than aloft (Wikelski et al. 2003); the total time spent on

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stopovers and the number of stopover sites visited largely determine the spatiotemporal course of migration. Effective conservation and management of migratory birds therefore depends on a fundamental understanding of stopover behaviour, including time spent resting and refuelling. Finally, stopover duration is a critical component in models of optimal bird migration (Ålerstam and Lindström 1990; Ålerstam and Hedenström 1998). Testing models of bird migration and reducing parameter uncertainty requires accurate estimates of stopover duration.

In stopover duration analysis, the key problem is estimating residence time before first capture and after last encounter (recapture or resighting). If birds are individually marked and uniquely identified at a stopover site, frequent sampling during the stopover provides a record of dates when caught (a capture history) for each bird which was caught or seen at least once. A capture–recapture analysis may then be used, with “age” meaning residence time (time since arrival). A Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) provides estimates of the probabilities of “survival” (retention at the site) from one sample to the next, and the probability of recapture at each sample. In the basic CJS model, these probabilities are assumed to depend on time (sample). This model was extended to multiple age classes by Pollock (1981). Lebreton et al. (1992) produced a comprehensive framework of likelihood models based on the CJS. They extended the basic CJS model to allow for multiple groups and covariates, and allowed survival and/or capture probabilities to be constant, to depend on time, known age and/or group (e.g. sex or site). They also introduced the idea of selecting from a wide class of models using Akaike’s Information Criterion (AIC, Akaike 1973). The basic CJS model has been used to estimate stopover duration (Kaiser 1995; Dinsmore and Collazo 2001; Rice et al. 2007). In these studies, the estimated daily probability of retention was used in the life expectancy formula of Seber (1982), stopover duration = $-1/\log_e(\text{daily retention probability})$. The life expectancy method is not unbiased however because the CJS model is conditional on first capture. If the “age” (time since arrival) is known at the time of first capture, CJS models provide estimates of “age-related survival”, where the probability of retention at a particular sample is assumed to be related to the duration of stopover so far. If, however, exact arrival times are unknown, assuming each newly caught bird has just arrived biases the estimates of the parameters of interest. It is necessary to estimate how long the bird was in residence before its first capture. Schaub et al. (2001) used Pradel’s (1996) recruitment parameters to get an overall estimate of stopover time, but see Efford (2005) and Pradel et al. (2005) for the limitations of this model.

We present new capture–recapture models which use information from each individual capture history to estimate the arrival times, and hence provide estimates of retention probabilities (which are dependent on time since arrival). The Jolly–Seber (JS) model (Jolly 1965; Seber 1965) provides estimates of the population size at each sample, and from these an estimate of the total number of birds stopping over may be obtained. Schwarz and Arnason (Schwarz and Arnason 1996; Schwarz 2001) provided a fully likelihood-based variant of the JS model, which we call

JSSA. This makes available maximum likelihood estimates of all the parameters, likelihood ratio tests and model comparisons based on AIC. The JSSA model also directly estimates N , the total number of birds stopping over, which is an advantage for our application. The likelihood framework gives profile likelihood intervals for N and other parameters (Cormack 1992).

This paper extends the JSSA model, providing a new collection of models in which capture and retention probabilities may depend on the residence time so far, even if arrival times are unknown. The models may also be applied to true births and deaths in populations with no migration, giving estimates of frailty and senescence.

Section 2 sets out the assumptions and notation of these models, Section 3 describes models in discrete time, and Section 4 introduces retention curves in continuous time. Statistical methods are in Section 5, Section 6 illustrates the models with real data, and Section 7 reports a simulation study. Evaluation and discussion are in Section 8.

2 Assumptions and Notation

2.1 Assumptions

Assumptions 1–6 are those of the JSSA model, but interpreting “birth” as arrival, “death” as departure, “survival” as retention at the site, “age” as time since arrival or residence time, and “lifetime” as stopover duration. We assume there are no actual births or deaths during the study.

1. K samples are taken at intervals which are large in relation to the time needed for the sample, so that samples may be regarded as instantaneous.
2. Arrivals and departures occur between samples, and departure is assumed to be permanent.
3. Each individual bird is uniquely and correctly identified.
4. There is a superpopulation of N birds, each available for capture on at least one sampling occasion.
5. Proportions $\beta_0, \beta_1, \dots, \beta_{K-1}$ of the N birds enter the population and are first available for capture at times 1, 2, \dots, K respectively ($\sum \beta_j = 1$).
6. Capture and departure events are independent between birds and between samples, and the birds are independent in their arrival times.
7. Sampling covers all the time when birds are present.

