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UTILITY OF OPEN POPULATION MODELS: LIMITATIONS POSED BY PARAMETER ESTIMABILITY IN THE STUDY OF MIGRATORY STOPOVER

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ABSTRACT.—Open population models using capture-mark-recapture (CMR) data have a wide range of uses in ecological and evolutionary contexts, including modeling of stopover duration by migratory passerines. In using CMR approaches in novel contexts there is a need to determine the conditions under which open population models may be employed effectively. Our goal was to determine whether there was a simple *a priori* mechanism of determining the conditions under which CMR models could be used effectively in the study of avian stopover ecology. Using banding data (n = 188 capture histories), we examined the challenges of using CMR-based models due to parameter inestimability, adequacy of descriptive power (Goodness-of-Fit, GOF), and parameter uncertainty. These issues become more apparent in studies with limited observations in a capture history, as is often the case in studies of avian stopover duration. Limited sample size and sampling intensity require an approach to reducing the number of fitted parameters in the model. Parameter estimability posed the greatest restriction on the utility of open population models, with high parameter uncertainty posing a lesser challenge. Results from our study also indicate the need for >10 observations per estimated parameter (approximately 3 birds captured or recaptured per day) to provide a reasonable chance of successfully estimating all model parameters. *Received 13 July 2005, accepted 20 May 2006.*

Migratory birds frequently use stopovers to complete migration successfully between their breeding and wintering grounds. Stopover sites provide refuge from predators, protection against inclement weather, and food resources to allow fat deposition to fuel migratory flight. It is thought that many migrating passerines cannot store enough fat to complete their migration in a single transit, but must refuel by foraging at stopover sites along their routes (Dunn 2001, Schwilch and Jenni 2001). Providing evidence for the use of stopover sites for refueling, Moore and Aborn (2000) documented increased activity patterns and differential habitat use by lean versus fat migrants. Lean migrants needing to refuel may stay longer at stopover sites than fat migrants (Moore and Kerlinger 1987, Yong and Moore 1997), and the rate of mass gain also may affect stopover duration. The length of time that migrants stay at stopover sites will affect the total duration of migration and may affect the ability of birds to obtain quality territories. Species-specific stopover patterns may reflect both intrinsic characteristics and ecological factors associated with individual stopover sites (Kaiser 1999). Schaub et al. (2001) argue for accurate estimates of stopover duration to test models of optimal migration strategy, specifically the trade-off between time spent in flight or at stopovers.

Although the importance of *en route* migratory stopover sites is well recognized (Moore 2000, Petit 2000, Sillett and Holmes 2002, Heglund and Skagen 2005), all sites are not equal. Mehlman et al. (2005) recommend that important stopover sites be identified based on the relative migrant abundance, the availability of resources that allow birds to replenish fat reserves, and the location of the site relative to other sites and ecological barriers. However, specific criteria for assessing, and statistical approaches for comparing, sites have not been established. Furthermore, there is a recognized need for research on how sites differ by season, species, and species demography (Mehlman et al. 2005, Partners in Flight Research Working Group 2002).

Since the mid-1980s, numerous researchers have described the basics of the stopover ecology of migratory landbirds at individual sites along the northern coast of the Gulf of Mexico

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(Moore and Kerlinger 1987, Moore et al. 1990, Kuenzi et al. 1991), the New England coast (Morris et al. 1994, 1996; Parrish 2000), the Great Lakes coasts (Jones et al. 2002, Bonter 2003), and in western states (Winker et al. 1992, Finch and Yong 2000). Most of these studies provide simple analyses of stopover duration based on recapturing banded birds. Calculating the amount of time lapsing between the first capture and the last recapture (Cherry 1982) has been the traditional method of estimating stopover duration at a given site; however, including only recaptured birds provides conservative estimates of stopover duration because birds not recaptured have not necessarily left the field site. If only recaptured birds are used in analyses (regularly $<5\%$ of all banded migrants are recaptured), this simple approach might provide a biased view of site use because $>95\%$ of migrants are excluded from analyses.

The limitations of the minimum stopover approach have resulted in the suggestion that open population models based on capture-mark-recapture (CMR) data be used to estimate stopover duration (Lavee et al. 1991, Holmgren et al. 1993, Kaiser 1995, Schaub et al. 2001). The Pradel (1996) extension of the Cormack-Jolly-Seber (CJS) models allows for a range of models of the probabilities of animal capture, arrival, and departure within each interval of a given study period. A number of useful statistics may be derived from the stochastic models, including mean time animals are present in the study area, mean capture probability, and temporal patterns of arrival, departure, and population size. These models also could allow meaningful comparisons of several stopover characteristics among sites.

Although the assumptions used in deriving open population models are widely known (e.g., Pollock et al. 1990, Cooch and White 2005), the conditions under which these models can be used are rarely discussed. Characteristics of the data (i.e., capture/recapture histories)—especially sample size, number of temporal sampling intervals available, recapture/resighting/recovery rate, etc.—may greatly impact the potential usefulness of these models. To use a given open population model, first all the model parameters must be estimated. Typically, parameter estimates are obtained using numerical maximum likelihood methods; characteristics of the capture history and the model's mathematical structure will determine the number of parameters that can be reliably estimated. Parameters that are inestimable due to limitations of a given capture history are extrinsically non-identifiable (McCullagh and Nelder 1989, Viallefont et al. 1998). Capture histories that involve long periods of time, particularly those with relatively few captures and/or recaptures, often prevent successful estimation of all parameter values; the resulting extrinsic non-identifiability of parameters either precludes the use of open population models or requires reducing the number of parameters.

One approach to reducing the number of parameters that must be fitted for a given model is to pool observations over several consecutive observation periods (e.g., Schaub and Jenni 2001, Schaub et al. 2001). However, pooling may bias the parameter estimates and preclude comparing models with different pooling intervals (Hargrove and Borland 1994, Morris et al. 2005b). The difficulty associated with the need to establish this basic temporal interval has been recognized in the paleontological literature (Connolly and Miller 2001, Xu et al. 2005), where it has been addressed by determining whether or not analysis results remain consistent as the pooling interval is changed. Additional detailed discussion of pooling and its effects appears to be lacking in both the statistical and ecological literature. An alternative to pooling is to use multiple-day constancy (MDC; Fig. 1), which holds parameter values fixed over a given ''constancy'' interval, thus reducing the number of parameters while retaining all information in the capture history (Morris et al. 2005a). Regardless of the method used to reduce the number of parameters, decreasing the number of parameters in a model will increase the likelihood that all parameters can be successfully estimated, by reducing the incidence of extrinsic non-identifiability.

