Estimating Temporary Emigration Using Capture-Recapture Data with Pollock's Robust Design

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ESTIMATING TEMPORARY EMIGRATION USING CAPTURE–RECAPTURE DATA WITH POLLOCK'S ROBUST DESIGN

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Abstract. Statistical inference for capture–recapture studies of open animal populations typically relies on the assumption that all emigration from the studied population is permanent. However, there are many instances in which this assumption is unlikely to be met. We define two general models for the process of temporary emigration: completely random and Markovian. We then consider effects of these two types of temporary emigration on Jolly–Seber estimators and on estimators arising from the full-likelihood approach to robust design data.

Capture–recapture data arising from Pollock's robust design provide the basis for obtaining unbiased estimates of demographic parameters in the presence of temporary emigration, and for estimating the probability of temporary emigration. We present a likelihood-based approach to dealing with temporary emigration that permits estimation under different models of temporary emigration and yields tests for completely random and Markovian emigration. In addition, we use the relationship between capture probability estimates based on closed and open models under completely random temporary emigration to derive three ad hoc estimators for the probability of temporary emigration. Two of these should be especially useful in situations where capture probabilities are heterogeneous among individual animals. Ad hoc and full-likelihood estimators are illustrated for small-mammal capture–recapture data sets.

We believe that these models and estimators will be useful for testing hypotheses about the process of temporary emigration, for estimating demographic parameters in the presence of temporary emigration, and for estimating probabilities of temporary emigration. These latter estimates are frequently of ecological interest as indicators of animal movement and, in some sampling situations, as direct estimates of breeding probabilities and proportions.

Key words: capture–recapture; demographic parameters; Microtus pennsylvanicus; *models; open populations;* Peromyscus leucopus; *Pollock's robust design; statistical estimation; temporary emigration.*

INTRODUCTION

An assumption implicit in capture–recapture models for open populations is that all emigration from the area subjected to sampling efforts is permanent (e.g., Seber 1982, Pollock et al. 1990). In reality, however, there are many different sampling situations in which this assumption is unlikely to be met. For example, stationary traps or nets sample the specific study areas on which they are located. However, the areas traversed by animals in their daily or weekly travels may not correspond exactly to the study area, with some time being spent in sampled areas and some time spent in areas not exposed to sampling efforts. Depending on exactly when the sampling is done, the animal may or may not be exposed to sampling efforts during a spe-

cific sampling period. Sometimes, migratory animals are sampled annually at breeding or wintering locations. It may be that they return to sampled locations (e.g., breeding colonies) during some years but not during others (e.g., Hestbeck et al. 1991). In other cases, a form of temporary emigration is induced by the capture process. For example, Spendelow and Nichols (1989) sampled Roseate Terns (*Sterna dougalii*) at a breeding colony by trapping and observing birds at nests. Nonbreeding birds had capture–observation probabilities of 0, and were effectively temporary emigrants.

Temporary emigration can lead to biased estimates of population size, number of recruits, and, in some cases, survival rate when standard design (e.g., Seber 1982, Pollock et al. 1990) and certain robust design (Kendall et al. 1995) models for open populations are used. Here, we present capture–recapture models and estimators that incorporate temporary emigration and, hence, yield estimates that are generally not biased by such movement. We present estimators for the propor-

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tion of animals in the target population at period i that are temporary emigrants. This parameter could be of some biological interest as an indicator of animal movement. In some situations (e.g., the sampling of breeding bird colonies), the proportion of temporary emigrants can be equated with the proportion of animals not breeding (Lebreton et al. 1990, Clobert et al. 1994), and this quantity is very important to animal population ecology.

We consider two models of temporary emigration. In one model, temporary emigration is viewed as a nonMarkovian process (completely "random emigration" of Burnham 1993), whereas in a second model, it is viewed as a first-order Markov process (Markovian emigration). We briefly consider bias in estimators of the Jolly–Seber (JS) model (Seber 1982) and estimators of Kendall et al. (1995) under both models of temporary emigration. We then present capture–recapture models that include and permit estimation of parameters associated with temporary emigration. We also present ad hoc estimation methods for cases in which some assumptions underlying these models are not reasonable. Finally, we illustrate these methods with data from our studies of white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*).

BACKGROUND INFORMATION AND NOTATION

Pollock's robust design

Standard capture–recapture data obtained during the study of an open population (one that can experience gains and losses between sampling periods) do not contain sufficient information to estimate temporary emigration without potentially restrictive assumptions and constraints (Clobert et al. 1990, 1994). Our approach to estimating temporary emigration requires the extra information provided by Pollock's (1982) robust design (robust design). Under this design, we distinguish between primary and secondary sampling periods. Consecutive primary sampling periods are separated from each other by sufficient time to expect the sampled population to change through gains (birth and immigration) and losses (death and emigration). For example, small-mammal populations might be trapped every 8 wk, or a migratory bird population might be sampled every year. Capture-history data summarized over primary periods are used with models developed for open populations, such as the JS model.

Each primary period i ($i = 1, 2, \ldots, k$) includes l_i secondary sampling periods separated from each other by time intervals that are sufficiently short for the population to be effectively closed to gains and losses. For example, a small-mammal population might be trapped for five consecutive days (secondary periods) within each primary period. Data from secondary periods within a primary period can be analyzed using capture–recapture models developed for closed populations, such as those summarized by Otis et al. (1978).

Two models of temporary emigration

We define a superpopulation of N_i^0 animals that are "associated" with the area sampled by our capture–recapture efforts during primary sampling period i, in the sense that they have some non-negligible a priori probability of being in the area exposed to sampling efforts when period i begins. Further, N_i members of the superpopulation are, in fact, in the area exposed to sampling efforts during period i (and we assume they are there for the entire period, i.e., for all l_i secondary periods within primary period i). These N_i animals are captured during primary period i with probability p_i^*.