The extra assumption 7 prevents boundary effects from biasing estimates. Early birds arriving long before the first sample and late lingerers after the last sample would have their stopover durations underestimated.

The discussion to follow also assumes the samples are equally spaced in time, although unequal intervals may be modelled by adjusting all retention probabilities to a standard time unit.

2.2 Data

The data come in the form of a $D \times K$ capture matrix \mathbf{X} , where D is the number of distinct birds caught. Element x_{ij} is 1 if bird i is captured on occasion j , otherwise $x_{ij} = 0$. Row i of \mathbf{X} is the **capture history** (CH_i) for bird i , $i = 1, 2, \dots, D$.

Thus there are $N - D$ birds never caught, each with capture history $\mathbf{0}$, a K -vector of zeros. N is an unknown parameter.

2.3 Parameters

We use the JSSA N and β_j parameters, while the retention and capture parameters are extended to allow dependence on time since arrival as well as calendar time (sample). A bird which arrived a time units ago and is present at sample j is assumed to have probability p_{ja} of capture at sample j and ϕ_{ja} of retention from sample j to $j + 1$. These simplify to ϕ_j and p_j (the JSSA models) if there is no dependence on residence time, to ϕ_a and p_a if there is no calendar time dependence, and to ϕ and p if the probabilities are constant over both residence time and calendar time.

3 Models in Discrete Time

3.1 Capture Histories and Their Likelihoods

We now develop likelihoods for open population models which allow both time since arrival and calendar time to affect the capture and retention probabilities of the birds. Modelling individual capture histories in the JSSA framework enables us to allow for different possible arrival and departure times for each bird via random variables \mathcal{B} and \mathcal{D} . If bird i is first present and available for capture at sample b_i , and is last available for capture at sample d_i before departure, we denote its **presence history** PH_i by $\{b_i, d_i\}$. The ordered pair (b_i, d_i) is an unobserved realisation of the joint distribution of \mathcal{B}, \mathcal{D} . If retention is related to residence time, \mathcal{B} and \mathcal{D} are correlated. Suppose a bird has capture history CH_i with first capture at sample f_i and the last at ℓ_i ($1 \leq b_i \leq f_i \leq \ell_i \leq d_i \leq K$). Then the probability of this capture history, conditional on this presence history, is (omitting the i subscripts on b and d)

$$P(\text{CH}_i \mid \text{PH}_i = \{b, d\}) = \prod_{j=b}^d p_{ja}^{x_{ij}} (1 - p_{ja})^{1-x_{ij}} \quad (1)$$

where a is the time from arrival to sample j , e.g. if time is measured in days, $a = j - b + 1$ assuming “age” 1 day at arrival time. However, the JSSA model provides the probability of this presence history, allowing retention to depend on time since arrival:

$$P(\text{PH}_i = \{b, d\}) = P(\mathcal{B} = b \text{ and } \mathcal{D} = d) = \beta_{b-1} \left(\prod_{j=b}^{d-1} \phi_{ja} \right) (1 - \phi_{da}) \quad (2)$$

where, if $b=d$, the empty product $\prod_{j=b}^{d-1}$ is taken to be unity.

Hence the unconditional probability of bird i 's capture history with unknown arrival and departure times is found by summing $P(\text{CH}_i \mid \{b, d\}) \times P(\{b, d\})$ over all possible presence histories, using equations 1 and 2:

$$P(\text{CH}_i) = \sum_{b=1}^{f_i} \sum_{d=\ell_i}^K \left\{ \beta_{b-1} \left(\prod_{j=b}^{d-1} \phi_{ja} \right) (1 - \phi_{da}) \left(\prod_{j=b}^d p_{ja}^{x_{ij}} (1 - p_{ja})^{1-x_{ij}} \right) \right\}. \quad (3)$$

Similar reasoning gives the unconditional probability of no captures, denoted by CH_0 :

$$P(\text{CH}_0) = \sum_{b=1}^K \sum_{d=b}^K \left\{ \beta_{b-1} \left(\prod_{j=b}^{d-1} \phi_{ja} \right) (1 - \phi_{da}) \left(\prod_{j=b}^d (1 - p_{ja}) \right) \right\}. \quad (4)$$

The summation over possible departure times in equations 3 and 4 is an extension of the use of the parameter χ_j = probability not seen after sample j in the JS model. The JSSA model's entry parameters, β_j , allow us to do a similar summation over the entry times before the first sighting.

