# Problems Associated with Pooling Mark-Recapture Data Prior to Estimating Stopover Length for Migratory Passerines[1]

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## Abstract

One measure of the importance of a stopover site is the length of time that migrants spend at an area, however measuring the time birds spend at a stopover site has proven difficult. Most banding studies have presented only minimum length of stopover, based on the difference between initial capture and final recapture of birds that are captured more than once. Cormack-Jolly-Seber (CJS) models have used multiple recaptures to estimate stopover length by migrants, and recently a new model (Stopover Duration Analysis, SODA) incorporating recruitment estimates has been suggested. Using banding data from Red-eyed Vireos (*Vireo olivaceous*), American Redstarts (*Setophaga ruticilla*), and Northern Waterthrushes (*Seiurus noveboracensis*) captured during fall migration on Appledore Island, Maine, during 1999 and 2000, we evaluated stopover estimates from minimum stopover and SODA methods. In particular, we investigated the effects of pooling data for analysis on stopover estimates. Results from our banding data and model simulations suggest that pooling may result in biased stopover estimates, by increasing estimates with increased pooling interval sizes. Furthermore, pooling may also increase the variance in the estimate. Thus pooling should be used with caution and avoided when possible.

*Key words:* mark-recapture, migratory passerines, pooling, stopover length.

## Introduction

Stopover sites may provide places for migrants to rest, avoid predators, and feed to build or rebuild fat stores that fuel migration. Adequate stopover sites may be critical for the successful completion of migration. The amount of time that individuals spend at a stopover site will impact the total time of migration. Furthermore, stopover length may provide a mechanism of evaluating the importance of stopover sites in conjunction with rates of mass change. Comparison of stopover lengths at different sites has been limited because of low recapture rates. Initially, minimum stopover length was calculated as the difference between date of capture and date of final recapture (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987). The use of Cormack-Jolly-Seber models on mark-recapture data has been recommended to provide a better estimate of stopover length (Lavee et al. 1991, Holmgren et al. 1993, Kaiser 1995, Pradel et al. 1997) because the models include all individuals, not simply those that are recaptured. Furthermore, using information about days on which birds were likely to be present, but not captured, these models also incorporate capture probabilities. However, like minimum stopover, these models do not evaluate the likelihood that a bird had been at the site prior to the date of capture. Schaub et al. (2001) incorporated recruitment analysis into models using mark-recapture data to develop a stopover duration analysis (SODA), which estimates total stopover length rather than only stopover after initial capture (referred to as stopover after).

Schaub et al. (2001) and Schaub and Jenni (2001) used SODA to estimate the length of stopover by several species of migrants using data pooled over 5-d intervals. Pooling involved reducing the number of "days" in a capture history by combining birds captured during particular time intervals. For example, data pooled over 3-day intervals would result in all birds captured or recaptured on days 1, 2, and 3 being combined into new interval 1, birds captured or recaptured on days 4, 5, and 6 being combined into new interval 2, and so on. Pooling decreases the number of parameters in time-dependent models, thus allowing comparison of models that include time-dependent as well as constant parameters. A similar method of subdividing long banding periods into smaller periods has been advocated in other long term banding studies involving population models (e.g., Tavecchia et al. 2001). Because many migrants stop for relatively short time periods, we were interested in the effects of pooling on stopover estimates. Specifically, we were interested in whether pooling data prior to fitting SODA models would affect the estimate obtained, and if so, what effect increasing the pooling interval would produce.

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## Methods

The Appledore Island Migration Banding Station was operated during fall migration (mid-August to the end of September) on Appledore Island, Maine, in 1999 and 2000. Appledore Island is the largest island in the Isles of Shoals, is dominated by shrubby vegetation, and is approximately 10 km southeast of Portsmouth, New Hampshire. A detailed description of the field site is available in Morris et al. (1994). We captured migrants in mist nets (12 m net, 30 mm mesh) that were opened around sunrise, closed around sunset, and checked at least once every thirty minutes throughout the day. We took all birds captured to a central location for banding. For each bird captured and recaptured, we recorded band number, species, age, sex, and a variety of morphometric measurements. For this study we used capture and recapture data for Red-eyed Vireos (*Vireo olivaceous*), American Redstarts (*Setophaga ruticilla*), and Northern Waterthrushes (*Seiurus noveboracensis*) captured during fall migration on Appledore Island, Maine, during 1999 and 2000.

