

**MIGRATING BIRDS STOP OVER  
 LONGER THAN USUALLY  
 THOUGHT: COMMENT**

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The seasonal long-distance movements of migratory birds are punctuated by periods of rest and refueling termed stopovers. The duration of these periods is an important variable in the biology of migratory species. Capture–recapture provides data for the estimation of stopover duration in the many species for which individual tracking is not feasible. Schaub et al. (2001) proposed a new method for the analysis of such data. This note suggests that the method leads to erroneous estimates of mean stopover duration.

Estimation of stopover duration in the absence of mortality is mathematically identical to estimation of life expectancy in the absence of emigration. Life expectancy at birth is defined as

$$L_0 = \int_0^{\infty} p(a) da \quad (1)$$

where survivorship  $p(a)$  is the probability of surviving at least to age  $a$  ( $a$  is continuous and  $p(0) = 1$ ) (Keyfitz 1985, Lotka 1998). Relating this to stopover duration, we interpret “age” as time since arrival, and the survivorship curve  $p(a)$  as the proportion of birds remaining in the population  $a$  time units after arriving.

The Cormack–Jolly–Seber (CJS) open population model (Cormack 1964, Seber 1982) provides estimates of survivorship that underlie both the analysis of Schaub et al. (2001) and this note. The stopover population is subject to recruitment and loss between samples. Stopover durations are assumed to be short, so that mortality may be ignored, and the rate of departure is given by  $1 - \phi_t$ , where  $\phi_t$  is the time-specific CJS “survival” parameter (probability that an animal in the population at time  $t$  will also be in the population at time  $t + 1$ ). Because “survival” is time dependent under this model, the cohort of birds arriving at time  $i$  experiences a particular “survivorship” curve that may be designated  $p_i(a)$ . In the stopover case that we

consider here,  $p_i(a)$  may be estimated from the sequence of CJS estimates of departure forward from the time of arrival. This entails the assumption that departure rate is unaffected by capture or by time since arrival. Stopover duration for birds arriving at time  $i$  is given by Eq. 1, substituting  $p_i(a)$  for  $p(a)$ . Schaub et al. (2001) derived a formula for a quantity they termed  $Sa_i$  that expresses the integral of Eq. 1 in terms of the time-specific CJS survivals  $\phi_i, \phi_{i+1}, \dots, \phi_n$ , where there are  $n$  estimable  $\phi$ :

$$Sa_i = \sum_{k=i}^n \left( \prod_{j=i}^{k-1} \phi_j \right) \left( -\frac{1 - \phi_k}{\ln \phi_k} \right) + \left( \prod_{j=i}^n \phi_j \right) \frac{-1}{\ln \phi_{n+1}}. \quad (2)$$

Departures are assumed to follow a Poisson process in the intervals between sampling times. The value  $\phi_{n+1}$  is the survival rate projected beyond the end of the study; Schaub et al. (2001) suggested using a moving average of the last three estimated  $\phi$ :

$$\phi_{n+1} = \frac{\phi_{n-2} + 2\phi_{n-1} + 4\phi_n}{7}. \quad (3)$$

Schaub et al. (2001) did not define  $Sa_i$  explicitly, but it is clear from their text and Eq. 4 that they intended the definition in my Eq. 2. “ $Sa$ ” used without a subscript in their Appendix and Eq. 2 actually refers to  $Sa_1$ .

Unfortunately, Schaub et al. (2001) proceeded to argue against  $Sa_i$  as an estimate of stopover duration. Their argument may be paraphrased as follows. The likelihood of a capture history in the CJS model is conditioned on first capture. Birds are first caught on average some time after arriving.  $Sa_i$  therefore estimates only that component of stopover duration that follows (first) capture (they omit the qualifier “first”), and there must be another nonzero component of stopover duration ( $Sb_i$ ) before capture.  $Sb_i$  may be estimated with “seniority”  $\gamma_i$ , estimates from reverse-time CJS analysis (Pradel 1996), by substituting  $\gamma$  for  $\phi$  in the formula for  $Sa_i$ .