Under the completely random emigration model (terminology of Burnham 1993), we define a parameter, γ_i, denoting the probability that a member of the superpopulation is not in the area exposed to sampling efforts during period i (i.e., is a temporary emigrant). Thus, the expected number of animals exposed to capture in period i is $E(N_i) = (1 - \gamma_i)N_i^0$.

Under the Markovian emigration model, we envision a first-order Markov process in which the probability of being a temporary emigrant in period i is γ_i' for the $N_{i-1}^0 - N_{i-1}$ animals that were temporary emigrants in period $i - 1$, and γ_i'' for the N_{i-1} animals that were in the area exposed to sampling efforts in period $i - 1$. This model is similar in some respects to the dependent-sighting probability model of Sandland and Kirkwood (1981). It is also similar to a model presented by Whitehead (1990), for which he produced estimates, but his model assumes that the superpopulation is closed for the entire study and that N_i remains relatively constant. An important assumption underlying both of our models of temporary emigration is that the probability (ϕ_i) of an animal in the superpopulation in period i surviving to, and remaining in the superpopulation at, period $i + 1$ is the same for all animals in the superpopulation at period i, and does not differ by temporary emigration status.

Additional notation

The previous and following notation builds on the notation of Seber (1982:196), Otis et al. (1978), and Kendall et al. (1995). Let

M_i^0 = number of animals marked before primary period i and in the superpopulation during period i ($i = 2, 3, \ldots, k$; $M_1^0 = 0$),

M_i = number of animals from M_i^0 in the area exposed to sampling efforts (not temporary emigrants) during primary period i,

B_i^0 = number of animals entering the superpopulation between primary periods i and $i + 1$ and still in the superpopulation at $i + 1$ ($i = 1, 2, \ldots, k - 1$),

B_i = number of animals from B_i^0 in the area exposed to sampling efforts during primary period $i + 1$,

u_i = number of animals captured during primary period i, that were unmarked prior to period i,

m_{hi} = number of animals captured in primary period i that were last captured in primary period h ($h = 1, 2, \ldots, i - 1$; $i = 2, 3, \ldots, k$), and

m_i = $\Sigma_{h=1}^{i-1} m_{hi}$, the number of individuals from M_i captured in primary period i.

X_{hi}^ω = number of m_{hi} individuals (or u_i for $h = 0$) that have capture history $\omega \in \Omega$ over the l_i secondary samples within primary period i, where Ω is the set of all possible sequences of l_i 1's (for capture) and 0's (for no capture); $X_i^\omega = \Sigma_{h=0}^{i-1} X_{hi}^\omega$.

R_i = number of individuals released with marks during primary period i ($i = 1, 2, \ldots, k - 1$),

p_{ij} = probability that an animal is captured in secondary sample j of primary period i, given that it is alive and in the sampled area during period i ($j = 1, 2, \ldots, l_i$; $i = 1, 2, \ldots, k$), -

q_{ij} = $1 - p_{ij}$,

p_i^* = probability that an animal is captured in at least one of the l_i secondary samples of primary period i ($p_i^* = 1 - \Pi_{j=1}^{l_i} q_{ij}$), given that the animal is located in the sampled area during period i,

q_i^* = $1 - p_i^* = \Pi_{j=1}^{l_i} q_{ij}$,

p_i^0 = probability that an animal is caught in primary period i, given that the animal is alive and in the superpopulation at period i ($i = 1, 2, \ldots, k$),

χ_i = probability that an animal alive in primary period i is never seen again after period i under the Jolly–Seber model, with no temporary emigration;

χ_i = $1 - \phi_i (1 - q_{i+1}^* \chi_{i+1})$ for $i = 1, 2, \ldots, k - 1$; $\chi_k = 1$,

χ_i^e = probability that an animal alive in primary period i is never seen again after period i under the completely random model of temporary emigration;

χ_i^e = $1 - \phi_i(1 - [1 - (1 - \gamma_{i+1}) p_{i+1}^*]\chi_{i+1}^e)$ for $i = 1, 2, \ldots, k - 1$; $\chi_k^e = 1$.

For our purposes, p_{ij}, ϕ_i, γ_i, γ_i', and γ_i'' are considered fixed parameters, whereas N_i, N_i^0, M_i, M_i^0, B_i, and B_i^0 are considered unknown random variables (except that $M_1 = M_1^0 = 0$).

Effects of Temporary Emigration on Existing Estimators

Jolly–Seber model

The JS model (Seber 1982, Pollock et al. 1990, Lebreton et al. 1992) is the model most commonly used to estimate population size, survival rates, and recruit-

ment for capture–recapture studies on open populations. For data collected under the robust design, the JS model ignores the patterns of capture over secondary periods, considering only whether an animal was caught at some point during a given primary period. The model assumes that any emigration from the population during the study is permanent. With the exceptions of Balser (1981: 23) and Burnham (1993), little has been done to examine the effect of temporary emigration on JS estimators.

Completely random emigration.—Given that an animal is alive and is one of the N_i^0 animals in the superpopulation at time i, its probability of being captured is $p_i^0 = (1 - \gamma_i)p_i^* = $ Pr(capture | alive and in superpopulation), where $(1 - \gamma_i) = $ Pr(in study area | alive and in superpopulation), and $p_i^* = $ Pr(capture | alive and in study area).

We approximated large-sample expectations of JS estimators (Seber 1982:200) under the completely random emigration model, using expected values of JS summary statistics (e.g., see Carothers 1973, Arnason and Mills 1981). This resulted in:

$$E(\hat{M}_i^{js}) \approx M_i^0 = M_i/(1 - \gamma_i) \geq M_i$$

$$E(\hat{N}_i^{js}) \approx N_i^0 = N_i/(1 - \gamma_i) \geq N_i$$

$$E(\hat{p}_i^{js}) \approx p_i^0 = p_i^*(1 - \gamma_i) \leq p_i^*,$$

$$E(\hat{\phi}_i^{js}) \approx \phi_i$$

$$E(\hat{B}_i^{js}) \approx B_i^0 = B_i/(1 - \gamma_i) \geq B_i. \qquad (1)$$

Thus, under the completely random emigration model, JS estimators estimate quantities associated with the entire superpopulation, N_i^0, not simply with the population found in the area exposed to capture efforts in period i. Assuming survival rate is the same for those in and out of the study area, $\hat{\phi}_i^{js}$ remains unbiased.