Individuals that were captured at least one day after initial capture were used to calculate recapture percentages and minimum stopover length and all individuals captured were included in mark-recapture modeling of stopover length. Minimum stopover length was calculated by subtracting the initial capture date from the date of final recapture. This is a conservative estimate of the time a bird spent on Appledore because we could not assume that we captured an individual on its first day on the island nor could we assume that final recapture occurred on its last day on the island (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987).

Raw data were converted into capture history files for each species each year. A capture history is a matrix that indicates whether a bird was captured during a particular capture interval. Thus, in our initial capture history files, each capture interval corresponded to a single day of banding. To investigate the effects of pooling, data were pooled into intervals ranging between two and seven days, thus all captures and recaptures occurring within a single pooling interval were treated as a single capture event. The data file was truncated at the end of the last complete pooling interval. We created a new software program, Program FITMAN, in MATLAB (Anonymous 1992) that fit capture-recapture models by maximizing the log likelihood of the data, given the model, over the parameters using a Nelder-Mead simplex method. To validate FITMAN's performance, the parameter values produced by this program were then compared with those produced by Program MARK version 2.1, Program SURGE version 4.2 (Lebreton et al. 1992), and Pro-

gram SODA (Schaub et al. 2001). We used AIC methods to choose the best model(s) for each data set. Once models were chosen, stopover length estimates were calculated following Schaub et al. (2001), and standard errors and 95 percent confidence intervals were determined using bootstrapping. In addition to estimating stopover length using banding data, we also estimated stopover length using simulated data sets, which used p (probability of capture), $\phi$ (probability of survival, in this case probability of a particular bird remaining at a stopover site), and $\gamma$ (seniority estimate, in this case the probability that a particular bird was present on the previous day) values determined by modeling unpooled banding data using an appropriate model.

## Results

Red-eyed Vireos, American Redstarts, and Northern Waterthrushes were regularly captured and recaptured on Appledore Island during fall migration during these two years (*table 1*). Minimum stopover lengths calculated from recaptured individuals were generally shorter than those estimated using SODA models, although several estimates were similar between the two methods and minimum stopover was longer than SODA estimates for American Redstarts during fall 1999 (*table 1*). The most frequently chosen SODA model across all species, both years, and three pooling intervals utilized constant p and $\phi$ and time-dependent $\gamma$ (*table 1*).

For all three species studied, stopover length estimates based on mark-recapture banding data increased with increasing pooling interval (*fig. 1, table 1*). Additionally, results of simulations based on American Redstart banding data from fall 2000 showed increased stopover estimates with increased pooling interval (*fig. 2*). Estimates from data pooled over 7-d intervals were 33 to 100 percent higher than those obtained from unpooled data. The least amount of bias occurred in the p, $\phi$, $\gamma$ model, which was not chosen for any species in either year. Furthermore, the variance of the estimate also increased as pooling interval increased (*fig. 2*). The analytic approach used by Hargrove and Borland (1994) and extended here (*Appendix I*) also predicts an upward bias in stopover estimates caused by pooling (*fig. 3*). Thus, models using banding data, simulations based on banding data, and an analytic approach all suggest that pooling results in an upward bias in the estimate of stopover length.

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Table 1—*Comparison of stopover estimates using 1, 3, and 5 day pooling intervals.*

