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MULTIPLE-DAY CONSTANCY AS AN ALTERNATIVE TO POOLING FOR ESTIMATING MARK–RECAPTURE STOPOVER LENGTH IN NEARCTIC–NEOTROPICAL MIGRANT LANDBIRDS

Sara R. Morris,[1] David A. Liebner, Amanda M. Larracuente, Erica M. Escamilla, and H. David Sheets

Canisius College, 2001 Main Street, Buffalo, New York 14208, USA

Abstract.—Capture–mark–recapture models require estimation of parameters that may be either constant or time-dependent. Open-population models have been adapted for use in estimating stopover duration of migratory songbirds. However, with data collected over an extended period or with relatively few recaptures, small sample sizes may preclude use of fully time-dependent models. Pooling is commonly used to reduce the number of parameters estimated in time-dependent models. In pooling, all captures and recaptures during a specified interval are treated as a single capture event, which results in a loss of information about recaptures within the interval. Additionally, pooling of banding data of migratory songbirds appears to bias stopover-length estimates upwards. An alternative to pooling is use of multiple-day-constancy models. Advantages of this approach include maintenance of all recapture data, simultaneous Akaike's Information Criterion-based comparison of models using different constancy intervals, and unbiased stopover estimates. *Received 15 June 2003, accepted 6 October 2004.*

Key words: capture–mark–recapture, migration, open population models, stopover duration.

Constancia de Múltiples Días como una Alternativa a la Combinación de Datos de Captura-Recaptura para Estimar la Duración de las Paradas de Aves Migrantes Neárticas–Neotropicales Terrestres

Resumen.—Los modelos de captura-marcado-recaptura requieren la estimación de parámetros que pueden ser ya sea constantes o dependientes del tiempo. Los modelos de poblaciones abiertas han sido adaptados para estimar la duración de las paradas de aves canoras migrantes. Sin embargo, con datos colectados a lo largo de un período extenso o con relativamente pocas capturas, los tamaños de muestra pequeños pueden impedir el uso de modelos totalmente dependientes del tiempo. Usualmente se combinan estos datos para reducir el número de parámetros estimados en modelos dependientes del tiempo. Al combinar los datos, las capturas y recapturas obtenidas durante un intervalo de tiempo determinado son tratadas como un evento de captura único, lo que conduce a una pérdida de información de las recapturas dentro del intervalo determinado. Además, la combinación de los datos de anillado de aves canoras migratorias parece sobrestimar la duración de las paradas. Una alternativa a la combinación de datos es usar modelos de constancia de múltiples días. Las ventajas de este enfoque incluyen el mantenimiento de todos los datos de recaptura, la comparación de modelos basados en el Criterio de Información de Akaike usando intervalos de constancia diferentes y estimaciones no sesgadas de la duración de los períodos de escala migratoria.

[1]E-mail: morriss@canisius.edu

Stopover sites 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 successful completion of migration. Understanding the time birds spend at stopover sites is important because it will affect total migration time, and stopover duration is the most important factor in determining overall migration speed (Schaub and Jenni 2001). Protracted migration may negatively affect migrants, because migrants that arrive late to breeding and wintering grounds may face increased competition and poorer-quality territories. Furthermore, researchers can use time spent at different stopover sites to compare the relative quality of those sites. However, determining the length of time migrants spend at stopover sites has been difficult. Minimum stopover length (i.e. difference between date of capture and date of final recapture) has been used to estimate length of time migrants spend at a given site (e.g. Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987), but it is widely recognized as a conservative estimate. Because birds may not be captured on their initial date of arrival and may stay on site beyond their final date of recapture, minimum stopover length is an underestimate of the time spent at a stopover site. Furthermore, minimum stopover length is based only on individuals that are recaptured, and thus does not incorporate data from the large proportion of migrants that are not recaptured at a site.