Variances of JS estimators should be larger in the presence of temporary emigration. From Eq. 1, we can see that as γ_i increases, p_i^0 becomes smaller relative to p_i^*; i.e., the effective sampling probability and resultant sample sizes decrease.

Markovian emigration.—When the probability of being a temporary emigrant in period i is different for those that were temporary emigrants in period $i - 1$ (γ_i') than for those that were available for capture in period $i - 1$ (γ_i''), intuition tells us that there will be potentially large bias in the JS estimators. Large-sample approximations of this bias are not nearly as simple and informative as the expressions in Eq. 1 for the completely random emigration model. Numerical approximations to the bias of JS estimators under Markovian emigration, presented in a subsequent section, indicate a strong dependence on the relationship between γ_i' and γ_i''.

Full-likelihood approach

When data are collected under the robust design, it is possible to build a model for the entire sampling process that incorporates information provided by both levels of sampling (primary and secondary periods). Kendall et al. (1995) constructed several product–multinomial models for data collected under the robust design. We have included part of the likelihood function for model M_t' (time variation in capture probabilities within and between primary periods), where there are only two secondary samples taken per primary period (Kendall et al. 1995):

$$L_1 = \prod_{i=1}^{k-1} \binom{R_i}{m_{i,i+1}, \ldots, m_{ik}} (\phi_i p_{i+1}^*)^{m_{i,i+1}}$$

$$\times (\phi_i q_{i+1}^* \phi_{i+1} p_{i+2}^*)^{m_{i,i+2}} \ldots$$

$$\times (\phi_i q_{i+1}^* \ldots \phi_{k-1} p_k^*)^{m_{ik}} (\chi_i)^{R_i - r_i}$$

and

$$L_2 = \prod_{i=2}^{k} \binom{\mu_i}{X_{0i}^{10}, X_{0i}^{01}, X_{0i}^{11}} \prod_{h=1}^{i-1} \binom{m_{hi}}{X_{hi}^{10}, X_{hi}^{01}, X_{hi}^{11}}$$

$$\times \left(\frac{p_{i1} q_{i2}}{p_i^*}\right)^{X_i^{10}} \left(\frac{q_{i1} p_{i2}}{p_i^*}\right)^{X_i^{01}} \left(\frac{p_{i1} p_{i2}}{p_i^*}\right)^{X_i^{11}}. \quad (2)$$

L_1 describes the capture process between primary periods and is part of the JS model (Seber 1982: 198). L_2 conditions on cohorts of previously marked animals captured in a given primary period, and describes the capture process over the two secondary periods for each cohort. The p_{ij}'s are common to both L_1 (through $p_i^* = 1 - q_{i1} q_{i2}$) and L_2. We call conditional maximum likelihood estimation under this model a "full-likelihood" approach, because it uses information from primary and secondary levels of sampling simultaneously.

For the sake of clarity, we will follow Lebreton et al. (1992) in the remainder of our discussion, denoting different models by their constituent parameters. Under this nomenclature model M_t', $(L_1 \times L_2)$ described in Eq. 2 would be denoted by (ϕ_i, p_{ij}), indicating that the model includes time-specific survival and capture probability parameters. Models that include time-independent parameters would be designated by removing the subscript from the parameter; e.g., (ϕ, p_{ij}) would denote a model with constant survival rate and time-dependent capture probabilities.

Completely random emigration.—When there is completely random emigration, the p_i^*'s in L_1 and L_2 will not be equivalent, and therefore we can expect bias in estimators. The p_i^* in L_1 will reflect p_i^0 (Eq. 1) and will incorporate temporary emigration, whereas the p_i^* in L_2 will still reflect $1 - q_{i1} q_{i2}$ and will not include temporary emigration. Therefore, we anticipate the expected value of $\hat{p}_i^{fl}$ (fl = full likelihood) under the joint likelihood function, $L_1 \times L_2$, to be intermediate:

$$p_i^0 = (1 - \gamma_i) p_i^* < E(\hat{p}_i^{fl}) < p_i^*. \quad (3)$$

Combined with Eq. 2, Eq. 3 implies that

$$N_i < E(\hat{N}_i^{fl}) < N_i^0$$

and

$$M_i < E(\hat{M}_i^{fl}) < M_i^0. \quad (4)$$

In addition, we anticipate bias in estimators for ϕ_i and B_i; because of the difference in the p_i^* between L_1 and L_2, the measured fit of the model will likely be poor.

Markovian emigration.—As in the JS case, the effect of Markovian emigration depends on the relationship between γ_i' and γ_i''. In addition, the effect is even more difficult to predict than the JS case because the estimators for model (ϕ_i, p_{ij}) are not explicit (i.e., they must be computed iteratively). We do not pursue this prediction here, because our principal purpose is to provide a means to adjust for this effect directly. Numerical examples illustrating the direction and magnitude of full-likelihood estimators under both completely random and Markovian emigration are presented in a subsequent section.

ESTIMATION IN THE PRESENCE OF TEMPORARY EMIGRATION

Completely random emigration: time dependence or trap response in capture probabilities

It was noted in previous sections that temporary emigration causes problems with both the JS and full-likelihood approaches. We have already shown in Eq. 1 that $E(\hat{p}_i^{js}) = (1 - \gamma_i) p_i^* = p_i^0$, the probability of capture given presence in the superpopulation, but regardless of presence in the sampled area during period i. When the data are collected using the robust design, the closed-model parameters (e.g., $1 - \Pi_{j=1}^{l_i} [1 - p_{ij}]$ under model M_t of Otis et al. 1978) reflect the conditional probability of capture given presence in the area exposed to sampling efforts, p_i^*.