I show by examples that this argument must be wrong, before returning to consider why. First, consider an idealized example in which emigration is a Poisson process and the  $\phi_t$  remain constant at  $\phi$ . The model is exponential in time (Seber 1982). A property of such models is that the conditional expectation of future life is constant over time (Johnson and Kotz 1970: 208). Thus, under the model, a bird that has already stopped over for several days has the same expectation of time to departure as a newly arrived bird. The mean stopover duration  $S$  may be estimated using a standard expression for life expectancy (e.g., Seber 1982):

$$S = -1/\ln(\phi). \quad (4)$$

Schaub et al. (2001) point out that their expression for  $Sa_i$  reduces to this expression under conditions of

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TABLE 1. Estimated stopover duration using three different methods with a simulated steady-state population.

Parameter	Estimated stopover duration (d)	
	Actual value 4 d	Actual value 8 d
$S$ (Eq. 4)	4.008 (0.003)	8.012 (0.007)
Sa + Sb (Schaub et al. 2001)	8.017 (0.006)	16.022 (0.014)
Minimum stopover duration (d)	3.739 (0.002)	5.844 (0.004)

Notes: Values are means (and SE) of 1000 simulations. The quantities for Sa and Sb were conceived by Schaub et al. (2001) as additive components of stopover duration: the expected duration of residence after and before first capture of a bird, respectively.

constant  $\phi$ . Let us further assume a steady-state population with constant  $\gamma_i = \gamma$  in which immigration balances emigration ( $\phi = \gamma$ ). Then  $Sb_i = Sa_i = -1/\ln(\phi)$  for all  $i$ . In this idealized case, the method of Schaub et al. (2001) yields an estimate ( $Sb_i + Sa_i$ ) exactly double that of Eq. 4.

#### Simulation of steady-state populations

For a more concrete example, I simulated populations with known stopover duration. The performance of Eq. 4 was compared to that of the method of Schaub et al. (2001) and the ad hoc method of “minimum stopover duration” (see references in Schaub et al. 2001).

In each of 1000 simulations, 20 notional daily samples were taken from a population of 800 birds with capture probability 0.5. Stopover durations of expected value 4 and 8 d were simulated by drawing pseudorandom values from an exponential distribution with appropriate mean. Arrival times of the initial population were distributed according to the expected distribution under the model. Animals that “emigrated” were replaced with an equal number of recruits. Emigration rate ( $1 - \phi$ ) was estimated by fitting the constant-parameter CJS model  $\phi(\cdot) p(\cdot)$  by maximum likelihood. Seniority ( $\gamma$ ) was estimated by applying the same algorithm to the reversed capture histories (Pradel 1996). So-called “minimum stopover duration” was the mean of intervals between initial capture and final recapture for all animals “caught” at least twice in the simulations.

Eq. 4 provided reasonable estimates of mean stopover duration for simulated durations from the exponential distribution that is intrinsic to survival under the CJS model (Table 1). Addition of estimated time since arrival ( $Sb_i$ ) led to approximate doubling of the estimated stopover duration, as predicted above. The naïve empirical approach (“minimum stopover duration”) yielded values closer to the true stopover duration. This may be the fortuitous result of negative and positive biases that nearly cancel for the particular parameter values of the simulations, and should not be taken as validating the method (Schaub et al. 2001).