| Species[1] | Year | n | Recapture rate (%) | Minimum stopover (d) | 1 d Model (AIC wt) | 1 d Stopover estimate mean ± S.E. (d) | 3 d Model (AIC wt) | 3 d Stopover estimate mean ± S.E. | 5 d Model (AIC wt) | 5 d Stopover estimate mean ± S.E. |
|---|---|---|---|---|---|---|---|---|---|---|
| REVI | 1999 | 231 | 26.8 | 3.97 ± 3.01 | $p, \phi, \gamma_t$ (1.0000) | 5.93 ± 2.53 | $p, \phi, \gamma_t$ (1.0000) | 6.93 ± 0.84 | $p, \phi, \gamma_t$ (0.9999) | 8.85 ± 2.30 |
| REVI | 2000 | 354 | 16.9 | 2.70 ± 1.83 | $p, \phi, \gamma_t$ (1.0000) | 2.76 ± 0.71 | $p, \phi, \gamma_t$ (1.0000) | 5.01 ± 0.93 | $p, \phi, \gamma_t$ (0.4659) | 8.65 ± 4.40 |
| | | | | | | | | | $p, \phi_t, \gamma$ (0.2600) | 6.05 ± 1.55 |
| | | | | | | | | | $p, \phi_t, \gamma_t$ (0.1757) | 10.45 ± 4.95 |
| | | | | | | | | | $p_t, \phi_t, \gamma_t$ (0.0817) | 8.30 ± 7.80 |
| AMRE | 1999 | 99 | 12.1 | 3.08 ± 3.63 | $p, \phi, \gamma_t$ (1.0000) $p_t, \phi, \gamma_t$ (NC)* | 1.88 ± 0.74 | $p, \phi, \gamma_t$ (1.0000) | 5.31 ± 2.52 | $p, \phi, \gamma_t$ (0.9998) | 10.90 ± 6.70 |
| AMRE | 2000 | 210 | 21.4 | 3.11 ± 2.55 | $p, \phi, \gamma_t$ (1.0000) | 3.25 ± 0.51 | $p, \phi, \gamma_t$ (1.0000) | 4.74 ± 0.60 | $p, \phi_t, \gamma$ (0.8887) | 8.10 ± 3.90 |
| | | | | | | | | | $p_t, \phi_t, \gamma$ (0.0549) | 8.50 ± 5.90 |
| | | | | | | | | | $p_t, \phi, \gamma_t$ (0.0349) | 5.50 ± 2.25 |
| | | | | | | | | | $p, \phi_t, \gamma_t$ (0.0188) | 6.35 ± 1.60 |
| NOWA | 1999 | 153 | 22.2 | 4.15 ± 2.86 | $p, \phi, \gamma_t$ (1.0000) | 7.11 ± 11.76 C?* | $p, \phi, \gamma_t$ (1.0000) | 6.06 ± 1.05 | $p, \phi, \gamma_t$ (0.9899) | 7.15 ± 1.25 |
| NOWA | 2000 | 251 | 17.9 | 4.64 ± 3.50 | $p, \phi, \gamma_t$ (1.0000) | 6.66 ± 7.08 C?* | $p, \phi, \gamma_t$ (1.0000) | 5.94 ± 0.78 | $p, \phi, \gamma_t$ (1.0000) | 7.85 ± 1.50 |

*The notation NC means No Convergence, indicating that this model did not converge during the model choice procedure. The notation C? indicates a suspicion of convergence problems in the bootstrap procedure.
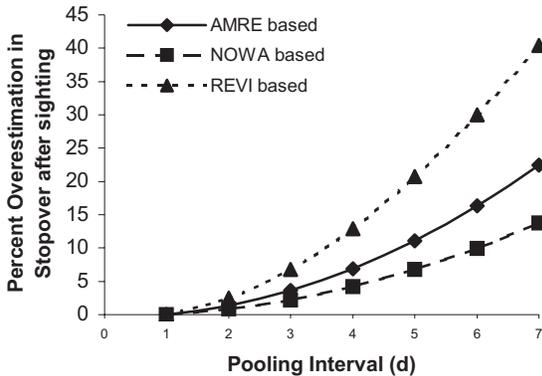
[1]REVI = Red-eyed Vireo; AMRE = American Redstart; NOWA = Northern Waterthrush