Under the completely random emigration model, this expectation, coupled with our ability to estimate p_i^* using closed models such as M_t and M_b (denote this estimator $\hat{p}_i^{cl}$) (Otis et al. 1978), leads to the following ad hoc estimator for γ_i:

$$\hat{\gamma}_i = 1 - \frac{\hat{p}_i^{js}}{\hat{p}_i^{cl}}. \quad (5)$$

An appropriate variance estimate based on the delta method (Seber 1982:7) would be

$$\widehat{var}(\hat{\gamma}_i) = \left(\frac{1}{\hat{p}_i^{cl}}\right)^2 \widehat{var}(\hat{p}_i^{js}) + \left(\frac{\hat{p}_i^{js}}{(\hat{p}_i^{cl})^2}\right)^2 \widehat{var}(\hat{p}_i^{cl})$$

$$- 2\left(\frac{\hat{p}_i^{js}}{(\hat{p}_i^{cl})^3}\right) \widehat{cov}(\hat{p}_i^{js}, \hat{p}_i^{cl}). \quad (6)$$

Findings of Kendall and Pollock (1992) suggest that the covariance term in Eq. 6 can be ignored.

The Eq. 5 estimator is intuitively appealing, and when $l_i = 2$, this estimator can be computed by hand.

TABLE 1. Comparison of large-sample properties of conditional maximum-likelihood estimators from $(\phi_i, p_{ij}, \gamma_i)$, (ϕ_i, p_{ij}), and Jolly–Seber models, where $(\phi_i, p_{ij}, \gamma_i)$ is the true model. Based on $N_i^0 \approx 500$ for all four primary periods, each consisting of two secondary periods.

| Parameters | Parameter value† | Model | | | | | |
| | | $(\phi_i, p_{ij}, \gamma_i)$ | | (ϕ_i, p_{ij}) | | Jolly–Seber | |
		% bias‡	% CV§	% bias	% CV§	% bias‡	% CV§
p_2^*	0.64	0	10.4	−7	6.0	−20	11.2
p_3^*	0.64	0	10.4	−7	6.0	−20	11.2
ϕ_1	0.60	0	9.4	−7	7.5	0	9.4
ϕ_2	0.60	0	10.5	−5	7.8	0	10.5
γ_2	0.20	0	51.6				
γ_3	0.20	0	51.6				

† Values of parameters not estimated are $p_1^* = p_4^* = 0.64$; $\phi_3 = 0.60$; $\gamma_4 = 0.20$.
‡ Here, 0% bias indicates unbiased to fifth decimal place.
§ Defined as 1 SE/estimate × 100.

However, we favor modeling the entire sampling process, described here. In the presence of temporary emigration, L_2 from Eq. 2 is still appropriate because it conditions on animals that have been captured (i.e., animals not outside the study area). However, the p_i^* in L_1 are no longer equivalent to the p_i^* of L_2 (Eq. 2). We can build new models that allow for completely random temporary emigration by replacing each p_i^* in L_1 with $(1 - \gamma_i)p_i^*$ to create L_{1a}:

$$L_{1a} = \prod_{i=1}^{k-1} \binom{R_i}{m_{i,i+1}, \ldots, m_{ik}} [\phi_i(1 - \gamma_{i+1})p_{i+1}^*]^{m_{i,i+1}}$$

$$\times [\phi_i(1 - (1 - \gamma_{i+1})p_{i+1}^*)\phi_{i+1}(1 - \gamma_{i+2})p_{i+2}^*]^{m_{i,i+2}} \cdots$$

$$\times [\phi_i(1 - (1 - \gamma_{i+1})p_{i+1}^*) \cdots$$

$$\phi_{k-1}(1 - \gamma_k)p_k^*]^{m_{ik}} (\chi_i^e)^{R_i - r_i}. \tag{7}$$

Although γ_i and p_i^* occur together consistently in L_{1a}, they are not confounded under the complete model (i.e., $L_{1a} \times L_2$), because the p_i^*'s occur in L_2 as well. Under this new model, γ_i is identifiable (i.e., can be estimated) for $i = 2, 3, \ldots, k - 1$. Because information on p_1^* and p_k^* comes only from within-period information (L_2) (i.e., p_1^* and p_k^* are not identifiable under the standard JS model), γ_1 and γ_k cannot be estimated without additional assumptions. In fact, γ_k is confounded with ϕ_{k-1}. We designate this model $(\phi_i, p_{ij}, \gamma_i)$. We compute full-likelihood estimates under this model using program RDSURVIV, a modified version of program SURVIV (White 1983), written by J. E. Hines and W. L. Kendall to fit multinomial models to robust design capture–recapture data.

For the cases of temporary or permanent trap response in catchability, one could use this method to modify models M_b^t or M_b^{tb}, respectively, from Kendall et al. (1995) to account for temporary emigration.

The benefits of using estimators derived from model $(\phi_i, p_{ij}, \gamma_i)$ when temporary emigration occurs are illustrated in Table 1. Estimators from $(\phi_i, p_{ij}, \gamma_i)$ are approximately unbiased. Based on $\gamma_i = 0.2$ and the com-

plete randomness of temporary emigration, the −20% bias in $\hat{p}_2^{js}$ and $\hat{p}_3^{js}$ is consistent with bias arguments made in a previous section. The unbiasedness of $\hat{\phi}_1^{js}$ and $\hat{\phi}_2^{js}$ is also consistent with those arguments. As expected, $\hat{p}_2^{fl}$ and $\hat{p}_3^{fl}$ are negatively biased but not as severely as $\hat{p}_2^{js}$ and $\hat{p}_3^{js}$, and the $\hat{\phi}_i^{fl}$ are also negatively biased. Although unbiased, the precision of $\hat{\gamma}_2$ and $\hat{\gamma}_3$ is poor. Full-likelihood estimators $\hat{p}_2^*$ and $\hat{p}_3^*$ under model $(\phi_i, p_{ij}, \gamma_i)$ are more precise than $\hat{p}_2^{js}$ and $\hat{p}_3^{js}$, but they are less precise than $\hat{p}_2^{fl}$ and $\hat{p}_3^{fl}$. Bias and precision of all estimators were estimated using the analytic-numeric approach described by Burnham et al. (1987: 214).