#### Simulation of pulsed populations

The steady-state scenario ( $\phi_i = \gamma_i = \phi$ ) is artificial. I also simulated a more realistic stopover population pulse to assess the behavior of the proposed estimators. Stochastic populations ( $n = 1000$ ) were constructed by subjecting a small seed population ( $N_0 = 20$ ) to a per capita population growth rate  $\lambda_i$  that was initially high (1.69) and declined linearly to 0.50 over 18 time steps (Fig. 1a). Survival rate  $\phi_i$ , one component of  $\lambda_i$ , also declined linearly. The pulse was terminated by setting both  $\lambda_i$  and  $\phi_i$  to zero at the final time step. Precise stopover duration is difficult to monitor at the individual level even in simulations, because animals “arrive” and “depart” between sampling times. However, for a discrete pulse, the mean duration of residence may be calculated from the area  $A$  under the population curve (the total number of “bird days”) divided by the number of distinct individuals in the superpopulation,  $N$ . From the simulations, we have the true  $N_i$  (Fig. 1b) and the true number of new individuals present at each sample  $B_i$ . The  $B_i$  were adjusted for animals that both arrived and departed within a time step ( $B_i^* = B_i \log(\phi_i)/(\phi_i - 1)$ ; Schwarz et al. 1993), and  $N = \sum_{i=0}^{19} B_i^*$ , where  $B_0^* = N_0$ . Sampling and analysis followed the steady-state example except that the separate time-specific components of stopover  $Sb_i$  (“before”) and  $Sa_i$  (“after”) of Schaub et al. (2001) were estimated from the relevant terms in their Eq. 4 (see Eqs. 2 and 3). The final seniority  $\gamma_{20}$  was undefined because  $N_{20} = 0$ .

Simulations with the parameters in Fig. 1a resulted in a superpopulation ( $N$ ) of  $1406 \pm 2$  birds present for a total ( $A$ ) of  $4066 \pm 7$  bird-days. Average stopover duration ( $A/N$ ) was  $2.891 \pm 0.001$  days. The components of stopover duration as defined by Schaub et al. (2001) showed strong and opposite time trends (Fig. 1c), as expected from the structure of the population pulse. The average “total” duration ( $Sb_i + Sa_i$ ) varied over time between 4.67 and 7.78 days (1.61–2.69 times the overall true value).

#### Estimating average stopover duration

In this example, birds arriving earlier experienced lower departure probabilities and stayed longer than birds

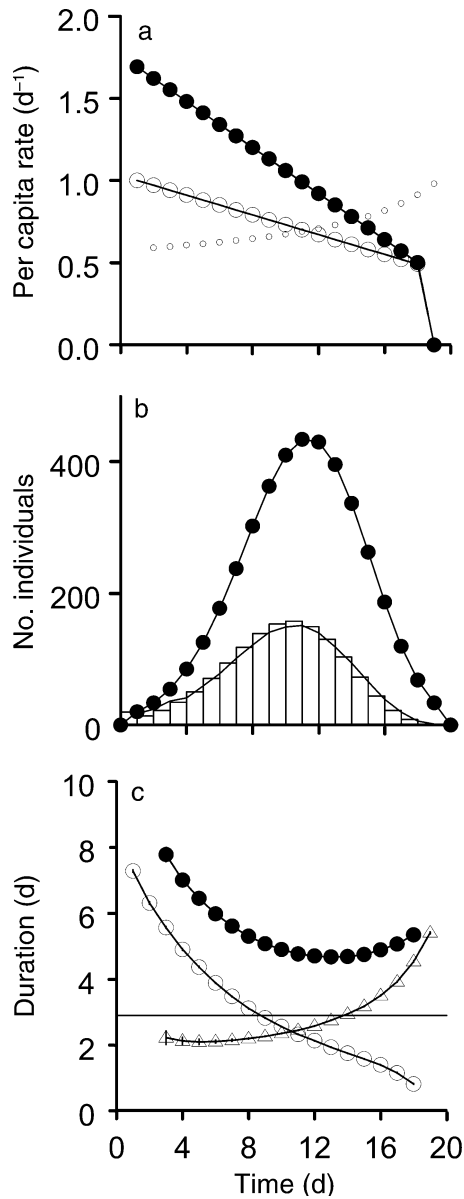


FIG. 1. Stopover duration of animals in a simulated population pulse. (a) Time-varying per capita population growth rate  $\lambda_t$  (solid circles) and survival rate  $\phi_t$  (large open circles). Small open circles indicate  $\gamma_{t+1} = \phi_t/\lambda_t$ . (b) Known population size  $N_t$  (solid circles) and recruitment  $B_t^*$  (bars). The superimposed curve is the distribution of arrival times ( $\beta_t$ ) estimated following Schwarz and Arnason (1996) and scaled to total  $N = 1406$ . Values shown are a mean of 1000 simulations. (c) Time-specific estimates of stopover duration following Schaub et al. (2001). Open circles, “after first capture”  $Sa_t$ ; open triangles, “before first capture”  $Sb_t$ ; and solid circles, total. Values shown are a mean of 879 simulations (the remaining 121 failed to yield valid estimates); bars (mostly obscured) indicate 95% confidence intervals. The horizontal reference line indicates the actual mean stopover duration.