Let h index the different observed capture histories, with n_h being the number of birds with capture history h , and write the parameters N , β , p and ϕ as a parameter vector θ . Then a multinomial model to allocate the N birds to their capture histories gives the full likelihood of θ given the capture matrix \mathbf{X} as

$$L(\theta \mid \mathbf{X}) = \frac{N!}{\prod_h n_h! (N - D)!} \times \left(\prod_{i=1}^D L_i \right) \times L_0^{N-D} \quad (5)$$

where $L_i = P(\text{CH}_i)$ (equation 3) and $L_0 = P(\text{CH}_0)$ (equation 4). If the a subscripts are dropped from equation 5, some algebra reduces the formula to the full likelihood for the JSSA model.

3.2 Linear Logistic Models for Retention and Capture Probabilities

The full model above may be labelled $\{\beta(t), \phi(t \times a), p(t \times a)\}$, to indicate β s dependent on time (sample), while ϕ and p both allow for time and age effects in an interactive way. However, there is not enough information in capture-recapture data to estimate the interactive parameters, and so we propose simplifications of ϕ and p with fewer parameters. An **additive** or **main effects** model on the logistic scale

(which is preferable to a raw scale for normality of estimators and avoidance of ϕ or p estimates outside $[0,1]$) could have ϕ_{ja} reparameterised as

$$\log \left(\frac{\phi_{ja}}{1 - \phi_{ja}} \right) = \tau_j + \alpha_a \quad (a, j = 1, 2, \dots (K - 1)) \quad (6)$$

where τ is the time effect and α is the age effect. A constraint is needed on α , perhaps a sum-to-zero constraint ($\sum \alpha_a = 0$) or a corner-point constraint ($\alpha_1 = 0$). Similarly capture probabilities may be modelled with additive time and age effects on the logistic scale:

$$\log \left(\frac{p_{ja}}{1 - p_{ja}} \right) = v_j + \zeta_a \quad (a, j = 1, 2, \dots (K - 1)) \quad (7)$$

Suitable notation for labelling these additive models would be $\phi(t + a)$ and $p(t + a)$.

Further simplifications could have

- $\phi(a)$ or $p(a)$, with probabilities depending on residence time but constant through calendar time,
- $\phi(t)$ or $p(t)$, with probabilities independent of residence time but varying through calendar time, or
- ϕ or p constant over changing residence time and calendar time, denoted by $\phi(.)$ and $p(.)$ in the model specification.

If all 2^K observable capture histories are actually seen, the models above are feasible, except for some minor parameter redundancy in early or late p or ϕ parameters (Catchpole and Morgan 1997). If no individual birds have a presence history with $f_i = 1$ and $l_i = K$, there is virtually no information about parameters beyond a certain maximum observed duration of stay ($M = \max (l_i - f_i + 1)$), and there is near-singularity of models (Catchpole et al. 2001); in this case parameters from “age” $M + 1$ onwards are not estimated. Also sparse data, with few different capture histories observed, can give substantial parameter redundancy. Schwarz and Arnason (1996) suggested various options for dealing with the two redundant parameters in the Jolly–Seber model $\{\beta(t), \phi(t), p(t)\}$, including setting $p_1 = p_K = 1$. However, as this gives an underestimate of β_0 , leading on to overestimates of the later β s (Jim Nichols, pers. comm.), we have set such end parameters to the mean of the estimable ones, on a logistic scale. For example, our JS model has $\text{logit}(p_1) = \text{logit}(p_K) = \text{mean}\{\text{logit}(p_2), \dots, \text{logit}(p_{K-1})\}$. Table 1 shows the numbers of estimable parameters in the models proposed so far.

Table 1 Numbers of independent parameters with K samples, an observed maximum stopover duration of $M \leq K$, and a large enough set of different capture histories to make the estimates feasible

	$p(.)$	$p(t)$	$p(a)$	$p(t + a)$
$\phi(.)$	$K + 2$	$2K *$	$K + M - 1$	$2K + M$
$\phi(t)$	$2K$	$3K - 3 * \dagger$	$2K + M - 2 *$	$3K + M - 4 * \dagger$
$\phi(a)$	$K + M$	$2K + M - 2 *$	$K + 2M - 2 * \dagger$	$2K + 2M - 4 * \dagger$
$\phi(t + a)$	$2K + M - 2$	$3K + M - 5 * \dagger$	$2K + 2M - 4 *$	$5K - 9 * \dagger$

All models assume $\beta(t)$. Some parameters are not estimable. Models marked $*$ must have p_1 or its logistic equivalent assigned, and models marked \dagger must have p_K or its logistic equivalent assigned.