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**Red-eyed Vireo**

**American Redstart**

**Northern Waterthrush**
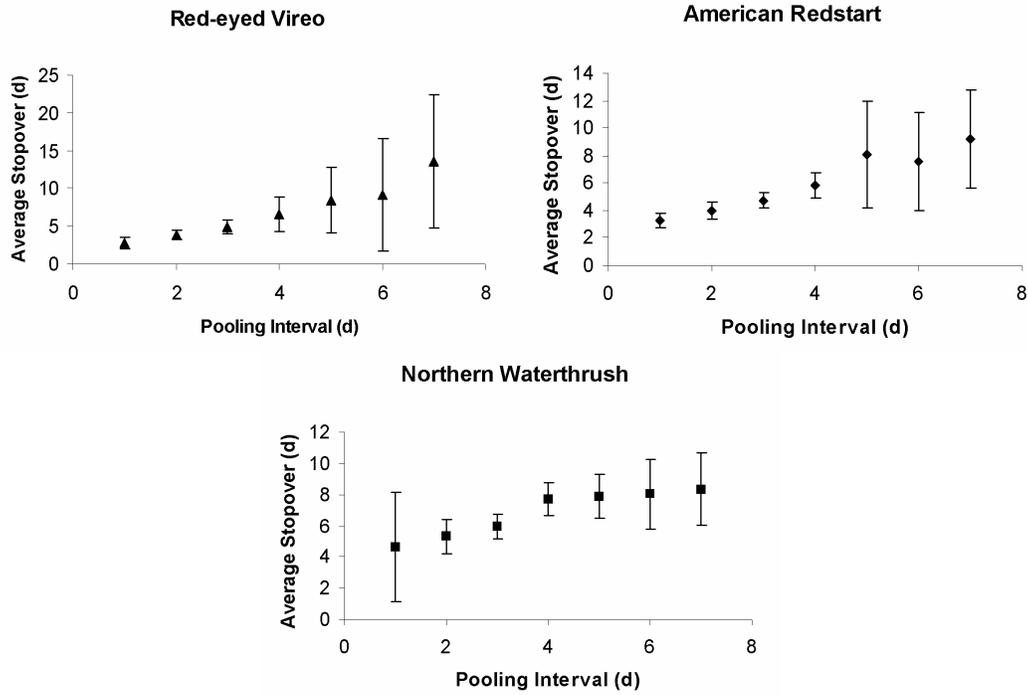
**Figure 1**—Comparison of stopover length estimates obtained from banding data that was pooled over different intervals and fitted to a p, $\phi$, $\gamma_t$ SODA model. Red-eyed Vireos, American Redstarts, and Northern Waterthrushes were captured and recaptured on Appledore Island, Maine, during fall 2000.

**phi(.) p(.) gamma(.)**

**phi(.) p(.) gamma(t)**

**phi(t) p(.) gamma(.)**

**phi(.) p(t) gamma(.)**
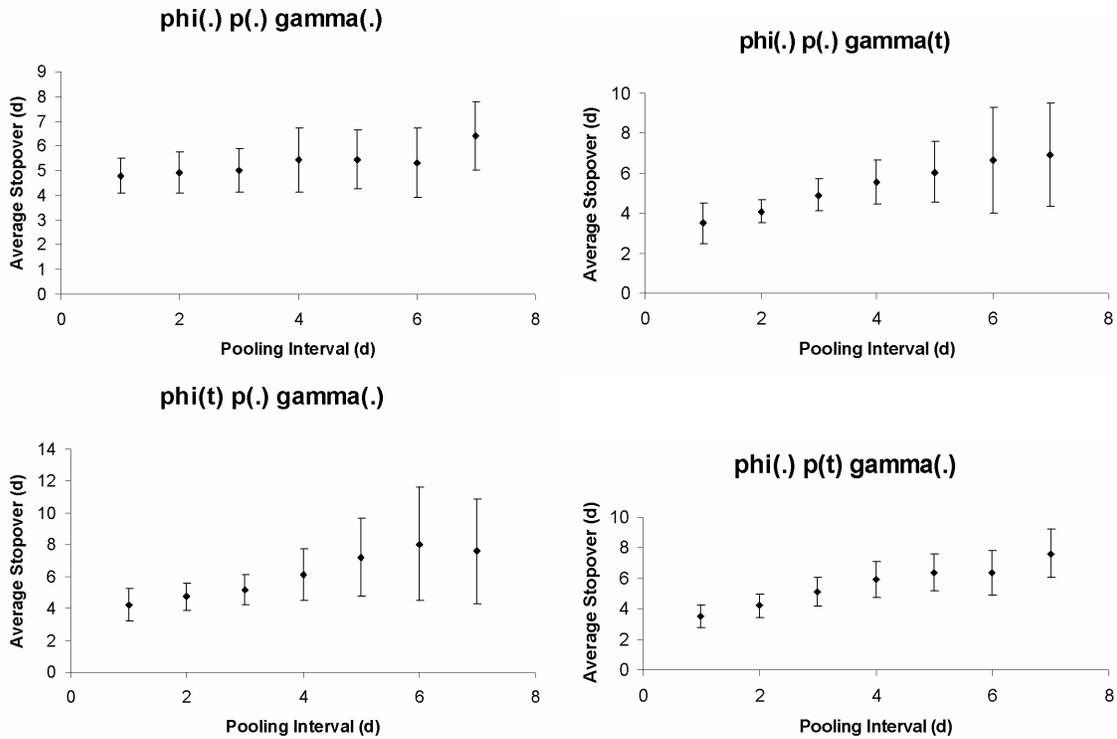
**Figure 2**—Results of simulations comparing stopover length estimates obtained from SODA models using different pooling intervals. Simulation data sets were created using parameter values obtained by fitting four different models to unpooled banding data of American Redstarts during fall 2000. By convention, constant parameters were designated as (.) and time-dependent parameters were designated at (t). The results presented represent the mean and S.E. of 250 simulations.