arriving later (see curve for  $Sa_t$  in Fig. 1c). We must therefore consider how to average stopover times  $S$  across the superpopulation of birds that were present at some time during migration. The expectation is given by

$$E(S) = \int_{-\infty}^{\infty} S(t)f(t) dt$$

where  $S(t)$  is the stopover duration of birds arriving at (possibly noninteger) time  $t$ , and  $f(t)$  is the probability density function of arrival times. We approximate this with data from discrete sampling times by weighting the time-specific  $Sa_t$  by the distribution of arrival times (Fig. 1b)

$$E(S) \approx \sum_{t=1}^s Sa_t \beta_{t-1} \tag{5}$$

where  $\beta_t$  represents the proportion arriving between times  $t$  and  $t + 1$ , and no birds arrive before  $t = 0$  or after  $t = s - 1$ . We assume that the departure probabilities of marked and unmarked birds are the same. Schwarz and Arnason (1996) parameterized the Jolly-Seber model in terms of the distribution of arrival times,  $\beta_t$ . Using maximum likelihood estimates of this parameter it is straightforward to apply Eq. 5 to stopover data, except for problems caused by nonidentifiability of  $\beta_0$  and  $\beta_{s-1}$  (in this example both were small and could safely be extrapolated from adjacent values). The resulting estimate ( $2.971 \pm 0.005$ ) is an improvement on the unweighted mean. Confidence intervals may be obtained by bootstrapping capture histories (e.g., Schaub et al. 2001).

*How did Schaub et al. get it wrong?*

The quantity  $Sa_t$  estimates stopover duration for birds arriving at time  $i$ , given the assumption that departure probability is time specific. Under the time-specific model for  $\phi$ , all birds present at  $i$  share the same prospects.  $Sa_t$  is therefore also the expected time from  $i$  to departure of all birds that arrived before  $i$  and were still present at  $i$ . By the logic of reverse-time analysis (Pradel 1996),  $Sb_t$  estimates the mean time since arrival for birds present at  $i$ . In a sense,  $Sb_t + Sa_t$  estimates the total stopover duration of these birds, but this sense is narrow and not obviously useful. Presence at  $i$  is conditional on having remained from arrival to  $i$ . Birds that arrived at the same times as those remaining at  $i$  and left before  $i$  are excluded from consideration.  $Sb_t + Sa_t$  is therefore a highly biased estimate of the expected duration across all individuals at the time of their arrival.

*Conclusions*

Theory and simulation both lead us to reject the method of Schaub et al. (2001). The term involving  $\gamma$  is superfluous. The magnitude of the error is easily determined from the relative values of  $\phi$  and  $\gamma$ . In

populations not undergoing net change,  $\phi \approx \gamma$  and the error is approximately +100%.

Several alternatives are available. The conventional estimator for life expectancy (Eq. 4) is appropriate for populations with constant  $\phi$ . It may also be adequate for variable populations with little net trend, as in the pulsed example. In this case, the geometric mean of the  $\phi(t)$  estimates may be substituted for the estimated  $\phi$ , but the fitted overall  $\phi(\cdot)$  (e.g., Schaub et al. 2001) is likely to be more precise, and is less vulnerable to bias when the sampling error is large. The formula derived by Schaub et al. (2001 Appendix, here as Eq. 2) provides estimates of stopover duration conditional on arrival time when  $\phi_t$  is variable. To estimate the population mean, time-specific estimates of stopover duration should be weighted by the relative frequency of arrivals at each time. The required weights are values of the  $\beta(t)$  parameters in the Jolly-Seber formulation of Schwarz and Arnason (1996).