When using open population models, goodness-of-fit (GOF) tests must be applied to determine whether the models have adequate descriptive power prior to biological applications. Two distinct approaches (analytical tests based on contingency tables and numerical tests based on comparing observed model misfit or deviance to estimates of misfit de-

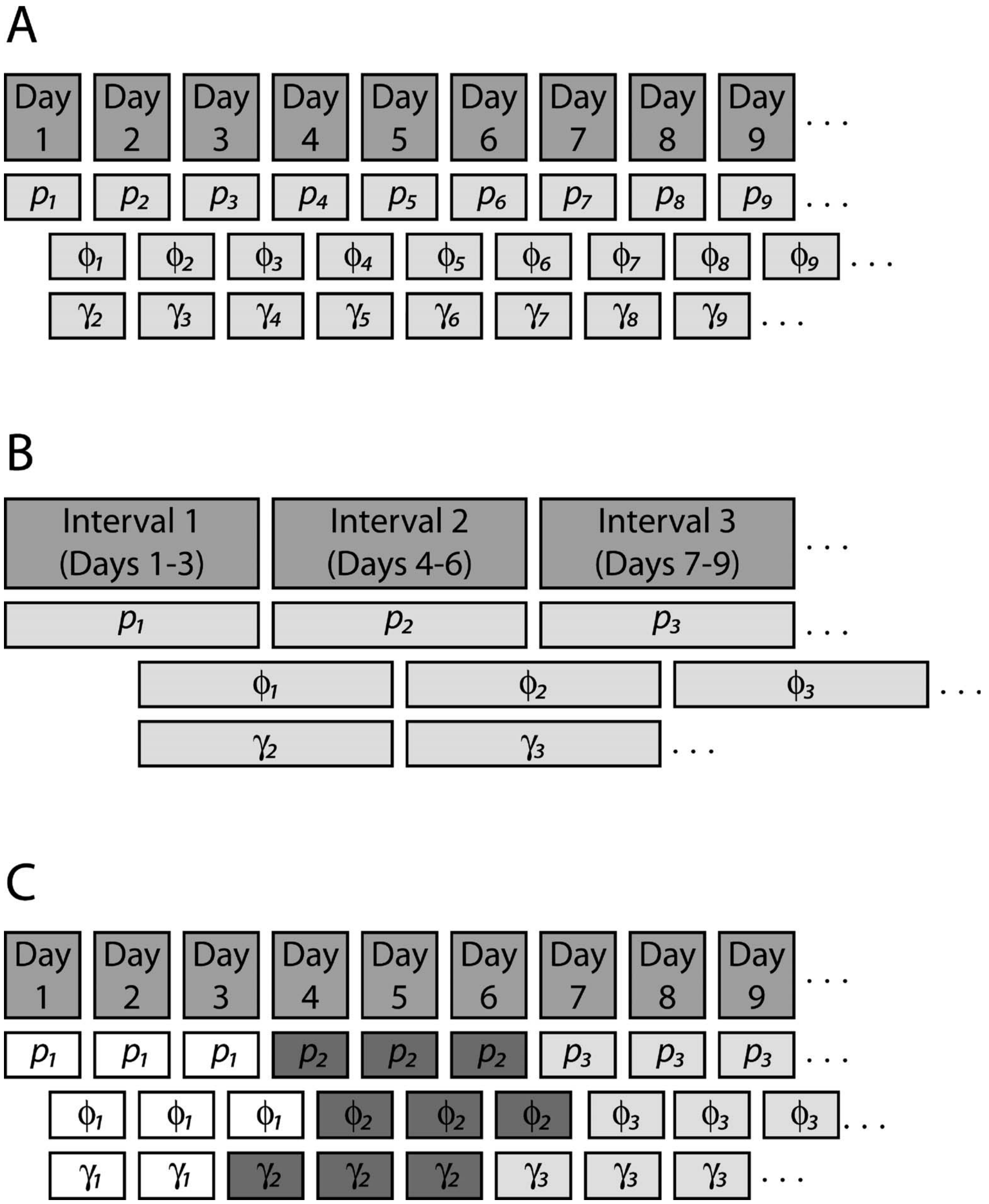

FIG. 1. Open population models may be used to estimate stopover duration by migratory birds by estimating daily rates of capture, arrival, and departure. Large numbers of parameters are required to work with (A) raw data, while both (B) pooled data (3-day pooling interval) and (C) multiple-day constancy (MDC, 3-day MDC interval) provide a reduction in the number of parameters in the open population models fitted to bird banding data. Since limited sample sizes make parameter estimation difficult, some reduction in the number of parameters may allow use of these models with smaller data sets. Both pooling and MDC approaches reduce the number of fitted parameters: p = probability of capture; ϕ = probability that a bird captured on one day remained until the following day (i.e., survival); and γ = probability that a bird captured on one day was there the day before (i.e., seniority). Pooling, however, loses information from multiple captures in the same interval, whereas MDC retains information on all captures. Figure adapted from Morris et al. (2005a).

rived from simulations) have been used to determine whether open population models fit the data. Once the most complex model passes the GOF test, selection of the most appropriate model (of those nested within this most complex model) for the data using Akaike's Information Criterion (AIC) can occur. Even when models can be chosen and fit, the variances of parameter estimates obtained from open population models may be too large for the estimates to be useful. The coefficient of variation (CV; the standard deviation of the estimate/the value of the estimate × 100) may be used to assess the potential utility of stopover estimates. A low CV is necessary for effective comparison of statistical measures among species, locations, and/or time periods. However, little attention has been paid to the dependence of the CV on the characteristics of the capture history.