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**Figure 3**—Dependence of the estimate of stopover after bias on pooling interval. The $\phi$ values were taken from fall 2000 Red-eyed Vireo (REVI), American Redstart (AMRE), and Northern Waterthrush (NOWA) banding data.

## Discussion

Minimum stopover is a conservative estimate of stopover length (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987). SODA models generally estimated longer stopovers than those calculated by recaptured individuals. Because SODA models include all individuals captured, not only those that were recaptured, it has been suggested that these models are likely to provide a better overall estimate of the stopover length of migrants (Schaub et al. 2001). Thus these models are likely to improve understanding of how stopover sites are being used by migrants. It is, however, interesting to note both minimum stopover and SODA estimates provide similar patterns of variation in stopover across years and species, although the two methods provide different stopover length estimates for a given year and species.

Banding data are collected over many days, and thus time-dependent models require estimating numerous parameters. For example, a banding station open for 45d in the fall would require the estimation of 47 parameters to fit a p, $\phi$, $\gamma_t$ model, which may be difficult with the sample sizes of various species of migrants. To reduce the number of parameters estimated in SODA models, pooling data has been utilized (Schaub et al. 2001, Schaub and Jenni 2001). One disadvantage of this method is that recapture data is typically lost when capture and recapture occur during the same pooling interval. Longer pooling intervals result in greater loss of information about recapture. Furthermore, the choice of pooling interval is often haphazard, because direct comparison of models using different interval length is precluded.

In this study, SODA stopover estimates obtained from pooled banding data were higher than those from un-pooled data, suggesting an upward bias in stopover estimates with pooling interval (*fig. 1, table 1*). Furthermore, simulations using population parameters derived from original banding data also predict this upward bias in stopover estimates with increasing pooling interval (*fig. 2*). Thus, SODA stopover length estimates obtained from fitting banding data and simulated data may be overestimates if the data were pooled prior to fitting the model. The extent of the bias is a result of numerous factors that include pooling interval, but also include p, $\phi$, and $\gamma$. Smith and Anderson (1987) suggest that biases in survival rates using band recovery data are greatest when mortality during a long banding period is high. During stopover, departure of birds (analogous to mortality) is often dependent on weather conditions and thus may vary substantially across several days. If these days are within a single pooling interval, the differences in departure could result in substantial bias in the survival estimates.

The dependence of the stopover after bias on pooling interval can be seen given the $\phi$ values obtained from models fitted to the fall 2000 Red-eyed Vireo, American Redstart, and Northern Waterthrush banding data (*fig. 3*). The extent of the overestimation varied among the three species because of differences in the p, $\phi$, and $\gamma$ values for each species. The Hargrove and Borland (1994) results are based on an assumption of constant population size as well as constant capture and survival probabilities. Migration data do not meet these assumptions, particularly with regard to constant population size. Most migratory stopover sites have a highly variable population size during the migratory season, with very few birds present under certain conditions and large numbers of migrants present in others. Both the analytic and computer-numeric (simulation) results reveal the same predicted upward bias in stopover length when data are pooled prior to model fitting. Because the field data, the simulations, and the analytic approach to estimating stopover length all yield an increasing stopover estimate with increased pooling interval, our results suggest that this is a substantial problem that must be addressed. Furthermore, because all of our results suggest that pooling may result in overestimation of stopover length, it should be avoided whenever possible. When it is not possible to avoid pooling, the pooling interval should be minimized.