3.3 Using Covariates

Covariates in calendar time may be incorporated into this scheme, as shown in Lebreton et al. (1992). For example, a time effect in the probability of capture due to weather or varying search effort could be accounted for by modifying equation 7 to

$$\log \frac{p_{ja}}{1 - p_{ja}} = \zeta_a + \lambda x_j + \delta w_j$$

where x_j is search effort and w_j is a relevant weather covariate at sample j . The parameters λ and δ are logistic regression coefficients. An example for retention parameters could use a measure of weather between samples ($w_j =$ weather between samples $j - 1$ and j) as a covariate. One such modification of equation 6 is

$$\log \frac{\phi_{ja}}{1 - \phi_{ja}} = \alpha_a + \delta_a w_j.$$

The different slopes (δ_a rather than δ) provide for a differential effect of severe weather conditions on retention – perhaps birds which arrived more recently are more likely to delay departure if the weather is poor.

3.4 Comparing Different Groups of Birds

The data may come from two or more populations which are separated spatially, temporally, taxonomically or sexually. These groups are modelled as in Lebreton et al. (1992) but using the full likelihoods of Sections 3.1 and 3.2. The joint likelihood is formed as the product of the individual likelihoods for each group. Comparison between groups of retention and/or capture probabilities is effected by starting with a global model allowing each group its own parameters, and then fitting submodels with various constraints on parameters. For example, we could compare the residence time-related retention probabilities of different groups, while still allowing each group its own N , β and p parameters. The constrained model would have the same retention parameters across the groups. These groups could be females and males, or populations at different locations, or different sub-species. With migratory birds, we may look for changes over the years in the total number

stopping over, by comparing a constrained model with equal N over different years with a model having N fluctuating, or on a linear trend over time.

4 Retention Curves in Continuous Time

Traditional survival curve analysis and lifetime modelling provides a method of smoothing the discrete retention probabilities into a retention curve depending on the time since arrival, using fewer parameters.

Suppose a continuous random variable X for the stopover duration of an individual has distribution function $F(x)$ = probability of departure by age x , and probability density function $f(x) = \frac{dF(x)}{dx}$ ($x > 0$). The retention function, probability of retention for at least x time units, is $S(x) = 1 - F(x)$, and the hazard function (instantaneous departure rate) is $h(x) = \frac{f(x)}{S(x)}$.

The retention probabilities from discrete-time capture–recapture may be constrained to lie on such curves, using

$$\phi_x = P(\text{duration} > x + 1 \mid \text{duration} > x) = \frac{S(x+1)}{S(x)}. \quad (8)$$

Standard survivorship (retention) curves of Types I, II and III (see, e.g. Richter and Söndgerath 1990) may be modelled with a Weibull distribution for the stopover duration random variable X ($X > 0$). The distribution function $F(x) = 1 - \exp\left\{-\left(\frac{x}{\gamma}\right)^\kappa\right\}$ has scale parameter $\gamma > 0$ and shape parameter $\kappa > 0$, and gives retention function $S(x) = 1 - F(x) = \exp\left\{-\left(\frac{x}{\gamma}\right)^\kappa\right\}$ and hazard rate (instantaneous departure rate) $\mu = \frac{f(x)}{S(x)} = \left(\frac{\kappa x^{\kappa-1}}{\gamma^\kappa}\right)$. The value of κ gives the type of retention curve, with $\kappa > 1$ for a Type I retention curve (high retention rate until near the end of the stopover, then high departure rate, a J-shaped hazard curve), $\kappa = 1$ for Type II retention (constant hazard rate), and $\kappa < 1$ for Type III (lowest retention soon after arrival, a reverse J-shaped hazard curve). The case $\kappa = 1$ with an exponential retention curve and constant hazard rate $1/\gamma$ is implicit in all models, such as the JS, where departure probability is assumed to be unrelated to time since arrival. If the κ estimate from the data gives a rejection of $H_0: \kappa = 0$ in favour of $H_A: \kappa > 1$, there is evidence for high retention soon after arrival and lower retention later.

The connection with discrete time data is $\phi_a = \exp\left\{-\left(\frac{a+1}{\gamma}\right)^\kappa + \left(\frac{a}{\gamma}\right)^\kappa\right\}$ where ϕ_a is the probability of retention from “age” a to $a + 1$. The assumed arrival time for a bird first available for capture at sample b is midway between samples $b - 1$ and b , and for those present at the first sample it is the time of the first sample minus half the average interval between samples.

Type IV retention has highest departure rates when either recently arrived or after staying a while with high retention, a “bathtub” shaped hazard curve (Richter and Söndgerath 1990). One example is the 6-parameter Siler curve (Siler 1979), which

also allows for a trend in retention over time to be tested. The retention probability from “age” a (at time t) to $a + 1$ is

$$\phi_{at} = \exp \left[\frac{\beta_1}{\gamma_1} \{e^{-\gamma_1(a+1)} - e^{-\gamma_1 a}\} - \beta_2 a - \frac{\beta_3}{\gamma_3} \{e^{-\gamma_3(a+1)} - e^{-\gamma_3 a}\} - \beta_4 t \right]. \quad (9)$$

If the data select a bathtub curve in preference to a Weibull, there is evidence for two types of bird, transients which depart soon after arrival, and stayers with high retention before ultimate departure.