Although ϕ_{k-1} and γ_k are confounded under model $(\phi_i, p_{ij}, \gamma_i)$, one can estimate ϕ_{k-1} through the use of various constraints (e.g., by setting $\gamma_k = \gamma_{k-1}$), but of course such constraints should be justified by the data.

Estimation of γ_i under model $(\phi_i, p_{ij}, \gamma_i)$, as described here, is roughly equivalent to the ad hoc method described in Eq. 5. However, we recommend the full-likelihood approach because (1) variances are estimated directly and, therefore, should be less biased, and (2) estimation and hypothesis testing under more restrictive models (e.g., setting γ_i constant over time) is straightforward using model $(\phi_i, p_{ij}, \gamma_i)$.

Completely random emigration: unexplained heterogeneity in capture probabilities

The preceding estimators for γ_i assume that the open-model $\hat{p}_i^{js}$ based on primary periods provide unbiased estimates of p_i^0, and that the closed-model $\hat{p}_{ij}^{cl}$ can be used to compute unbiased estimates of p_i^* (i.e., $\hat{p}_i^{cl} = 1 - \Pi_{j=1}^{l_i}[1 - \hat{p}_{ij}^{cl}]$). These assumptions frequently do not hold in the case of heterogeneous capture probabilities among individuals, or multiple sources of variation in catchability (i.e., combinations of heterogeneity, trap response, and/or time). For these cases, we consider additional ad hoc estimators.

Our additional ad hoc estimators are based on the use of robust closed-model estimators, such as those presented by Otis et al. (1978), Pollock and Otto (1983),

Chao (1988), Chao (1989), Rexstad and Burnham (1991), Chao et al. (1992), and Lee and Chao (1994), to estimate the numbers of survivors from previous releases of marked animals that are in the sampling area at some period i. Let $M_{i+\Delta}^{(R_i)}$ denote the number of those R_i animals released with marks during primary period i that are alive and in the area exposed to sampling efforts in some later period, $i + \Delta$. The $M_{i+\Delta}^{(R_i)}$ can be estimated using closed-population models in conjunction with capture–recapture data over the secondary samples within primary period $i + \Delta$. For example, assume that there is evidence of heterogeneous capture probabilities and that model M_h (Burnham and Overton 1978) is appropriate for the data from secondary capture periods during primary period $i + 1$. Then, we can estimate $M_{i+1}^{(R_i)}$ by using only capture–recapture data obtained in period $i + 1$ for animals released in period i (members of R_i), in conjunction with one of the estimators for model M_h (Burnham and Overton 1978, Chao 1988).

We base our ad hoc estimator of γ_i on the following three conditional expectations:

$$E(M_{i+1}^{(R_i)} \mid R_i) = R_i \phi_i (1 - \gamma_{i+1})$$

$$E(M_{i+2}^{(R_i)} \mid R_i) = R_i \phi_i \phi_{i+1} (1 - \gamma_{i+2})$$

$$E(M_{i+2}^{(R_{i+1})} \mid R_{i+1}) = R_{i+1} \phi_{i+1} (1 - \gamma_{i+2}). \qquad (8)$$

The expected number of survivors in period $i + \Delta$, of animals released in period i, is simply given by the product of R_i with the probability of surviving from i to $i + \Delta$, $(\Pi_{k=i}^{i+\Delta-1} \phi_k)$, and the probability of not being a temporary emigrant during period $i + \Delta$, $(1 - \gamma_{i+\Delta})$.

These expectations (Eq. 8) lead to the following estimator:

$$\hat{\gamma}_{i+1} = 1 - \left[\left(\frac{\hat{M}_{i+1}^{(R_i)}}{R_i} \right) \left(\frac{\hat{M}_{i+2}^{(R_{i+1})}}{R_{i+1}} \right) \bigg/ \left(\frac{\hat{M}_{i+2}^{(R_i)}}{R_i} \right) \right] \qquad (9)$$

with the variance estimator based on the delta method given by

$$\widehat{\text{var}}(\hat{\gamma}_{i+1}) = \left[\frac{\hat{M}_{i+2}^{(R_{i+1})}}{R_{i+1} \hat{M}_{i+2}^{(R_i)}} \right]^2 \widehat{\text{var}}(\hat{M}_{i+1}^{(R_i)})$$

$$+ \left[\frac{\hat{M}_{i+1}^{(R_i)}}{R_{i+1} \hat{M}_{i+2}^{(R_i)}} \right]^2 \widehat{\text{var}}(\hat{M}_{i+2}^{(R_{i+1})})$$

$$+ \left[\frac{\hat{M}_{i+1}^{(R_i)} \hat{M}_{i+2}^{(R_{i+1})}}{R_{i+1} (\hat{M}_{i+2}^{(R_i)})^2} \right]^2 \widehat{\text{var}}(\hat{M}_{i+2}^{(R_i)}). \qquad (10)$$

Because the $M_{i+\Delta}^{(R_i)}$ are estimated from separate data sets, we have excluded covariance terms from Eq. 10.

The numerator of the portion of Eq. 9 in brackets estimates the probability that an animal released with a mark in period i survives until $i + 2$ and does not temporarily emigrate during either sampling period $i + 1$ or $i + 2$ [i.e., the approximate expected value of the numerator is $\phi_i (1 - \gamma_{i+1}) \phi_{i+1} (1 - \gamma_{i+2})$]. The denominator of the portion of Eq. 9 in brackets estimates the probability that an animal released in period i sur-

vives until $i + 2$ and is not a temporary emigrant during $i + 2$ [i.e., the approximate expected value is given by $\phi_i \phi_{i+1} (1 - \gamma_{i+2})$]. Unlike our initial ad hoc estimator (Eq. 5), the Eq. 9 estimator for γ_{i+1} is based entirely on estimates from capture–recapture models for closed populations, and should thus be useful in the presence of heterogeneity, or combinations thereof with trap response and/or temporal variation in capture probability.