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# Appendix 1— Estimation of the Bias in the Stopover After Sighting Estimate Due to Pooling

Hargrove and Borland (1994) presented derivations of the bias in the parameter estimates caused by pooling based on an open-population model where

a)  the population size was assumed constant; and

b)  the probability of survival ($\phi$) and capture (p) were assumed constant throughout the study.

We have not attempted to extend Hargrove and Borland's results to derive an estimate of the bias in the seniority estimate ($\gamma$, Pradel 1996), but because the seniority may be calculated by "time-reversing" the data set and calculating the survival parameter for the time-reversed data set, we would expect similar biases in the estimate of seniority. Given estimates of the bias in the survival probability ($\phi$) and the seniority, it would be possible to estimate the bias in the total stopover before and after sighting (Schaub et al. 2001). However, purely from the estimate of the bias in the survival probability, it is possible to estimate the bias in the stopover after sighting estimate, since the expected stopover after sighting for a model with constant survival probability is simply $-1/\ln(\phi)$ (Seber 1982).

Hargrove and Borland's derivation of the bias in the survival probability produced by pooling is:

$$\Phi_p = \Phi \lambda_4 \tag{A1}$$

where $\Phi = \phi^k$, which is the probability of surviving k days (where k is the pooling interval) based on the daily survival probability; $\Phi_p$ is the estimated survival over k days obtained from the pooled data; and $\lambda_4$ is a function defined by Hargrove and Borland (1994) and shown in equation A3. The bias in the estimate obtained from the pooled data is thus:

$$\Phi_p / \Phi = \lambda_4 \tag{A2}$$

Following the notation used by Hargrove and Borland (their equations A.12 and A.8):

$$\lambda_4 = \lambda_1 / (\Phi(\lambda_1 + k(1-\phi)/\phi) \tag{A3}$$

$$\lambda_1 = p/(1-(1-p)\phi) + k\Phi Q(1-\phi)/(\phi(1-\Phi Q)) \tag{A4}$$

where $Q = (1-p)^k$.

From these results we know that the stopover after sighting (SOA) estimate is

$$SOA = -1/\ln(\phi) = -1/\ln(\Phi^{1/k}) = -k/\ln(\Phi) \tag{A5}$$

So that the pooled estimate of the stopover after sighting is

$$
\begin{aligned}
SOA_p &= -k/\ln(\Phi_p) = -k/\ln(\lambda_4\Phi) = -k/(\ln(\lambda_4) + \ln(\Phi)) \\
&= -k/(\ln(\lambda_4) + (k)\ln(\phi)) \\
&= -1/((1/k)\ln(\lambda_4) + \ln(\phi))
\end{aligned}
\tag{A6}
$$

and the bias in the stopover after estimate is

$$
\begin{aligned}
SOA_p/SOA &= [-1/((1/k)\ln(\lambda_4) + \ln(\phi))]/[-1/\ln(\phi)] \\
&= \ln(\phi)/((1/k)\ln(\lambda_4) + \ln(\phi)) \\
&= 1/(\ln\lambda_4/(k\ln(\phi)) + 1)
\end{aligned}
\tag{A7}
$$

# Appendix 2— The Relationship of Population Size to the Seniority Parameter

Pradel's (1996) approach to the open-population models includes seniority ($\gamma$), which is the estimate of the probability that a bird sighted was present during the previous sighting interval. Under this model, the population on day i+1 ($n_{i+1}$) is related to the population on day i ($n_i$) by

$$n_i = \gamma_{i+1} n_{i+1} \tag{A8}$$

and

$$n_{i+1} = n_i / \gamma_{i+1} \tag{A9}$$

Knowing $n_1$ and the values of the $\gamma_i$ (obtained from the model fitting procedure), we can calculate the expected population at all later times by iterative use of equation A9. This allows us to use a set of $\gamma_i$ and $\phi_i$ values to produce a computer simulation that has the same expected population profile (set of relative $n_i$ values) as the field data from which the p, $\phi$, and $\gamma$ values were obtained.

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