The Weibull curve may also be adapted for time trends by allowing the shape parameter to vary by calendar time, $\gamma = \gamma_0 + \gamma_1 t$. A significantly non-zero γ_1 could show if, say, later arrivals spend less time at the site.

5 Statistical Analysis

5.1 Model Comparison and Parameter Estimation

Model selection among these likelihood-based models may be done using Akaike’s Information Criterion (AIC) or some variant of that (Lebreton et al. 1992; Burnham and Anderson 2002). For confirmatory studies, all the models have the usual likelihood ratio tests (χ^2 tests) available for comparing two models or for testing parameters. Maximum likelihood estimates of parameters arise from the model fitting, with estimated standard errors available from the inverse of the estimated Hessian matrix.

Following Lebreton et al. (1992), the models are fitted using the logits of the retention and capture probabilities. This gives better convergence properties, and more appropriate confidence intervals. The greater normality of the estimators on the logit scale means the associated symmetric confidence intervals (± 1.96 standard errors) are realistic. The centres and endpoints of the logit confidence intervals are back-transformed to the $[0,1]$ scale to give asymmetric confidence intervals for the original probabilities. Similar advantages result from using $\log(N)$ as a parameter in the optimisation, with back-transformation giving an asymmetric confidence interval for N .

Profile likelihood intervals (PLI) are also strongly recommended for interval estimation with these models (Cormack 1992). They also provide the asymmetric intervals appropriate to the data.

5.2 Stopover Duration Estimation

For specific models, estimates of mean stopover duration have been used in the past. If a model with ϕ constant has been selected, mean stopover duration may be estimated by

$$-\frac{1}{\log_e \phi}$$

(Seber 1982). If a fitted stopover duration curve (e.g. Weibull or Siler) was selected, the mean of that distribution may be used. If a discrete-time model with ϕ_a was chosen, with the final $\phi_K = 0$ (valid if sampling continued to the final departures), a probability branching diagram gives estimates of the mean and standard deviation of stopover duration.

However, for any of the models in this paper, the parameter estimates and equation 2 provide estimates of the joint distribution of arrival and departure times, $P(B = b \text{ and } D = d)$. To obtain the (discrete) derived distribution of stopover duration $S = D - B + 1$, the probabilities of histories with a common duration are summed. With unequal spacing of samples the support of the distribution has irregular spacing, but fitting a retention curve in continuous time will give a distribution, mean and variance for the stopover duration.

6 Real Data Example

At the Cabo Rojo salt flats in Puerto Rico, 113 previously-banded semipalmated sandpipers (*Calidris pusilla*) were sighted over 18 weeks in 1992–3. These data represent overwintering residency rather than a short stopover.

Analysis of resightings by Rice et al. (2007) using CJS models (Lebreton et al. 1992) selected as the best models $\phi(\text{fat})p(t)$ (with a covariate of body fat, $\Delta AIC_c = 0$), and $\phi(\cdot)p(t)$ ($\Delta AIC_c = 0.66$).

Our models differ by including estimation of arrival time, and by using first sighting information more fully. The model selected by AIC was $\{\beta(t), \phi(t + a, \text{Weibull}), p(a)\}$ (Table 2), where a Weibull model for retention has its scale parameter on a linear trend over time. This allows for later cohorts to be on a longer or shorter stopover duration, while keeping the shape of the curve constant.

In this example, the parameter estimates indicate that the later arrivals are staying longer. This model choice is being driven by a number of early arrivals being seen only once, while a large group arriving about the middle of the study were seen frequently until the end.

The distribution of stopover time was found for the best four models, giving the means and standard deviations shown in Table 3.

However, this real data set has high capture probabilities, around 0.8 per sample, leading to an estimate of N , $\hat{N} = 113 = D$, which is the number actually seen. This

Table 2 Relative AIC values for semipalmated sandpipers (*Calidris pusilla*) at Cabo Rojo

	$p(\cdot)$	$p(t)$	$p(a)$	$p(t + a)$
$\phi(\cdot)$	13.90	19.25	10.39	9.34
$\phi(t)$	15.62	21.79	9.43	9.96
$\phi(a)$	21.52	22.94	17.84	15.11
$\phi(t + a)$	20.43	24.85	14.53	14.62
$\phi(a, \text{Weibull})$	15.69	20.66	11.98	9.31
$\phi(a, \text{Siler})$	21.58	26.36	18.02	16.15
$\phi(t + a, \text{Weibull})$	10.99	20.26	0.00	9.99
$\phi(t + a, \text{Siler})$	20.43	24.92	15.28	14.17