Use of Cormack-Jolly-Seber models on capture–mark–recapture (CMR) data has been recommended as providing a better estimate of stopover length (Lavee et al. 1991, Holmgren et al. 1993, Kaiser 1995, Pradel et al. 1997), because such models include all individuals, not simply those that are recaptured. Furthermore, Cormack-Jolly-Seber models incorporate capture probabilities using information about days on which birds were likely to have been present but not captured. However, like minimum stopover length, Cormack-Jolly-Seber models do not evaluate the likelihood that a bird had been at the site before the date of capture. Schaub et al. (2001) incorporated recruitment analysis in models using CMR data to develop stopover duration analysis (SODA). Recruitment analysis is an extension of CMR models developed by Pradel (1996), which incorporates estimates of probability of arrival (represented by parameter γ, seniority) as well as estimates of probabilities of capture (represented by p) and departure (represented by ϕ). Thus, SODA produces an estimate of total stopover length that incorporates time at a stopover site prior to initial capture, rather than only stopover after initial capture.

When one is working with small sample sizes in data (1) collected over a long period or (2) with a low number of recaptures, the number of parameters estimated in time-dependent models may inhibit the ability to select a model that fits the data. Overfitted models (i.e. those with large numbers of parameters for the sample size) tend to lead to inflation of variance, which (though worrisome) is less problematic than underfitted models that lead to bias in parameter estimates (Burnham and Anderson 1998). One solution when faced with limited sample sizes is pooling, which reduces the number of parameters that need to be estimated in time-dependent models by a factor of the number of days in the pooling interval. Schaub et al. (2001) and Schaub and Jenni (2001) used SODA to estimate length of stopover by several species of migrants using data pooled over five-day intervals. However, if a bird is captured and recaptured in the same pooled period, that recapture is lost, and there is evidence that pooling can bias estimates of parameters (Hargrove and Borland 1994, Morris et al. 2005). Here, we investigate use of multiple-day-constancy (MDC) models rather than pooling using SODA models to estimate stopover length by migrating songbirds. Whereas pooling results in an altered capture history, MDC involves alterations to the model by holding parameters constant for several days. Thus, MDC produces the same reduction in parameters without the loss of information about recaptures that occurs during pooling.

Methods

Banding data.—We used banding data from Appledore Island, Maine, to estimate fall stopover length for Red-eyed Vireo (*Vireo olivaceus*), American Redstart (*Setophaga ruticilla*), and Northern Waterthrush (*Seiurus noveboracensis*) from 1996 to 2000. Appledore, an offshore island ~10 km southeast of Portsmouth, New Hampshire, is the largest island in the Isles of Shoals archipelago. The perimeter of the island is dominated by exposed rock and low forbs, and the interior by shrubs and low trees. The Appledore Island Migration Banding Station operated from mid-August to the end of September or early October. Mist netting occurred daily, except during inclement weather. Volunteers checked the nets at least once every half-hour from before sunrise to after sunset and brought all birds captured and recaptured back to a central location for banding. Morris et al. (1994, 1996) provide additional information about the study site and the banding operation.

Stopover length estimation.—We used three methods to estimate stopover duration, minimum stopover, SODA using pooling, and SODA using MDC. Stopover duration was estimated using the traditional calculation of minimum stopover length, which is determined by subtracting date of final capture from date of initial capture (Cherry 1982, Moore and Kerlinger 1987). Stopover was also estimated using a modified version of SODA proposed by Schaub et al. (2001). Following Schaub et al. (2001), CMR data were modeled using a survival and seniority model for open populations developed by Pradel (1996). The Pradel model describes the dynamics of the CMR history using parameters p (probability of capture), ϕ (probability of survival; here, probability of a particular bird remaining at a stopover site), and γ (seniority; here, probability that a particular bird was present on the previous day). Maximum-likelihood estimates (MLEs) of the parameters for the given CMR data were obtained with numerical optimization techniques, using software developed for the present study. We developed software tools (called FITMAN) for CMR analysis, including goodness-of-fit testing, model choice, and parameter estimation using MATLAB (MathWorks, Nantick, Massachusetts). Parameter estimates were used to determine expected stopover for individuals present at the capture site for each capture occasion. To estimate average stopover for all migrants, we used a weighting scheme in which stopover estimates for each day were weighted using the probability that an individual in the sampled population would first arrive on that day.