In this study, we examined capture histories from migration banding data to determine the utility of open population models for estimating avian stopover duration. We used a large number of field capture histories ($n = 188$) from migration banding datasets rather than relying on computer simulations. Whereas computer simulations would provide greater control over parameters, we wanted to be sure to cover a wide range of natural conditions represented by empirical data. Specifically, we were interested in determining how data characteristics affect parameter estimability (through extrinsic non-identifiability), the ability of models to pass GOF tests, and the CV of stopover duration estimates. Estimating the range of sample sizes and recapture rates to which open population models can be fitted may help us determine whether these approaches are appropriate for a particular capture history. To that end, our results indicate the conditions under which open population models can be used effectively with banding data.

METHODS

Data collection.—Migrating birds were captured in mist nets at Appledore Island, Maine (1996–2002); Star Island, New Hampshire (1999 and 2000); and Hamlin Beach State Park, near Rochester, New York (1999 and 2000). Mist nets were operated daily during the spring and fall migration seasons except during inclement weather. All birds captured or recaptured were transported to a central location for banding and data collection.

For species with a sample size >50 individuals in a single season, we created a capture history that indicated whether any one individual was captured on a given day. Using this capture history, we calculated minimum stopover by subtracting the date of first capture from the date of final capture, following Cherry (1982). Additionally, we calculated a variety of descriptive statistics that were used for discriminant function analyses (see below).

Capture-mark-recapture.—The first step in the analysis was to determine the most complex model for which all parameters could be estimated. Numerical maximum likelihood methods were used to fit Pradel's (1996) extension of the CJS open population models to each capture history. Pradel's model requires estimation of sighting (p = probability of capture), seniority (γ = probability that the bird was present at a stopover site during the previous day), and survival (ϕ = probability of remaining at a stopover site until the next day). We considered time-dependent open population models with MDC intervals (Morris et al. 2005a) ranging from 1 to 7 days. In the MDC approach to time-varying parameters, the parameters are fixed over the MDC interval. However, all captures and recaptures within and between MDC intervals have an influence on the likelihood function and, hence, the parameter estimates. Each of these time-dependent models (in which sighting, survival, and seniority probabilities were all free to vary from one constancy interval to the next) was fitted to the capture history, and the number of extrinsically non-identifiable parameters was identified using an estimate of the rank of the Hessian matrix (Viallefont et al. 1998). Rank deficiency in the Hessian matrix was estimated by using finite-difference methods, and then tested using the singular value decomposition method (Viallefont et al. 1998). Rank deficiency was taken as indicating extrinsic parameter non-identifiability in a model. While some parameters in Pradel's extension of the CJS model are non-identifiable due the model's structure (i.e., intrinsic inestimability), this form of inestimability is part of the model, and does not negatively impact its further use. We are concerned here with extrinsically inestimable parameters in banding data. Inestimability makes it difficult to use either the Schaub et al. (2001) formulation of the stopover duration or the more recent estimate put forward by Efford (2005). Although Efford's approach appears simpler than that of Schaub et al. (2001), it still requires an estimate of the distribution of arrival times, thus necessitating the estimation of the same number of parameters (See Efford's equation 5 and discussion). To be useful in estimating stopover duration (Schaub and Jenni 2001, Schaub et al. 2001), all intrinsically estimable parameters in a model had to be completely identifiable, so those capture histories with non-identifiable parameters due to the structure of the data in all MDC intervals tested were judged unusable for further analysis.

We used software written by HDS and DAL using MATLAB (The MathWorks, Inc. 1992) to implement Pradel's population growth rate (PGR) method (Pradel 1996). We compared the performance of our software to that of MARK (White and Burnham 1999, Cooch and White 2005) and SURGE (Lebreton et al. 1992, Pradel and Lebreton 1993, Cooch et al. 1997); it produced identical results for a number of capture histories, both from our data and from example files distributed with MARK. When using very sparse data, our software and SURGE had similar convergence properties, with results depending less on sample size than they did in MARK, which may be attributable to differences in the particular link function (the default choice) we used in MARK (Cooch and White 2005); this particular difference in performance was not investigated in depth.

Since capture histories included a range of sample sizes and durations, comparing capture histories required a time-invariant measure of sampling intensity. We used the number of observations (sum of all capture and recapture events) per estimated parameter in a 7-day, time-dependent MDC model as the measure of observations per parameter. The 7-day MDC model had the lowest number of parameters of any model used in the estimability determination procedure discussed above. We divided the capture histories into three categories, based on the number of observations (#) per estimated parameter: (1) $2 < \# \leq 5$, (2) $5 < \# \leq 10$, and (3) $\# > 10$. Our highest category (>10 observations per parameter) roughly corresponds with three birds of that species captured or recaptured per day. This categorization allowed us to examine the dependence of estimability on the ratio of observations to parameters, and does not require that the sampling intervals used in a study be in units of days.

Capture histories were tested for GOF by assessing the ability of time-dependent (i.e., the most complex) models to fit the data. Both analytical tests (based on contingency tables) and numerical tests (based on parametric bootstrap procedures) have been used in conjunction with CMR models. The first approach is to use contingency tables to test whether assumptions of the open population models are violated. Specifically, contingency tables are used to test the assumptions that each marked animal in the population at time t has (1) the same probability of recapture, and (2) the same probability of survival (Pollock et al. 1990). Several variations on these tests have been incorporated into the programs RELEASE (Lebreton et al. 1992, Burnham et al. 1987), MARK (White and Burnham 1999), and U-CARE (Choquet et al. 2005). The contingency tables can be pooled to produce an overall chi-square statistic for the capture history as a whole, as well as testing specific hypotheses about violations of model assumptions. When faced with sparse data, the contingency tables may be pooled to improve their performance, particularly when the number of expected outcomes in one or more categories of the contingency table is very low. Pooling contingency tables, however, does not always result in tables with enough entries in each cell to be useful. All of our capture histories that had estimable models for MDC intervals of ≤7 days were submitted to GOF testing using the contingency table methods in U-CARE (Choquet et al. 2005).