Table 3 Means and standard deviations of estimated distributions of stopover times (weeks) for Cabo Rojo semipalmated sandpipers (*Calidris pusilla*), using the best four models

Model	Δ AIC	Mean Duration	Standard Deviation
$\phi(t + a, Weibull), p(a)$	0.00	10.09	3.50
$\phi(a, Weibull), p(t + a)$	9.31	9.97	3.43
$\phi(c), p(t + a)$	9.34	10.04	3.59
$\phi(t), p(a)$	9.43	10.33	3.69

data set is not providing a good test of the value of these models for estimation of N . It is also not really necessary to distinguish true arrival time from time of first capture, as most birds were seen very soon after arrival. The simplest model, $\phi(.)p(.)$, gave stopover time estimates fairly similar to those from the four models above.

Because of the differences in the analyses, detailed comparisons with the model of Rice et al. (2007) are not meaningful.

7 A Simulation Study

A simulation study was run to evaluate the model selection procedure, estimation of N and estimation of stopover duration. Three scenaria were tried, encompassing low and high K values (either 5 or 10) and different patterns of entry probabilities, with details given in Table 4. All simulations used $n = 200$ birds and the generating model $\{\phi(a)p(.)\}$ with constant capture probability 0.4 and retention probabilities 0.9, 0.8, 0.2, 0.1, 0. This gave high retention for two intervals, followed by low retention. No birds were retained for more than four intervals (five samples).

At each replication, a population was simulated to give a capture matrix of observed birds, which was then analysed with all 16 discrete-time models. A model fit was ruled inadmissible if any parameter estimate was at the boundary of the parameter space, which happened sometimes with sparse generated data. Table 4 gives an overview of model selection and estimation of N from the simulations.

In all three scenaria, the generating model was selected by AIC more times than any other, with improvement of the proportion of times selected as K increased. Overall, the best two models were the generating model $\{\phi(a), p(.)\}$ and the model $\{\phi(.), p(a)\}$. Strong correlations between ϕ estimates and adjacent p estimates introduce “leakage” of parameters (see e.g. Sidhu et al. 2007); if we insist on constant ϕ , the failure to observe long-staying birds is attributed instead to capture probabilities, and the $p(a)$ estimates become zero from a certain “age” onwards. In this case, common sense would dictate that birds do not suddenly become uncatchable when they have stayed for a certain time – a far more reasonable explanation is that they have departed. Models with constant ϕ or ϕ dependent on time only are unrealistic

Table 4 Simulation Study Results. The generating model was $\phi(a), p(\cdot)$, and in each replication the 16 models were fitted. All scenarios had the same retention probabilities $\phi(a) = (0.9, 0.8, 0.2, 0.1, 0)$, and constant capture probability 0.4. Entry probabilities β were $(.3, .2, .2, .1)$ for Scenario A, $(.15, .15, .1, .1, .1, .1, .05, .05)$ for Scenario B, and $(.05, .1, .1, .15, .15, .15, .1, .1, .05, .05)$ for Scenario C. Coverage is from a 95% log-based confidence interval for n , back-transformed

Scenario	A	B	C
Number of samples, K	5	10	10
Number of birds, N	200	200	200
Entry pattern (details in caption)	low–high	low–low	high–low
Retention probabilities	.9 .8 .2 .1 0	.9 .8 .2 .1, 0	.9 .8 .2 .1, 0
Capture probability	0.4	0.4	0.4
Number of replications	100	100	100
Model selection results:			
% reps, correct model 1st choice	33	45	38
% reps, correct model 2nd choice	38	30	36
% reps, correct model 3rd choice	24	16	22
Analysis by correct model:			
Coverage for N	0.95	0.94	0.93
Average % bias of \hat{N}	−0.07%	−2.71%	−1.58%

for stopover duration analysis. If the unrealistic model $\{\phi(\cdot), p(a)\}$ is excluded, the selection of $\{\phi(a), p(\cdot)\}$ improves considerably.

The coverage of the nominal 95% confidence intervals for n (log based and back-transformed) was acceptable with analysis by the true (generating) model (Table 4), and was almost always nearer 0.95 than coverage from the other 15 analysing models.