Goodness-of-fit testing.—Before working with any model of CMR observations, it is necessary to test the goodness-of-fit of the most complex model under consideration, to determine whether it has sufficient descriptive power and whether there is evidence that the basic assumptions of the CMR methods have been violated. The null model used in goodness-of-fit testing is that the observed data exhibit no greater deviance from the fitted model than would be expected if the fitted model were actually the underlying cause of the observed data. Such tests must be treated with some degree of caution, in that failure to reject the null hypothesis should not be taken as proof that the null is in fact true, only that there is insufficient evidence to reject it.

Three approaches to goodness-of-fit testing appear in the CMR literature (Cooch and White 2002). The first assumes that model deviance follows a chi-square distribution and looks for evidence of a higher deviance than expected by chance (Burnham et al. 1987). However, model deviance may not always follow a chi-square distribution (Cooch and White 2002). The second approach is to use a series of contingency-table tests of specific assumptions of the CMR models, as discussed in Burnham et al. (1987) and Lebreton et al. (1992) and implemented in RELEASE (Burnham et al. 1987). The third approach (the one used here) is to use a parametric bootstrap test of the significance of the observed deviance. The most complex model under consideration is fitted to the data and the deviance is calculated (White 2001). The model is used to generate a computer-simulated data set (capture history) of the same size as the original data set, on the basis of the generating model and its fitted parameters. The same model is then fitted to each bootstrap set created, and the deviance of the bootstrap set is calculated. The model deviance of the original data set is then compared with the range of deviances generated by the bootstrap sets; if the observed deviance exceeds the 95% confidence interval of the bootstrap sets, the observed data are judged to exhibit greater deviance than expected by chance.

When working with MDC models (see below), a full time-dependent model with a constancy of one day is typically the most complex (fully parameterized) model under consideration and is used in the goodness-of-fit calculation. In some instances, a longer constancy interval (hence a less parameterized model) may prove more appropriate, depending on sample size and duration of the study.

Multiple-day constancy as an alternative to pooling.—In MDC modeling, CMR parameters are held constant over several consecutive intervals when the model is fitted to the data. Rather than altering data by pooling results over a number of intervals, we alter the model by requiring that the parameters be fixed over those intervals. A comparison of the two approaches is shown schematically in Figure 1.

The MDC approach achieves the same reduction in number of parameters in a CMR model as pooling does, but without the loss of information about recapture that occurs in pooling. If we consider a 45-day record of bird banding data, where birds are captured, marked, and released daily, fitting a model of sighting (p), survival (ϕ) and seniority (γ) to the data would require estimation of 45 sighting values and 44 values each for survival and seniority, for a total of 133 parameter values. Note that it is not possible to estimate seniority for the first interval and survival for the last interval, which reduces the number of days for which we estimate parameter values. Additionally, it is not possible to arrive at statistically independent estimates of the last sighting probability and the last survival value, nor first sighting and first seniority; thus, the number of independent parameters is further reduced by 2, so that there are only 131 independent parameters. Pooling the data over three-day intervals or using a three-day constancy model would reduce that to 43 values (15 sighting values and 14 each for survival and seniority), 41 of which are statistically independent. Again, we cannot estimate survival for the last interval of three days or seniority for the first interval. In fitting a model to the data, values of sighting, survival, and seniority are chosen that maximize the likelihood (based on a multinomial model of the population) of the pooled capture history, given the model.