None of the methods mentioned so far allows for the likely dependence of departure probability on time since arrival (Kaiser 1995, Schaub et al. 2001). This is equivalent to age-dependence of survival when age is unknown, an estimation problem for which S. Pledger (*unpublished manuscript*) has recently suggested a solution. Empirical "area under the curve" estimators from fisheries may also apply (e.g., Lady and Skalski 1998, Manske and Schwarz 2000).

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## MIGRATING BIRDS STOP OVER LONGER THAN USUALLY THOUGHT: REPLY

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Efford (2005) pinpoints in his comment that our method for estimating the stopover duration of a migrant at an intermediate migration site presented in 2001 (Schaub et al. 2001) and implemented in software SODA (Choquet and Pradel 2000) overestimates the stopover duration of a migrating bird when emigration is a Poisson process. He establishes formally that the estimate is then twice the true stopover duration and thus recommends getting back to the formula for "life expectancy" originally proposed by Kaiser (1995). Indeed, this latter formula yields the correct estimate in the particular case raised by Efford (2005), i.e., when stopover duration follows a Poisson distribution.

However, the problem we confronted in our 2001 paper is different. We did not assume that the stopover duration of the birds follows a Poisson distribution. Rather, we had in mind a situation where most birds spend approximately the same time at the stopover site.

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TABLE 1. Estimation of stopover duration for a flock of birds arriving the fifth day of a study and departing the eighth day by the life expectancy formula (Sa) and Schaub et al. formula (Sa + Sb).

Day	Departure probability	Arrival probability	Sa	Sa + Sb
5	0	1	3	3
6	0	0	2	3
7	0	0	1	3
8	1	0	0	3

Notes: It is assumed that detection is perfect. Estimates of arrival and departure probabilities by the Cormack-Jolly-Seber model are also given.

In that case, the “life expectancy” estimator (Sa) does not perform well. This can be seen on a simple example. Let us consider an indeterminate number of birds arriving simultaneously on a study site one day and departing together after exactly three days’ stay. Let us suppose furthermore that capture probability is 1. Then, the time-dependent Cormack-Jolly-Seber model is valid and yields estimates of “survival” and “seniority” probabilities, reinterpreted as departure and arrival probabilities, as in Table 1. The application of the “life expectancy” formula produces estimates of stopover duration which are correct only for day 5 while the Schaub et al. formula yields correct estimates all the time.

Hence both suggestions for estimating stopover duration are specific to the underlying distribution of the stopover duration. At the present time, there is no statistical method to assess the correct distribution from empirical data. Yet, at least for small passerines, there is experimental evidence that birds tend to spend an equal amount of time at stopover sites (Bairlein 1986). Moreover, wind and rain have a strong impact on bird migration resulting in synchronized waves of arriving and departing birds and likely synchronized stopover duration among birds (Richardson 1990).

As correctly pointed out by Efford (2005), neither of the proposed methods explicitly models departure as function of time the bird has already spent at the stopover site. From a biological point of view, it is very likely that the departure decision is dependent on

the time the bird was already at the stopover site given the strong endogenous rhythms controlling many aspects of bird migration (Gwinner 1990) and the need to arrive at an optimal time either in the wintering or the breeding site. The method we have proposed is an approximate attempt to adjust for this possible dependence (Table 1), but as discussed by Efford (2005) and herein, it will not perform well in every situation.

Clearly, there is a need for more research to understand better in which situations the different estimates of stopover duration are biased and to develop an approach that is more general. The situation originally examined by Efford (2005) and the one we have just considered are of course overly simplistic. In a real situation, there are birds arriving at different dates and departure is a stochastic rather than a deterministic process. Provided one has a fairly good idea of what must be the real situation, simulations such as those in Efford’s comment may help assess which method should work better. Another option is of course to find better formulae. Eq. 5 proposed by Efford (2005) is a candidate.

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