To evaluate the estimation of stopover duration, we compare the true distribution of duration (from the generating model) with the estimated distribution from the analysing models, averaged over the 100 simulated populations. The comparisons of true and estimated stopover duration distributions are shown for Scenario B ($K = 10$) in Fig. 1. The probabilities from fitting the correct model $\{\phi(a), p(\cdot)\}$ are much closer to the true probabilities than those from analysis by three competing models $\{\phi(\cdot), p(\cdot)\}$, $\{\phi(\cdot), p(a)\}$ and $\{\phi(a), p(a)\}$. The simulated populations were also analysed using the correct $\{\phi(a), p(\cdot)\}$ model but with a simplified likelihood model using only the birds seen at least once; no attempt was made to estimate N or allow for the unseen birds in the likelihood. Arrival and departure times were estimated only for the seen birds, and ϕ and p parameters were estimated from this incomplete data set. The estimated stopover duration probabilities were calculated, averaged over the 100 simulations, and the trace of this “seen” model is also shown in Fig. 1. The resulting overestimation of stopover duration probably occurs because the unseen birds are largely those with short stopovers, so estimation without allowing for them gives a positive bias.

The means and standard deviations of these generating and analysing distributions are in Table 5. Note the 23% overestimation of the mean stopover duration which results from considering only the seen birds.

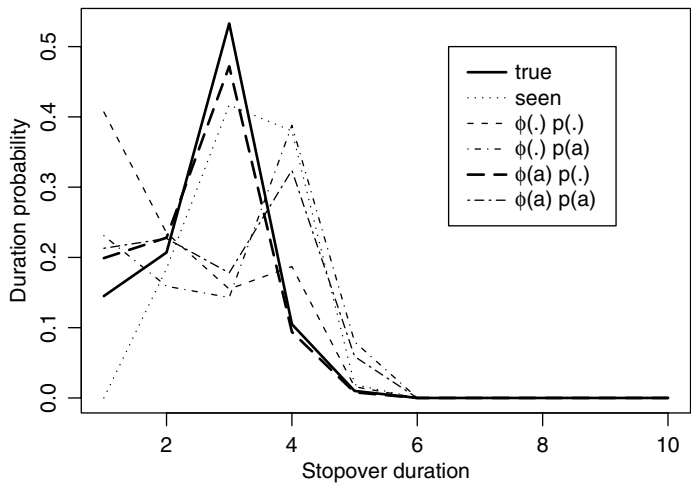


Fig. 1 True and estimated distributions of stopover duration, Scenario B. The true (generating) model is $\{\phi(a), p(\cdot)\}$. Five analysing models were fitted for each simulated population, and the probabilities estimated from averages over the 100 simulations. Analysis by the true model gives a close fit. The “seen” model ignored the unseen birds

Table 5 Means and standard deviations of the true stopover duration distribution and the estimated distributions

Model	Mean	Standard deviation
True model		
$\{\phi(a), p(\cdot)\}$	2.63	0.79
Analysing model:		
Seen birds only	3.23	0.59
$\{\phi(\cdot), p(\cdot)\}$	2.17	1.43
$\{\phi(\cdot), p(a)\}$	2.93	1.78
$\{\phi(a), p(\cdot)\}$	2.49	0.88
$\{\phi(a), p(a)\}$	2.79	1.59

8 Discussion

We have introduced new models, aimed at improving accuracy of estimation of the total number of birds using a stopover site, and the duration of stopover. Likelihood-based models are employed, bringing a range of benefits: AIC comparisons, likelihood ratio tests, and the estimation of the distribution of stopover duration rather than just a mean and standard deviation. The use of joint likelihoods allows for comparisons of different groups of birds, perhaps two sexes, different species, or the same species over different years. Tests may be constructed to see if, for example, there is a trend over the years of the numbers stopping over.

In the survival literature, it is known that individual heterogeneity of survival, if not allowed for in a model, has consequences for the estimation of survival parameters

(Burnham and Rexstad 1993; Pledger and Schwarz 2002; Efford 2005). In stopover applications, the birds with intrinsically longer stopover times provide the information about the upper end of the retention curve. Since they are not representative of the whole group, an increasing instantaneous departure rate for the whole population can be masked. Our models allow for heterogeneity of retention via an “age” effect, using the (unknown) true time since arrival rather than the time since first capture.

It is necessary to sample over the whole time of the stopover, to eliminate boundary effects. If the sampling starts late, and some birds have already been present a long time before a first opportunity for capture, their arrival times are underestimated. Similarly if sampling finishes too soon, birds still present at the last sample will be assumed to depart soon, when in fact they may stay much longer.

The models are performing well, as shown by a simulation study with substantial turnover in the population. Compared with existing models (with constant or time-dependent retention and capture probabilities), the new models allowing for retention to depend on residence time give a much more accurate estimation of distribution, mean and variance of stopover duration.