The second alternative is to use numerical simulations to determine whether the observed model deviance is consistent with the deviance distribution obtained by using the model in a parametric bootstrap procedure (also called a Monte Carlo simulation). The model deviance is the difference between the observed log-likelihood and the log-likelihood for a ''saturated'' model, and it serves as a model's measure of fit. In such a procedure (as implemented in MARK and our software), the model is used to generate a series of simulated capture histories of the same size as the original capture history. The model is fit to each of the simulated capture histories in turn, and a confidence interval for the deviances observed over the simulated data is obtained. If the observed deviance is high (above the 95% upper bound of the simulation deviances), then it may be possible to continue the analysis by computing an estimated variance inflation factor ($\hat{c}$) and using this to adjust the statistics of model choice (White 2002, Cooch and White 2005). Data sparseness also affects this parametric bootstrap approach to GOF testing because the model must be fit to the simulation data during the estimation of the range of deviances. Each capture history was tested for GOF at the lowest MDC interval for which the model parameters were identifiable, using software written by HDS and DAL. Parameter identifiability was monitored during the GOF testing procedure, as it also poses a problem when conducting Monte Carlo simulations. Similarly, capture histories exhibiting evidence of a lack-of-fit (i.e., those with deviances outside the 95% confidence intervals from the simulations) over all seven intervals were not subjected to further analysis. We did not make use of the $\hat{c}$ estimation procedure (White 2002, Cooch and White 2005), as it turned out that only two capture histories fell into this category of results.

After a time-dependent model was shown to exhibit GOF, we compared competing models to determine which model was optimal for producing stopover estimates. Model selection compared all prospective models over several MDC intervals for each capture history, beginning with the smallest MDC interval that passed GOF. We excluded prospective models that had both constant seniority and survival because they predict a population size that is constant or monotonically increasing or decreasing. Based on field observations, we know that during the migration period the population present at a stopover site increases to a maximum value and then declines to zero, making any model predicting constant population size or a monotonic pattern of change in population size biologically unreasonable (see Burnham and Anderson 1998 for a discussion of the exclusion of biologically unreasonable models). The lowest AIC_c value indicated the most appropriate model for a given capture history, thus determining the appropriate MDC interval and whether each parameter was constant or time-dependent. In addition to determining which model was the most appropriate, the AIC_c score was used to assign a relative AIC_c weight (w) to each model, which reflects the relative probability that each model is correct. If the AIC_c weight of the chosen model was <0.95, we also included additional models with relatively high AIC_c weights. Thus, the number of models included was determined by a cumulative AIC_c weight of 0.95, so that all models with a reasonable chance of being correct were considered. We used a bootstrapping procedure to determine the total stopover duration estimate and the standard deviation of this estimate (following Schaub et al. 2001).

Schaub et al. (2001) present a derivation of the expected total stopover duration calculated as a daily value; we report the average total stopover duration over the migration season. In our method, the daily stopover is weighted by the estimated probability of arrival times, using the estimated population growth rate as presented by Pradel (1996). Efford (2005) argues that the total stopover duration (Schaub et al. 2001) produces an overestimate of the actual duration. Efford (2005) advocates using a weighted average of Schaub et al.'s "stopover-after" estimate using a weighting derived from Schwarz and Arnason's (1996) estimates of the distribution of arrival times (Equation 5 in Efford 2005). We also present the stopover-after statistic, again weighted using the estimated population growth rate as derived from Pradel (1996). Conceptually, this approach is the same as that presented by Efford, although the computations may differ slightly, as the Pradel (1996) parameterization of the problem differs from that used by Schwarz and Arnason (1996).

In addition to having adequate descriptive power and being estimable, the chosen model must yield a useful statistic for comparisons. The coefficient of variation (CV) was used to determine usefulness of the total stopover statistic estimated for each species in each season. CV was calculated by dividing the standard error of the total stopover estimate by its mean and multiplying by 100. In this study,

TABLE 1. Summary of the utility of open opulation models in three categories representing the number of observations (#) per estimated parameter for a given capture history from avian banding data. To be applicable, models had to have estimable parameters and pass goodness-of-fit (GOF) testing. As the number of observations per parameter increased, the number of capture histories that could be analyzed using open population models also increased. Parameter inestimability in both model fitting and GOF testing poses the greatest impediment to the use of open population models at these sample sizes. Bird banding data were collected during spring and fall migration on Appledore Island, Maine (1996–2002); Star Island, New Hampshire (1999–2000); and Hamlin Beach State Park, New York (1999–2000). The banding data were used to create capture histories, which indicate whether and individual bird was captured on a particular day; a separate capture history was created for each bird species for which there were >50 captures at a single location during a specific season.

	No. observations per estimated parameter		
Capture histories that:	$2 < \# \leq 5$ ($n = 42$)	$5 < \# \leq 10$ ($n = 81$)	<10 ($n = 65$)
Had inestimable parameters	24 (57%)	29 (36%)	16 (25%)
Were inestimable in simulation GOF	15 (36%)	30 (37%)	6 (9%)
Failed simulation GOF	0 (0%)	0 (0%)	2 (3%)
Failed U-CARE "transients" test	0 (0%)	1 (1%)	4 (6%)
Had an applicable model	3 (7%)	21 (26%)	37 (57%)
Had a CV <50% in total stopover duration[a]	1 (2%)	7 (9%)	15 (23%)
Had a CV >50% in total stopover duration[a]	2 (5%)	14 (17%)	22 (34%)
Had a CV <50% in stopover-after[b]	1 (2%)	9 (11%)	18 (28%)
Had a CV >50% in stopover-after[b]	2 (5%)	12 (15%)	19 (29%)

[a] Total stopover estimates are based on open population models and estimates from stopover duration analysis (SODA) described in Schaub et al. (2001); CV (coefficient of variation) = (SE/mean) × 100.

[b] Stopover-after estimates are based on open population models and estimates using equation 5 from Efford (2005).

only CV values ≤50% were considered useful because comparing different stopover estimates is impossible when CV values are substantially >50%. CV values could, of course, be determined for any estimated parameters in the model; we focus here on the derived statistic (stopover duration) relevant to the study of migration ecology.