We present an additional estimator that may be useful in certain situations. In particular, there are some deviations from assumptions underlying open-population, capture–recapture models (e.g., heterogeneous capture probabilities, permanent trap response) that produce substantial bias in estimated capture probabilities (i.e., under our completely random emigration model, $E[\hat{p}_i^{js}]$ $\neq \hat{p}_i^0$), but yield survival estimates, $\hat{\phi}_i^{js}$, with little (heterogeneity, see Carothers 1973, Hwang and Chao 1995) or no (permanent trap response, see Nichols et al. 1984a) bias. In such cases, it is possible to estimate temporary emigration probability as

$$\hat{\gamma}_{i+1} = 1 - \left[\left(\frac{\hat{M}_{i+1}^{(R_i)}}{R_i} \right) \bigg/ \hat{\phi}_i^{js} \right] \qquad (11)$$

with delta method variance estimate (ignoring covariance term) given by

$$\widehat{\text{var}}(\hat{\gamma}_{i+1}) = \left[\frac{1}{R_i \hat{\phi}_i^{js}} \right]^2 \widehat{\text{var}}(\hat{M}_{i+1}^{(R_i)}) + \left[\frac{\hat{M}_{i+1}^{(R_i)}}{R_i (\hat{\phi}_i^{js})^2} \right]^2 \widehat{\text{var}}(\hat{\phi}_i^{js}). \qquad (12)$$

The ratio in parentheses in Eq. 11 is estimated using closed-model estimators, as in Eq. 9, and estimates the probability of surviving from period i to $i + 1$ and remaining in the area exposed to sampling efforts at period $i + 1$.

Completely random emigration: estimator selection

Selection of an estimator (from the full-likelihood approach or Eq. 5, or Eqs. 8 or 10) for γ_i should be based on the relative bias and precision of the component estimators. The ratios, $\hat{M}_{i+\Delta}^{(R_i)}/R_i$, condition on subsets of the animals caught at $i + \Delta$, whereas estimation of the p_{ij} (and thus p_i^*) using Eqs. 5 or 7 uses all of the animals caught in any primary period, i. In addition, we expect the open-model estimates, $\hat{p}_i^{js}$ and $\hat{\phi}_i^{js}$, to be precise relative to the closed-model estimates, $\hat{p}_{ij}^{cl}$ and $\hat{M}_i^{cl}$, at least for the closed models typically required for capture–recapture data (e.g., the model M_0 of Otis et al. [1978] provides precise estimates but is seldom adequate for real data). For these reasons, if capture probabilities can be adequately modeled as varying with time or based on trap response, we recommend the full-likelihood estimation approach (e.g., model $[\phi_i, p_{ij}, \gamma_i]$). In cases where $\hat{p}_i^{js}$ is likely to provide a poor estimate of p_i^0, but $\hat{\phi}_i^{js}$ is relatively unbiased, we recommend that $\hat{\gamma}_i$ be based on Eq. 11. In cases where none of the open-model estimates is likely to be unbiased, we recommend use of the estimator in Eq. 9.

In the discussion of model $(\phi_i, p_{ij}, \gamma_i)$ and the three

TABLE 2. Comparison of large-sample properties of conditional maximum-likelihood estimators from $(\phi_i, p_{ij}, \gamma_i')$, $(\phi_i, p_{ij}, \gamma_i)$, (ϕ_i, p_{ij}), and Jolly–Seber models, where $(\phi_i, p_{ij}, \gamma_i')$ is the true model and $\gamma_i'' < \gamma_i'$. Based on $E(N_1^0) = 500$ for all four primary periods, each consisting of two secondary periods.

| | | Model | | | | | | | |
| | | $(\phi_i, p_{ij}, \gamma_i')$ | | $(\phi_i, p_{ij}, \gamma_i)$ | | (ϕ_i, p_{ij}) | | Jolly–Seber | |
Parameter	Parameter value†	% Bias‡	% CV§	% Bias	% CV§	% Bias	% CV§	% Bias	% CV§
p_2^*	0.64	0	6.5	0	6.5	−6.7	6.0	−19	11.2
p_3^*	0.64	0	6.5	0	6.5	−6.7	6.0	−19	11.2
ϕ_1	0.60	0‖	13.4	−1.5	9.5	−8.2	8.1	−1.5	9.5
ϕ_2	0.60	0‖	16.9	−2.0	10.6	−7.0	8.4	−1.9	10.6
ϕ_3	0.60	0‖	18.9	¶		−16.0	11.3	¶	
γ_2''	0.20	0‖	63.9	−6.0	55.8	NA#		NA	
γ_3''	0.20	0‖	69.5	††	††	NA		NA	
γ_3'	0.30	0‖	207	††	††	NA		NA	

† Values of parameters not estimated are $p_1^* = p_4^* = 0.64$; $\phi_3 = 0.60$; $\gamma_4'' = 0.20$; $\gamma_4' = 0.30$.
‡ Here, 0% bias implies unbiased to at least the fifth decimal place.
§ Defined as 1 SE/estimate × 100.
‖ Based on setting $\gamma_4'' = \gamma_3''$ and $\gamma_4' = \gamma_3'$.
¶ Cannot estimate.
# Not applicable.
†† $\hat{\gamma}_3 = 0.1881$ (CV = 56%).

ad hoc estimators, we have focused on potential violations of open-model assumptions and consequent bias of $\hat{p}_i^{js}$ as an estimator for p_i^0 (Eq. 5) or of $\hat{\phi}_i^{js}$ (Eq. 11). However, it is also possible for assumptions underlying closed-population models and, thus, model $(\phi_i, p_{ij}, \gamma_i)$, to be violated, yielding biased estimates of p_{ij} or $M_{i+\Delta}^{(R)}$. For example, assume that animals immigrate to the study area between secondary samples within a primary period. This will yield a negative bias in $\hat{p}_{ij}$ and $\hat{p}_i^*$ from $(\phi_i, p_{ij}, \gamma_i)$, which also produces a negative bias in $\hat{\gamma}_i$.