These models may be extended in various ways. Allowance can be made for unequal spacing of samples, using smoothing or “lifetime” curves in continuous time. Adaptations are possible to allow for some occasions which have resighting only, with no attempt to capture new birds. Also, the capture–recapture data may be combined via likelihoods with count data of unmarked birds, using joint multinomial models for the capture–recapture and Poisson models for the counts. Joint likelihoods also allow the inclusion of extra information such as some birds having known arrival and departure times, perhaps from radiotelemetry information.

These models also apply to population dynamic studies, where age and survival have their true meanings, and are not interpreted as residence time and retention. With studies which are long in relation to the lifetime of the animal, and where there is little or no migration, the distribution of lifetimes may be estimated and the detection of senescence in animals of unknown age is possible.

Acknowledgments We thank Carl Schwarz, Neil Arnason and Jim Nichols for useful discussions of the Schwarz and Arnason model, and Hal Caswell for Siler curve information.

References

- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, Hungary.
- Ålerstam T, Hedenström A (1998) The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Ålerstam T, Lindström, Å (1990) Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 in Gwinner E. (eds) *Bird Migration: The Physiology and Ecophysiology*. Springer, Berlin, Germany.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, Berlin, Heidelberg, New York.
- Burnham KP, Rexstad EA (1993) Modeling heterogeneity in survival rates of banded waterfowl. *Biometrics* 49:1194–1208.

- Catchpole EA, Morgan BJT (1997) Detecting parameter redundancy. *Biometrika* 84:187–196.
- Catchpole EA, Kgosì PM, Morgan BJT (2001) On the near-singularity of models for animal recovery data. *Biometrics* 57:720–726.
- Cormack RM (1964) Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Cormack RM (1992) Interval estimation for mark-recapture studies of closed populations. *Biometrics* 48:567–576.
- Dinsmore SJ, Collazo JA (2001) The influence of body condition on local apparent survival of spring migrant sanderlings in coastal North Carolina. *Condor* 105:465–473.
- Efford MG (2005) Migrating birds stop over longer than usually thought: Comment. *Ecology* 86:3415–3418.
- Fredericksen M, Fox A, Madsen J, Colhoun K (2001) Estimating the total number of birds using a staging site. *Journal of Wildlife Management* 65:282–289.
- Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration – stochastic model. *Biometrika* 52:225–247.
- Kaiser A (1995) Estimating turnover, movements and capture parameters of resting passerines in standardized capture–recapture studies. *Journal of Applied Statistics* 22:1039–1047.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- Pledger S, Schwarz CJ (2002) Modelling heterogeneity of survival in band recovery data using mixtures. *Journal of Applied Statistics* 29:315–327.
- Pollock KH (1981) Capture–recapture models allowing for age-dependent survival and capture rates. *Biometrics* 37:521–529.
- Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth. *Biometrics* 52:703–709.
- Pradel R, Schaub M, Jenni L, Lebreton J-D (2005) Migrating birds stop over longer than usually thought: Reply. *Ecology* 86:3418–3419.
- Rice SM, Collazo JA, Alldredge MW, Harrington BA, Lewis, AR (2007) Local annual survival and seasonal residency rates of semipalmated sandpipers (*Calidris pusilla*) in Puerto Rico. *The Auk* 124:1397–1406.
- Richter O, Söndgerath, D (1990) Parameter Estimation in Ecology. VCH Verlagsgesellschaft mbH, Weinham, Germany.
- Routledge RD, Smith GEJ, Sun L, Dawe N, Nygren E, Sedinger JS (1999) Estimating the size of a transient population. *Biometrics* 55:224–230.
- Schaub M, Pradel R, Jenni L, Lebreton J-D (2001) Migrating birds stop over longer than usually thought: An improved capture–recapture analysis. *Ecology* 82:852–859.
- Schwarz CJ (2001) The Jolly–Seber model: more than just abundance. *Journal of Agricultural, Biological and Environmental Statistics* 6:195–205.
- Schwarz CJ, Arnason AN (1996) A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* 52:860–873.
- Seber GAF (1965) A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Seber GAF (1982) The Estimation of Animal Abundance and Related Parameters. Second edition. Macmillan, New York, USA.
- Sidhu LA, Catchpole EA, Dann P (2007) Mark-recapture-recovery modeling and age-related survival in Little Penguins (*Eudyptula minor*). *The Auk* 124:815–827.
- Siler W (1979) A competing-risk model for animal mortality. *Ecology* 60:750–757.
- Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH (2003) Costs of migration in free-flying song birds. *Nature* 423:704.
- Ydenberg RC, Butler RW, Lank DB, Smith BD, Ireland J (2004) Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proceedings of the Royal Society of London B* 271:1263–1269.