Discriminant function analyses.—We used discriminant function analyses to examine which conditions led to estimability of parameters in the original capture history and during GOF testing. We used a range of simple statistics that could be calculated without employing the complex CMR models. The variables included in these analyses were the number of individuals captured, number of days sampled, percent of individuals recaptured at least once, total number of captures and recaptures, total number of recaptures, number of captures per day, median captures per day, recaptures per day, number of days with no captures or recaptures, minimum stopover estimate, standard deviation of the minimum stopover estimate, standard deviation in the number of captures per day, and several measures of capture consistency, which we term "completeness." Completeness is the percentage of days on which there was ≥1 capture event, while "completeness two" refers to the percentage of days with ≥2 capture events. "Recapture completeness" and "recapture completeness two" refer to the percentage of days with ≥1 or ≥2 recaptures, respectively. Backwards stepwise discriminant analyses were performed in SYSTAT 10.2 (SYSTAT Software, Inc. 2002).

RESULTS

We examined the parameter estimability of 1- to 7-day MDC models applied to 188 capture histories representing 34 different species (97 capture histories from fall and 91 from spring migration). Of these, we were able to obtain estimable parameters of a completely time-dependent MDC model for 119 capture histories. The MDC interval at which models could be estimated varied among capture histories. The shortest interval that could be used ranged from 3 to 7 days (3-day $n = 15$, 4-day $n = 22$, 5-day $n = 40$, 6-day $n = 21$, 7-day $n = 21$). Parameter estimability was strongly dependent on the number of observations per parameter (Table 1). Estimability also played a large role in the outcome of GOF testing. Relatively few capture histories failed GOF testing in an absolute sense. Five capture histories showed evidence of differences in capture probabilities of previously recaptured individuals relative to new captures (the transience test) in U-CARE, and two had excess deviance in the parametric bootstrap test (simulation GOF). The remaining capture histories that ''failed'' GOF did so because of parameter inestimability in the bootstrap procedure. In these instances, the models could not be fit reliably to the simulated data (i.e., there were problems with estimability in $\geq$10% of the simulated capture histories). The ability of models to satisfy the GOF criteria was substantially greater for capture histories in our highest category (>10 observations per parameter) than in those in the other two categories ($2 < \# \leq 5$ and $5 < \# \leq 10$ observations per parameter; Table 1). Data sparseness also affected the contingency tests implemented in U-CARE; 42% ($n = 119$) of the capture histories with estimable parameters produced useful contingency tables, although the percentage varied among our three categories ($2 < \# \leq 5$: 0%, $n = 18$; $5 < \# \leq 10$: 38%, $n = 52$; >10: 61%, $n = 49$).

A discriminant function analysis of all capture histories with >10 observations per parameter produced a moderately effective, statistically significant discriminant function describing parameter estimability (Wilks' $\lambda = 0.53$, $F_{5,59} = 10.41$, $P < 0.001$) with positive loadings on duration, recapture completeness, and median captures per day. There were negative loadings on number of recaptured birds and minimum stopover. To extract biological information from discriminant function loadings, we examined a range of bivariate plots depicting the various loadings. The plots yielded only one clear biological interpretation: capture histories with high minimum stopover duration often had inestimable parameters (Fig. 2). Parameter estimability during GOF testing limited the number of capture histories that could be analyzed; however, a discriminant function analysis to predict parameter estimability during GOF testing of the 49 capture histories that were estimable and had >10 observations per parameter was not significant (Wilks' $\lambda = 0.83$, $F_{4,44} = 2.20$, $P = 0.085$).

Optimal models for the capture histories that passed GOF testing varied in the incorporation of time-dependent parameters and in the MDC interval used in the models. When the $\mathrm{AIC_c}$ was used to compare the estimable candidate models, regardless of the number of observations per parameter, 88 viable models were identified for the 61 capture histories. The total number of models exceeded the number of capture histories, as multiple models were considered for some capture histories. For 46 of the 61 capture histories, a single model had an overwhelming AIC_c weight (>0.95), indicating that a unique model was identified. Two alternative models were identified for seven capture histories, three alternative models were identified for six capture histories, and four and six models were identified for one capture history each. Parameters that were time-dependent also varied among the chosen models. All three parameters were time-dependent in 14 capture histories, two parameters were time-dependent in 38 capture histories (p and ϕ: 15; p and γ: 17; ϕ and γ: 6), and a single parameter was time-dependent in 36 capture histories (p: 0; ϕ: 13; γ: 23). The MDC time interval chosen for all 61 capture histories varied from 3 to 7 days (3-day $n = 5$; 4-day $n = 2$; 5-day $n = 18$; 6-day $n = 19$; 7-day $n = 44$). Although 52% of our original capture histories were collected during the fall, 75% of the capture histories with applicable models were collected during the fall.

Estimated total stopover duration values ranged from 0.76 to 17.08 days (Table 2), and the CV values were highly variable (ranging from 13% to 274%). Of the 61 capture histories that were useable after GOF testing, 23 had a total stopover CV of <50% (Table 1). Stopover-after estimates ranged from 0.38 to 10.13 days, which were shorter than the estimates of total stopover. Despite the difference in stopover duration estimates obtained by estimating total stopover and stopover-after, stopover-after had a slightly wider range of CV values than total stopover. CV values for stopover-after ranged from 13% to 365%. Most of the estimates involving CV values of <50% were capture histories from the fall migration season (18 of the 23 estimates for total stopover and 24 of 28 estimates for stopover-after), approximately mirroring the distribution of spring and fall capture histories (75% of estimable capture histories were collected during the fall). These useful estimates were

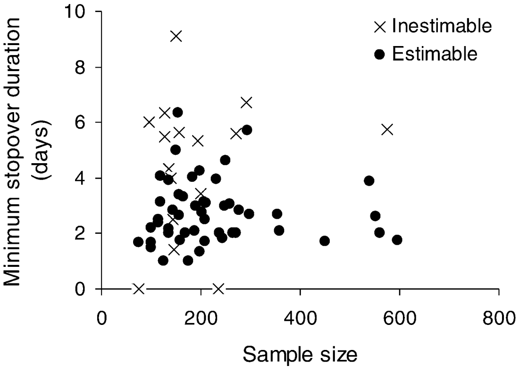

FIG. 2. The relationship between parameter estimability, minimum stopover duration (days), and sample size. Among capture histories of landbird species at migratory stopover sites that had 10 or more (by species) capture events per estimated parameter, those with high minimum stopover duration often had inestimable parameters.

obtained for a variety of species including two vireos, Red-breasted Nuthatch (*Sitta canadensis*), two kinglets, two thrushes, Gray Catbird (*Dumetella carolinensis*), many warbler species, and White-throated Sparrow (*Zonotrichia leucophrys*; Table 2).