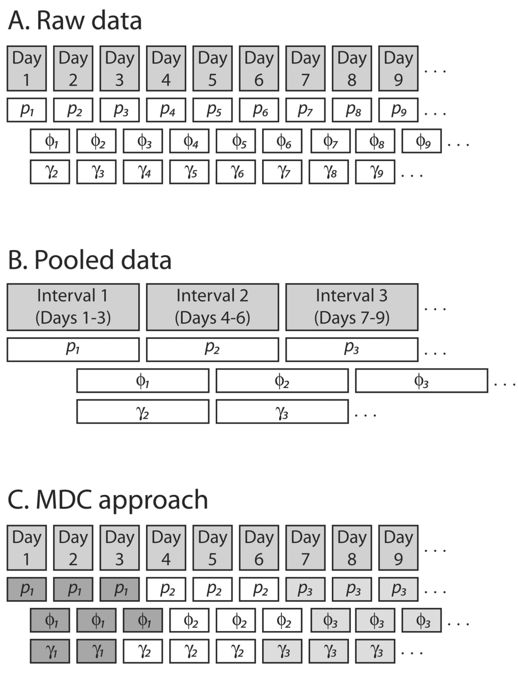

FIG. 1. Comparison of the relationship of the parameters to the observed data when using unpooled data, pooled data, and the MDC approach in fitting mark–recapture models to banding data. (A) Fully time-dependent model fitted to raw (unpooled) data. (B) Fully time-dependent model fitted to pooled data with a three-day pooling interval. (C) MDC model fitted to unpooled data with a three-day constancy interval.

Model choice.—For each species each season, we converted raw banding data into capture histories that indicated whether each bird was captured or not on each day of the banding season. For MDC models, those capture histories were used and parameters were fixed for one- to seven-day intervals in time-dependent models. Length of the final interval in a capture history was typically shortened to avoid discarding any data. To investigate pooling, original capture histories were modified by pooling over one-, three-, five-, and seven-day intervals.

Model fitting and selection was carried out using FITMAN. Models estimated parameters p, ϕ, and γ (see above), which were either time-dependent or constant in the model. FITMAN produced an Akaike Information Criterion (AIC) value for each model fit to a data set. Relative AIC values were compared to select the best model for each data set independently.

In CMR modeling, it is common to choose among various models, in which sighting, survival, and seniority are either constant or time-dependent, by using one of the forms of the AIC, which is an estimated information-theoretic distance between the model and the "truth" or "full reality" (Akaike 1973, Burnham and Anderson 1998). The value of the second-order variation of the AIC, the AIC_c (Sugiura 1978, Sakamoto et al. 1986, Burnham and Anderson 1998) is used here, because it is a more accurate estimator of the information-theoretic distance when sample sizes are small. The likelihood function is based on the parameter values in the model and the capture history of all observed animals (for a complete discussion, see Lebreton et al. 1992, Cooch and White 2002).

Burnham and Anderson (1998) emphasize the importance of restricting the models submitted to the AIC process to those that are biologically reasonable. The ϕ and γ parameters describe the rates of arrival and departure at a stopover site. Because banding data indicate that population size varies during the migration season, relative rate of arrival and departure of migrants at a stopover site must also vary, which implies that at least one of those parameters, ϕ or γ, must be time-dependent. Thus, we excluded models in which ϕ and γ were both constant.

Once models were chosen, FITMAN was used to estimate stopover length using the ϕ and γ values from the chosen model. Stopover length estimates and confidence intervals were generated by a bootstrap procedure within FITMAN.

Results

Models using pooled data.—The constant *p*, constant ϕ, and time-dependent γ model was the most frequently chosen model, regardless of pooling interval. Sighting probability (*p*) was not time-dependent in any chosen model. A single model was chosen for all data sets that were pooled over one-, three-, or five-day intervals; but in several instances, two models were chosen using seven-day pooled data (Table 1). Estimates of stopover length and variance appeared to increase with pooling interval (Fig. 2).

Models using multiple-day-constancy intervals.—Among models using MDC intervals, those with different intervals were directly comparable using AIC_c. In all but one case (Red-eyed Vireos in 1997), a single model was chosen for each data set (Table 2). Although $p.\phi.\gamma_t$ models were the most frequently chosen, the constancy interval chosen varied from one day to seven days. In all chosen models, γ was time-dependent. Time-dependent *p* appeared only once, as one of two possible models and in a model that used a constancy interval of seven days. Survival (ϕ) was time-dependent in only one chosen model (Table 2).

Comparison of stopover estimates.—Regardless of the method used to calculate stopover length, Northern Waterthrushes generally had longer estimated stopovers than either Red-eyed Vireos or American Redstarts (Fig. 2). However, stopover length did not differ significantly among species or among years, though the large standard errors in Northern Waterthrush estimates make comparisons difficult (Fig. 2). Stopover estimates were generally longer with open-population models than with minimum-stopover calculations (Fig. 2), though stopover patterns were similar, regardless of the method used to calculate stopover.