Because Eqs. 5, 9, and 11 are ratio estimators, they are biased even when underlying assumptions are met. This bias is a function of their component estimators and the variances of those components (Seber 1982: 7). From experience with estimators of similar structure, we anticipate that this bias will be small. Nevertheless, we are investigating this question and could adjust the estimators for bias if necessary.

Markovian emigration

We can also modify the models of Kendall et al. (1995) to account for Markovian emigration, where the probability of being outside the study area in primary period i is dependent on whether or not the animal was in the study area in period $i - 1$. Specifically, we can modify model (ϕ_i, p_{ij}) in a fashion similar to that of the previous section to create model $(\phi_i, p_{ij}, \gamma_i')$, combining L_2 with a new likelihood for the primary periods, L_{1b}. We illustrate L_{1b} by including selected expected cell frequencies:

$$E(m_{12}) = R_1\phi_1(1 - \gamma_2'')p_2^*$$

$$E(m_{13}) = R_1\phi_1\phi_2p_3^*$$

$$\times [\gamma_2''(1 - \gamma_3') + (1 - \gamma_2'')(1 - p_2^*)(1 - \gamma_3'')]$$

$$E(m_{23}) = R_2\phi_2(1 - \gamma_3'')p_3^*. \tag{13}$$

In $E(m_{13})$, the expression in brackets is split into one term for animals outside the study area in primary period 2 and another term for those in the study area but not captured in period 2.

As the number of primary periods becomes larger, cell probabilities become more complex. The appendix contains a fuller treatment of this model for an arbitrary number of primary periods, using matrix notation.

Estimation under this model requires additional constraints, such as $\gamma_k'' = \gamma_{k-1}''$, $\gamma_k' = \gamma_{k-1}'$. With this constraint, γ_i'' is identifiable for $i = 2, 3, \ldots, k$, and γ_i' is identifiable for $i = 3, 4, \ldots, k$. γ_2' is not identifiable because there are no marked animals in the superpopulation in primary period 2 that were not in the sampled area in period 1.

To illustrate estimation under Markovian emigration, Table 2 contains large-sample properties of full-likelihood estimators using the $(\phi_i, p_{ij}, \gamma_i')$, $(\phi_i, p_{ij}, \gamma_i)$, (ϕ_i, p_{ij}), and JS models for one set of parameter values where Markovian emigration exists, with $\gamma_i'' < \gamma_i'$. All estimators under model $(\phi_i, p_{ij}, \gamma_i')$ were unbiased. This was expected because we had also set the actual parameters $\gamma_4'' = \gamma_3''$ and $\gamma_4' = \gamma_3'$, but we feel that this is a reasonable strategy in general. Precision of the $\hat{\gamma}_i''$ and $\hat{\gamma}_i'$ was poor. This was especially true for $\hat{\gamma}_3'$, because animals present in period 3 and known to be temporary emigrants in period 4 cannot be observed directly.

We computed expected values for the same set of estimators described in Table 2, this time setting $\gamma_i'' > \gamma_i'$ (Table 3). Comparing Table 3 with Table 2, estimators for ϕ_i, γ_i'', and γ_i' under model $(\phi_i, p_{ij}, \gamma_i')$ were uniformly more precise when $\gamma_i'' > \gamma_i'$. This was expected, because $\gamma_i'' > \gamma_i'$ implies that more animals outside the study area in period i will be present and available for capture in subsequent periods than when $\gamma_i'' < \gamma_i'$. Bias of estimators under misspecified models $(\phi_i, p_{ij}, \gamma_i)$, (ϕ_i, p_{ij}), and JS was greater when $\gamma_i'' > \gamma_i'$, but for $\hat{\gamma}_i$ under model $(\phi_i, p_{ij}, \gamma_i)$, and for ϕ_i under the $(\phi_i, p_{ij}, \gamma_i)$ and JS models,

TABLE 3. Comparison of large-sample properties of conditional maximum-likelihood estimators from $(\phi_i, p_{ij}, \gamma_i')$, $(\phi_i, p_{ij}, \gamma_i)$, (ϕ_i, p_{ij}), and Jolly–Seber models, where $(\phi_i, p_{ij}, \gamma_i')$ is the true model and $\gamma_i'' > \gamma_i'$. Based on $E(N_i^0) = 500$ for all four primary periods, each consisting of two secondary periods.

Parameter	Parameter value†	$(\phi_i, p_{ij}, \gamma_i')$ % Bias‡	$(\phi_i, p_{ij}, \gamma_i')$ % CV§	$(\phi_i, p_{ij}, \gamma_i)$ % Bias	$(\phi_i, p_{ij}, \gamma_i)$ % CV§	(ϕ_i, p_{ij}) % Bias	(ϕ_i, p_{ij}) % CV§	Jolly–Seber % Bias	Jolly–Seber % CV§
p_2^*	0.64	0	6.9	0	6.9	−11.1	6.8	−31	13.7
p_3^*	0.64	0	6.9	0	6.9	−11.2	6.9	−31	13.6
ϕ_1	0.60	0‖	12.4	2.1	11.1	−10.7	9.2	2.1	11.1
ϕ_2	0.60	0‖	14.6	3.1	12.5	−7.4	9.3	3.1	12.5
ϕ_3	0.60	0‖	16.7	¶		−23.0	12.3	¶	
γ_2''	0.30	0‖	37.7	4.8	33.5	NA#		NA	
γ_3''	0.30	0‖	34.9	††		NA		NA	
γ_3'	0.20	0‖	194	††		NA		NA	

† Values of parameters not estimated are $p_1^* = p_4^* = 0.64$; $\phi_3 = 0.60$; $\gamma_4'' = 0.30$; $\gamma_4' = 0.20$.
‡ Here, 0% bias implies unbiased to at least the fifth decimal place.
§ Defined as 1 SE/estimate × 100.
‖ Based on setting $\gamma_4'' = \gamma_3''$ and $\gamma_4' = \gamma_3'$.
¶ Cannot estimate.
# Not applicable.
†† $\hat{\gamma}_3 = 0.3148$ (CV = 33%).

it was positive. Precision of estimators under misspecified models was poorer when $\gamma_i'' > \gamma_i'$.