DISCUSSION

Our study provided some insights about the conditions under which CMR models can be effectively used to estimate migratory–stopover duration. Dividing the data into three categories based on the number of observations per parameter revealed the importance of the observation:parameter ratio in predicting the utility of CMR models. Models with >10 observations per parameter were estimable and ~62% satisfied GOF testing; most ''failures'' to satisfy GOF were due to the difficulty of estimating parameters during the GOF procedure when using simulations. If our banding data are representative, then the presence of >10 observations per parameter (roughly three birds captured or recaptured per day) may connote a reasonable probability that CMR models will be useful for characterizing a given capture history.

Although we present analyses based on total number of observations (summed capture and recapture events) per parameter, we also conducted similar analyses using number of individual birds banded per parameter, yielding similar results. The capture histories were also divided into different categories based only on total sample size ($50 \leq n < 100$, $100 \leq n < 150$, and $n \geq 150$). The division by sample size alone was not effective, because sample size is a product of both sampling duration and sampling intensity.

Extrinsic parameter inestimability proved to be the largest impediment to using open population models in our study, affecting both the initial model fitting and GOF testing. The discriminant function analysis revealed that a long minimum stopover (>4 days) was a good indicator that the parameters would not be estimable. Because most birds that are recaptured at stopover sites have minimum stopovers of only a few days, long minimum stopover statistics likely represent multiple birds with unusually long stopovers. Such a scenario would yield a large stopover estimate CV and indicate large biological differences among migrants at a given stopover site. Examining the 16 capture histories with >10 observations per parameter but with inestimable parameters revealed that 3 histories had no recaptures at all and 2 histories had only 2 recaptures. Ten of the capture histories were from three Nearctic-Nearctic migratory species: five White-throated Sparrows (*Zonotrichia albicollis*), four Yellow-rumped Warblers (*Dendroica coronata*), and one Ruby-crowned Kinglet (*Regulus calendula*). Three of the other capture histories represented local breeding species. All of these factors led us to believe that the inestimability in these cases might have been related to heterogeneous migration behavior (either among individuals or subpopulations).

Unlike what we found for parameter estimability, there was no clear single factor explaining parameter inestimability in GOF testing. The discriminant function had low predictive power, with only a 67% chance of correctly predicting the outcome of the GOF test, again indicating the lack of strong factors influencing estimability in GOF. Biological factors related to heterogeneity of the captured specimens (Pollock et al. 1990, Cooch and White 2005) can easily lead to failures of GOF testing. Additionally, there may be statistical reasons for some of the observed failures in GOF testing. The GOF test is based on a Monte-Carlo simulation test run at a 95%

TABLE 2. Results of open population models applied to banding data to estimate stopover duration by migratory birds. Model choice, multiple-day-constancy (MDC) interval, and stopover estimates varied substantially both between and within species. In each case, only the most heavily weighted model is presented. Most models required the use of fairly long MDC intervals, indicating a need to substantially reduce the number of estimated parameters. Many of the resulting stopover duration estimates had high coefficients of variation (>50%), making comparisons difficult. Coefficients of variation were calculated by dividing the standard error of stopover duration, estimated by bootstrapping, by the stopover duration estimate. Bird banding data were collected during spring and fall migration on Appledore Island, Maine (1996–2002); Star Island, New Hampshire (1999–2000); and Hamlin Beach State Park, New York (1999–2000).