Discussion

Although pooling decreases the number of parameters in time-dependent models, and thus allows comparison of models that include time-dependent as well as constant parameters,

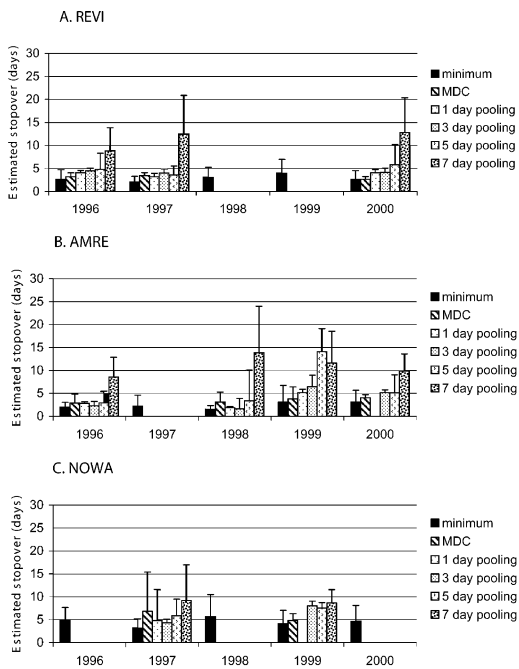

Fig. 2. Comparison of stopover estimates (mean and 95% confidence intervals) using different methods of estimating stopover for Red-eyed Vireos (REVI), American Redstarts (AMRE), and Northern Waterthrushes (NOWA) during fall migration on Appledore Island, Maine. Sample sizes are provided in Table 2.

Table 1. Model choice and stopover estimates using open-population models incorporating different pooling intervals for migrants on Appledore Island, Maine, during fall migration, 1996–2000.

		One-day pooling interval		Three-day pooling interval		Five-day pooling interval		Seven-day pooling interval	
Species	Year	Model chosen	Stopover estimate [a]	Model chosen	Stopover estimate [a]	Model chosen	Stopover estimate [a]	Model chosen	Stopover estimate [a]
Red-eyed Vireo	1996	$p.\phi.\gamma_t$	4.13 ± 0.48	$p.\phi.\gamma_t$	4.48 ± 0.60	$p.\phi.\gamma_t$	4.82 ± 3.50	$p.\phi.\gamma_t$	8.82 ± 5.04
	1997	$p.\phi.\gamma_t$	3.22 ± 0.73	$p.\phi.\gamma_t$	4.02 ± 0.87	$p.\phi_t\gamma.$	3.59 ± 1.95	$p.\phi_t\gamma.$	12.46 ± 8.40
								$p.\phi.\gamma_t$	8.96 ± 6.37
	2000	$p.\phi.\gamma_t$	4.06 ± 0.71	$p.\phi.\gamma_t$	4.16 ± 0.90	$p.\phi.\gamma_t$	5.86 ± 4.35	$p.\phi.\gamma_t$	12.81 ± 7.56
American Redstart	1996	$p.\phi.\gamma_t$	2.82 ± 0.37	$p.\phi.\gamma_t$	2.28 ± 0.96	$p.\phi_t.\gamma$	2.95 ± 2.55	$p.\phi_t\gamma.$	8.54 ± 4.34
	1998	$p.\phi.\gamma_t$	1.88 ± 0.24	$p.\phi_t\gamma.$	1.63 ± 2.28	$p.\phi_t\gamma.$	3.40 ± 6.65	$p.\phi.\gamma_t$	13.86 ± 10.15
								$p.\phi_t\gamma.$	14.77 ± 9.80
	1999	$p.\phi.\gamma_t$	5.17 ± 0.74	$p.\phi.\gamma_t$	6.44 ± 2.52	$p.\phi.\gamma_t$	14.10 ± 5.00	$p.\phi.\gamma_t$	11.62 ± 6.93
								$p.\phi_t\gamma.$	10.08 ± 8.89
	2000	NE [b]	NE [b]	$p.\phi.\gamma_t$	5.16 ± 0.60	$p.\phi_t\gamma.$	5.14 ± 3.90	$p.\phi_t\gamma.$	9.87 ± 3.71
Northern Waterthrush	1997	$p.\phi.\gamma_t$	4.83 ± 6.80	$p.\phi.\gamma_t$	4.33 ± 0.80	$p.\phi.\gamma_t$	5.88 ± 3.60	$p.\phi_t\gamma.$	9.17 ± 7.77
	1999	NE [b]	NE [b]	$p.\phi.\gamma_t$	8.01 ± 1.05	$p.\phi.\gamma_t$	7.54 ± 1.20	$p.\phi.\gamma_t$	8.68 ± 2.87

[a] Mean ± SE (days).