Species	Site[a]	Season	Year	*n*	Stopover duration (days)	Chosen model	Total stopover duration estimate (days)[b]	Stopover-after estimate (days)[c]
Traill's Flycatcher (*Empidonax alnorum* and *E. traillii*)	H	Spring	1999	54	14	$p_{\cdot}\ \phi_7\ \gamma_7$	3.47 ± 2.88	1.14 ± 1.88
Blue-headed Vireo (*Vireo solitarius*)	A	Spring	1996	101	12	$p_5\ \phi_5\ \gamma_5$	**1.73 ± 0.82**	1.33 ± 0.81
Red-eyed Vireo (*V. olivaceus*)	A	Fall	1996	297	41	$p_{\cdot}\ \phi_{\cdot}\ \gamma_3$	**4.11 ± 0.62**	**2.22 ± 0.28**
	A	Fall	1997	188	31	$p_7\ \phi_{\cdot}\ \gamma_7$	**3.42 ± 0.46**	**1.85 ± 0.30**
	A	Fall	1998	258	40	$p_5\ \phi_5\ \gamma_5$	5.37 ± 7.02	3.60 ± 6.87
	A	Fall	1999	231	43	$p_5\ \phi_5\ \gamma_5$	8.37 ± 10.85	**3.71 ± 1.38**
	A	Fall	2000	354	47	$p_{\cdot}\ \phi_{\cdot}\ \gamma_6$	**4.30 ± 1.08**	**2.17 ± 0.44**
	A	Fall	2001	277	43	$p_{\cdot}\ \phi_{\cdot}\ \gamma_3$	4.97 ± 3.51	**2.38 ± 0.50**
	A	Spring	1996	114	21	$p_{\cdot}\ \phi_7\ \gamma_7$	1.53 ± 1.19	0.59 ± 0.45
	A	Spring	1998	136	26	$p_7\ \phi_{\cdot}\ \gamma_7$	1.46 ± 1.03	0.81 ± 0.65
	A	Spring	1999	156	28	$p_7\ \phi_7\ \gamma_{\cdot}$	1.52 ± 0.89	0.76 ± 0.45
	A	Spring	2000	168	33	$p_7\ \phi_7\ \gamma_7$	11.24 ± 30.81	10.13 ± 30.70
	S	Fall	2000	116	42	$p_{\cdot}\ \phi_7\ \gamma_{\cdot}$	**2.30 ± 1.10**	1.22 ± 0.78
Red-breasted Nuthatch (*Sitta canadensis*)	A	Fall	1999	100	48	$p_{\cdot}\ \phi_7\ \gamma_{\cdot}$	**7.87 ± 3.46**	3.62 ± 1.82
Golden-crowned Kinglet (*Regulus satrapa*)	A	Fall	2000	100	9	$p_3\ \phi_3\ \gamma_{\cdot}$	**0.94 ± 0.46**	**0.45 ± 0.22**
	A	Fall	2001	61	18	$p_{\cdot}\ \phi_{\cdot}\ \gamma_7$	2.21 ± 1.14	1.22 ± 0.66
	H	Fall	1999	208	24	$p_5\ \phi_{\cdot}\ \gamma_5$	1.83 ± 1.77	**0.74 ± 0.28**
	H	Fall	2000	450	28	$p_5\ \phi_{\cdot}\ \gamma_5$	**2.22 ± 0.97**	**1.27 ± 0.54**
	S	Fall	2000	76	9	$p_7\ \phi_7\ \gamma_{\cdot}$	2.04 ± 1.98	0.98 ± 0.89
Ruby-crowned Kinglet (*R. calendula*)	H	Fall	2000	595	38	$p_5\ \phi_5\ \gamma_5$	4.12 ± 6.42	2.28 ± 2.71
	H	Spring	1999	209	21	$p_5\ \phi_{\cdot}\ \gamma_5$	2.04 ± 1.45	1.19 ± 1.05
	H	Spring	2000	198	29	$p_{\cdot}\ \phi_{\cdot}\ \gamma_4$	**1.82 ± 0.83**	0.96 ± 0.51
Gray-cheeked Thrush (*Catharus minimus*)	H	Fall	1999	118	27	$p_6\ \phi_6\ \gamma_{\cdot}$	**13.66 ± 4.33**	**6.82 ± 2.33**
Swainson's Thrush (*C. ustulatus*)	H	Fall	2000	116	35	$p_{\cdot}\ \phi_7\ \gamma_{\cdot}$	3.34 ± 2.67	1.68 ± 1.35
Hermit Thrush (*C. guttatus*)	H	Fall	1999	165	27	$p_7\ \phi_7\ \gamma_7$	**5.14 ± 1.25**	**2.97 ± 0.82**
	H	Fall	2000	135	19	$p_{\cdot}\ \phi_{\cdot}\ \gamma_6$	**13.20 ± 3.45**	**9.35 ± 3.07**
Gray Catbird (*Dumetella carolinensis*)	H	Fall	2000	70	29	$p_{\cdot}\ \phi_7\ \gamma_{\cdot}$	**17.08 ± 7.81**	**7.15 ± 3.54**
Cedar Waxwing (*Bombycilla cedrorum*)	A	Fall	1998	87	31	$p_7\ \phi_{\cdot}\ \gamma_7$	1.42 ± 0.85	0.77 ± 0.51
	A	Fall	2002	56	43	$p_{\cdot}\ \phi_{\cdot}\ \gamma_7$	4.95 ± 3.13	2.45 ± 1.44
	S	Fall	2000	76	42	$p_7\ \phi_{\cdot}\ \gamma_7$	1.04 ± 0.70	0.54 ± 0.40
Northern Parula (*Parula americana*)	A	Spring	1998	58	21	$p_7\ \phi_7\ \gamma_{\cdot}$	0.76 ± 0.62	0.38 ± 0.30

TABLE 2. Continued

Species	Site[a]	Season	Year	n	Stopover duration (days)	Chosen model	Total stopover duration estimate (days)[b]	Stopover-after estimate (days)[c]
Magnolia Warbler (*Dendroica magnolia*)	A	Spring	1997	237	35	$p_7\ \phi_7\ \gamma.$	1.58 ± 2.27	1.01 ± 2.05
	A	Spring	1998	561	33	$p.\ \phi_5\ \gamma_5$	**1.82 ± 0.58**	**1.02 ± 0.40**
	A	Spring	1999	265	28	$p_6\ \phi_6\ \gamma.$	2.23 ± 5.78	1.42 ± 5.19
	A	Spring	2001	358	39	$p_7\ \phi_7\ \gamma_7$	3.86 ± 7.76	1.76 ± 2.00
	H	Fall	2000	156	31	$p.\ \phi_5\ \gamma_5$	6.56 ± 3.66	3.27 ± 1.92
	H	Spring	2000	175	28	$p_7\ \phi_7\ \gamma_7$	1.78 ± 2.82	1.14 ± 2.37
	S	Spring	2000	159	30	$p_5\ \phi_5\ \gamma.$	2.00 ± 2.98	0.89 ± 0.75
Blackpoll Warbler (*D. striata*)	A	Fall	1996	78	32	$p_6\ \phi_6\ \gamma.$	**1.46 ± 0.50**	**0.73 ± 0.28**
	A	Fall	1998	120	32	$p.\ \phi_7\ \gamma.$	3.49 ± 2.89	1.77 ± 1.53
Black-and-white Warbler (*Mniotilta varia*)	A	Fall	1998	78	46	$p.\ \phi.\ \gamma_7$	**3.83 ± 1.54**	**1.99 ± 0.84**
American Redstart (*Setophaga ruticilla*)	A	Fall	1996	141	44	$p_7\ \phi_7\ \gamma_7$	2.72 ± 3.54	1.36 ± 0.74
	A	Fall	1997	142	41	$p.\ \phi.\ \gamma_5$	3.53 ± 2.19	**1.75 ± 0.81**
	A	Fall	1999	99	48	$p\ .\phi.\ \gamma_7$	4.67 ± 2.53	2.43 ± 1.38
	A	Fall	2000	210	40	$p_5\ \phi_5\ \gamma_5$	7.19 ± 14.75	5.01 ± 14.75
	A	Fall	2001	113	50	$p.\ \phi.\ \gamma_7$	3.59 ± 1.85	**1.78 ± 0.58**
	A	Fall	2002	144	47	$p_6\ \phi.\ \gamma_6$	**3.56 ± 1.33**	**1.94 ± 0.83**
	A	Spring	1997	103	29	$p.\ \phi_6\ \gamma.$	4.59 ± 3.69	3.02 ± 3.24
	A	Spring	1998	189	25	$p.\ \phi.\ \gamma_5$	**3.16 ± 0.63**	**1.79 ± 0.40**
	A	Spring	2000	143	34	$p_6\ \phi.\ \gamma_6$	3.65 ± 5.23	**1.46 ± 0.57**
Ovenbird (*Seiurus aurocapillus*)	A	Spring	1997	90	30	$p_6\ \phi_6\ \gamma_6$	6.27 ± 14.12	0.94 ± 1.02
Northern Waterthrush (*S. noveboracensis*)	A	Fall	1997	206	41	$p.\ \phi.\ \gamma_7$	5.24 ± 3.30	**2.55 ± 0.73**
	A	Fall	1999	153	46	$p.\ \phi.\ \gamma_7$	**7.49 ± 1.46**	**4.06 ± 0.90**
	A	Fall	2001	197	43	$p_7\ \phi_7\ \gamma.$	**8.86 ± 3.13**	**4.33 ± 2.09**
	A	Fall	2002	162	45	$p.\ \phi.\ \gamma_6$	7.89 ± 5.18	**3.97 ± 1.39**
	S	Fall	2000	100	43	$p.\ \phi.\ \gamma_7$	**3.06 ± 0.76**	**1.53 ± 0.39**
Wilson's Warbler (*Wilsonia pusilla*)	H	Fall	2000	50	25	$p.\ \phi_6\ \gamma_6$	3.27 ± 3.05	**1.32 ± 0.30**
	H	Spring	2000	100	23	$p_5\ \phi_5\ \gamma.$	**2.64 ± 0.69**	**1.35 ± 0.45**
White-throated Sparrow (*Zonotrichia albicollis*)	A	Spring	2002	247	28	$p_6\ \phi.\ \gamma_6$	3.15 ± 4.73	1.00 ± 0.52
	H	Fall	2000	539	35	$p_7\ \phi_7\ \gamma.$	**6.95 ± 2.75**	**3.47 ± 1.68**
	H	Spring	1999	126	21	$p_7\ \phi_7\ \gamma.$	0.93 ± 0.80	0.46 ± 0.39

[a] A = Appledore Island, Maine; H = Hamlin Beach State Park, New York; S = Star Island, New Hampshire.

[b] Mean ± SE of the total stopover estimate (following Schaub et al. 2001). Estimates in boldface had a CV of <50%. CV values were calculated as (SE/mean) × 100.

[c] Mean ± SE of the stopover-after estimate (using equation 5 in Efford 2005). Estimates in boldface had a CV of <50%. CV values were calculated as (SE/mean) × 100.

confidence level. It is worth noting that this simulation test has a Type I error rate of 5% (i.e., 5% chance of passing the GOF test when the model does not have adequate descriptive power); however, the expected Type II error rate (the chance that the model has failed GOF when, in fact, it has adequate descriptive power) is not known, so we cannot even say with certainty that the rate of GOF failure is greater than expected by chance. The contingency table GOF tests implemented in U-CARE also were severely limited by the sparseness of the data (only 42% of estimable capture histories could be tested using U-CARE).

For all capture histories used in this study, it was necessary to reduce the number of parameters in the fitted model from the number present in a fully time-dependent model to estimate all parameters successfully. Our results indicated that MDC intervals from 3 to 7 days were necessary to reduce the parameter count in the models sufficiently to estimate all parameters. Parameter reduction was necessary even for relatively large sample sizes (up to 595 specimens captured over 38 days). The only current alternative to the MDC method of reducing the number of parameters is pooling the data—with its attendant problems of possible parameter bias (Hargrove and Borland 1994, Morris et al. 2005b). If pooling is desirable in a given study, the MDC interval approach outlined here could be adapted to determine the minimum pooling interval necessary, based on parameter estimability. Regardless of the method, successful use of CMR models on banding data will often require some form of parameter reduction.

In our current work, the CV of total stopover duration measures the relative uncertainty in the derived parameter of interest. The CV includes both biological variability and variability due to parameter estimation uncertainty. Given our current available data, it is somewhat difficult to determine the extent of the biological contribution versus the sampling-related contribution. Again, long minimum stopover duration might indicate heterogeneity in the population. However, corresponding increases in (1) the fraction of capture histories with a CV of <50% and (2) the number of observations per parameter (Table 1) indicate some variation due to sample size. Overall, more estimates of stopover duration had a CV of <50% when using the stopover-after statistic (28 capture histories) than when using the total stopover statistic (23 capture histories). Thus, in addition to the theoretical points raised by Efford (2005), the statistic based on his equation 5 resulted in more useable estimates of stopover duration based on banding data.

Most of the capture histories that were estimable and had applicable models in this study were collected during fall migration (Table 2). Previous work on Appledore Island resulted in higher rates of recapture and documented longer minimum stopover durations during fall migration than in spring migration (Morris et al. 1994, Morris and Glasgow 2001); this may have helped increase the number of observations per parameter available in our study, which, in turn, may have resulted in higher estimability. We did not see a specific pattern related to avian biology that explained the pattern of capture histories with low CV values. Although most of the capture histories with low CV values were obtained during fall banding, this proportion was similar to the proportion of fall capture histories that had applicable models. The capture histories with low CV values represented a wide range of species (Table 2). Species that had low CV values over multiple seasons included those captured in high numbers, such as Red-eyed Vireo (*Vireo olivaceus*), American Redstart (*Setophaga ruticilla*), and Northern Waterthrush (*Seiurus noveboracensis*).

Our results document the difficulty associated with parameter estimability when using passerine banding data for capture-mark-recapture models of stopover duration. We are not implying that these methods cannot or should not be used on this type of data, but rather they should be used cautiously, particularly when sample sizes are small. Efford (2005) suggests using a constant ϕ model for populations with no consistent trend in ϕ, which would reduce problems with estimability. Researchers planning to use these methods in migration banding studies should attempt to maximize the number of captures and recaptures during sampling periods to increase the likelihood of parameter estimability.

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