[b] NE = not estimable. In some cases, density and evenness of capture (banding) histories are inadequate to estimate parameter values (Viallefont et al. 1998). That limitation affected two of our data sets, preventing the estimation of stopover in those cases.

Table 2. Recapture frequency, minimum stopover, and model choice and stopover estimates using the MDC approach with open-population models for migrants on Appledore Island, Maine, during fall migration, 1996–2000.

Species	Year	n	Number of recaptures[a]	Minimum stopover (days)	MDC Model[b]	Stopover estimate (days)[c]	Goodness-of-fit results (P)
Red-eyed Vireo	1996	297	74 (24.9)	2.69 ± 2.06	$p.\phi.\gamma_1$ (1.0000)	3.23 ± 0.82	0.47
	1997	189	49 (26.1)	2.08 ± 1.24	$p.\phi.\gamma_3$ (0.5259)	3.45 ± 0.67	0.86
					$p_7\phi.\gamma_7$ (0.4737)	3.42 ± 0.47	
	1998	258	54 (20.9)	3.07 ± 2.17			1.00
	1999	232	62 (26.8)	3.97 ± 3.01			0.98
	2000	354	60 (16.9)	2.70 ± 1.83	$p.\phi.\gamma_1$ (0.9999)	2.70 ± 0.56	0.94
American Redstart	1996	141	16 (11.3)	1.94 ± 1.12	$p.\phi.\gamma_3$ (1.0000)	2.92 ± 1.95	0.91
	1997	143	9 (6.3)	2.22 ± 2.39			0.99
	1998	158	6 (3.8)	1.50 ± 0.84	$p.\phi.\gamma_6$ (1.0000)	3.12 ± 2.15	0.52
	1999	99	12 (12.1)	3.08 ± 3.63	$p.\phi.\gamma_4$ (1.0000)	3.81 ± 2.62	0.94
	2000	210	45 (21.4)	3.11 ± 2.55	$p.\phi.\gamma_2$ (1.0000)	4.03 ± 0.67	0.65
Northern Waterthrush	1996	165	24 (14.5)	4.75 ± 2.91			1.00
	1997	206	29 (14.1)	3.14 ± 2.05	$p.\phi.\gamma_3$ (0.9999)	6.84 ± 8.54	0.91
	1998	270	44 (16.3)	5.61 ± 4.90			1.00
	1999	153	34 (22.2)	4.15 ± 2.86	$p.\phi_4\gamma_4$ (0.9893)	4.84 ± 1.50	0.83
	2000	251	45 (17.9)	4.64 ± 3.50			1.00

[a] Percentage in parentheses

[b] MDC models are not presented for seasons in which goodness-of-fit testing indicated that the models did not adequately describe the data. Subscripts in the models indicate the multiple-day-constancy interval that was chosen using AIC_c. AIC weight is given in parentheses.

[c] Mean ± SE

there are several problems with that method. Akaike's Information Criterion values can be compared only within a single pooling interval, because pooling alters the distribution of the data, precluding direct comparisons across different pooling intervals. Furthermore, previous work involving simulations and field data (Morris et al. 2005) indicates that pooling may introduce biases into stopover estimates. Data presented here (Fig. 2) show the same general pattern of increasing stopover estimates with increased pooling interval. As the pooling interval increases, stopover estimate and variance both increase. Hargrove and Borland (1994) conclude that the pooled estimates of population parameters are "acceptable" if the mortality during the pooling interval is <50%. In the study of migration, ϕ describes departure rather than mortality, so Hargrove and Borland's (1994) conclusions would require <50% departure during a pooling interval to produce "acceptable" parameter estimates, under their assumptions of a fixed population size and constant survival and sighting probabilities. Schaub and Jenni (2001) pooled banding data over five-day intervals. In several cases, their estimated total stopover durations were less than five days, indicating substantial departures during the five-day pooling interval.

Pooling alters the capture history used in calculating the likelihood of the data given the model. The same set of observations will have different capture histories and thus different likelihood functions when different pooling intervals are used. Because models of the same data set based on different pooling intervals describe different distributions, they cannot be compared with one another using AIC.

Because the MDC model is fitted to the original, unpooled capture history (regardless of the length of the constancy interval), models using different possible values of the constancy can be compared with one another using AIC. Rather than being arbitrary, the choice of constancy interval is systematic and based on the data; it is cast into the same framework used to make other choices about the probabilistic models describing the data. A variety of other approaches to model choice are possible and are discussed in Burnham and Anderson (1998), though few if any uses of those alternative approaches appear in the literature on open-population models or in the commonly used open-population software (White 2001, Cooch and White 2002). However, all the various approaches to model-selection function by comparing many models with one set of data, using a variety of criteria to choose among models. The act of pooling data alters the data itself, specifically the number of captures and recaptures per interval, so that the researcher is faced with the need to choose an optimal pooling interval as well as choosing among models. There is little discussion in the literature about the criteria used in pooling interval choice (Hargrove and Borland 1994); therefore, the choice of pooling interval often appears to be arbitrary. The need to choose among pooling intervals to reduce the number of estimated parameters in the model(s) is eliminated by the MDC approach, and all capture and recapture data are preserved. When compared with models using pooled data, MDC models retain information about additional recaptures within the interval that can be used to fit the models. Furthermore, MDC models avoid the pooling-induced bias described by Hargrove and Borland (1994) and Morris et al. (2005).

Both models using pooled data and MDC intervals are still subject to the difficulties associated with low recapture rates and long banding periods. Additional work with banding data may provide a clearer understanding of how well models are able to fit and describe stopover ecology of migrants. Using MDC models on Northern Waterthrush data from 1999 yielded an abnormally high stopover estimate and associated variance. Examination of the original capture history revealed six individuals with minimum stopovers of a week or more, including three with 10-day minimum stopovers. Inclusion of that many birds with uncharacteristically long stopovers may have contributed to difficulties in obtaining stable parameter estimates for the models employed and the increased bootstrap estimate of variance produced by the resampling procedures employed. Additionally, the inclusion of a time-dependent capture probability in the MDC model required estimation of a larger number of parameters than other data sets, contributing to the higher variance. Furthermore, the Northern Waterthrush data from both 1997 and 1999 exhibited a minimum in the variance of the stopover estimate obtained using data pooled over three-day intervals, which suggests that a three-day pooling interval would be an optimal choice for those data sets. The MDC results for those years (three- and four-day constancy, respectively) are consistent with that supposition. However, the minimum in variance in stopover across different pooling intervals is only suggestive, because there are no objective criteria for selecting among different pooling intervals.

The utility of open-population models requires numerous assumptions about the behavior of individuals. The biology of individual animals may not be consistent with the statistical requirements of the models. For example, open-population models require that all individuals have similar capture probabilities and that marking does not affect likelihood of subsequent capture. The capture histories we present here include individuals that were captured on consecutive days and others that were captured only several days after initial capture, which suggests that there was not a tendency toward increased or decreased likelihood of capture. However, the possibility of altered capture probabilities will need to be addressed prior to large-scale use of these methods. Another assumption of the models is that arrival and departure events of individuals are independent of the behavior of other individuals. Because the study species are solitary rather than flocking birds and are not known to migrate in family groups, that assumption is likely to hold here. In species that migrate in flocks or family units, the assumption of independent behavior is likely to be violated.

Many questions about stopover ecology of migrants may benefit from use of open-population models. Such models can be used to determine the dependence of stopover on other variables, including age, sex, body size, mass, or condition. Incorporation of other variables into the models increases the number of parameters that must be estimated, thus making the models harder to fit. Use of MDC to decrease the number of fitted parameters will allow more biological questions about stopover behavior to be addressed by open-population models.

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