EXAMPLE ANALYSES

Peromyscus leucopus

White-footed mice, *Peromyscus leucopus*, were trapped approximately monthly from 1978 through 1983 in lowland hardwood forest at Patuxent Wildlife Research Center, Maryland, on two trapping grids, each a 14 × 14 checkerboard of trapping stations. Adjacent stations in each row or column were separated by ≈15.2 m (50 feet). A single Sherman live trap containing cotton and corn was placed at each station. Traps were baited and set one evening, run the next day and reset, run the following day and closed. Animals were marked with individually coded monel fingerling tags placed in their ears. Animals with entirely gray pelage (young animals) were excluded from analyses, and males and females were pooled for analyses.

Capture probability estimates from standard open-capture–recapture models (e.g., JS) tended to be high (typically >0.6) for both grids, except during relatively cold periods (e.g., overnight temperatures <0°C), when capture probability estimates frequently declined to <0.3. With respect to capture–recapture modeling, two scenarios were possible during these cold periods: (1) all animals could have exhibited reduced activity and, hence, lower capture probabilities, and (2) some animals could have stayed belowground and in dens (perhaps entering torpor), becoming temporary emigrants. Indeed, torpor in *Peromyscus* is frequently associated with cold temperatures and short day length, shows substantial variation among individuals within populations, and has been cited as a reason for poor trappability (Hill 1983). In this example analysis, we use the robust design to distinguish between these two pos-

sibilities and provide a means of estimating relevant parameters, regardless of which scenario holds.

We selected capture–recapture data from September 1980 through March 1981 (Table 4), an interval that included three sampling periods of low capture probabilities during winter months. For grids 1 and 2, respectively, JS estimates of capture probability (from program JOLLY, Pollock et al. 1990) were 0.93 and 1.00 (2-d trapping period beginning 28 September), 0.82 and 0.87 (4 November), 0.27 and 0.14 (6 December), 0.11 and 0.11 (3 January), 0.29 and 0.24 (31 January), 0.77 and 0.79 (1 March), and 0.81 and 0.74 (28 March). We analyzed both data sets (grids 1 and 2) using the full-likelihood approach previously described, with several different models. Following the model nomenclature described earlier, we fit models (ϕ_i, p_{ij}), $(\phi_i, p_{ij}, \gamma_i)$, and $(\phi_i, p_{ij}, \gamma_i')$. We did not conduct an exhaustive search of possible restrictive models, but we did fit models with survival and emigration parameters constant over time, denoted by the absence of an i subscript in the model definition notation.

We followed the approach recommended by Burnham and Anderson (1992) and Lebreton et al. (1992), selecting the model with the lowest Akaike's Information Criterion (AIC) as the most useful model for each data set. Low-AIC models are parsimonious, in that they fit the data reasonably well with a relatively small number of parameters. We computed likelihood ratio (LR) test statistics between competing models as a means of testing hypotheses of ecological interest (Lebreton et al. 1992). Such LR tests are appropriate only for nested models where the null hypothesis model is a special case of the alternative hypothesis model, and can be obtained by constraining parameters of the more general, alternative hypothesis model. Finally, we report Pearson χ^2 goodness-of-fit (GOF) test statistics using the cell-pool-

TABLE 4. Capture–recapture statistics for *Peromyscus leucopus* caught at Patuxent Wildlife Research Center, Maryland, September 1980–March 1981. Numbers in parentheses indicate the frequencies of the three observable two-period capture histories (11, 10, 01) within each primary sampling period, i, for new captures, u_i, and recaptures, m_{hi}.

Sampling date	Sample period (h)	Number released (R_h)	Number unmarked (u_h)	Number of R_h next captured at period i, m_{hi}					
				$i = 2$	$i = 3$	$i = 4$	$i = 5$	$i = 6$	$i = 7$
Grid 1									
28 Sep 1980	1	22	22 (18, 0, 4)	15 (8, 1, 6)	0	0	0	0	0
4 Nov 1980	2	16	1 (0, 0, 1)		3 (1, 1, 1)	0	0	6 (5, 1, 0)	0
6 Dec 1980	3	7	4 (1, 0, 3)			2 (0, 0, 1)†	3 (2, 0, 1)	2 (1, 1, 0)	0
3 Jan 1981	4	5†	8 (0, 1, 7)				2 (0, 0, 2)	2 (2, 0, 0)	0
31 Jan 1981	5	9†	8 (1, 1, 6)					6 (5, 1, 0)	2 (1, 0, 1)
1 Mar 1981	6	25	9 (5, 3, 1)						18 (7, 7, 4)
28 Mar 1981	7		1 (0, 1, 0)						
Grid 2									
28 Sep 1980	1	20	20 (14, 2, 4)	10 (2, 1, 7)	0	0	0	1 (1, 0, 0)	0
4 Nov 1980	2	15	5 (1, 1, 3)		2 (0, 0, 2)	2 (0, 0, 2)	0	4 (2, 2, 0)	1 (1, 0, 0)
6 Dec 1980	3	6-	4 (3, 0, 1)			0	2 (1, 0, 1)	1 (0, 1, 0)	1 (0, 1, 0)
3 Jan 1981	4	6	4 (0, 0, 4)				2 (0, 1, 1)	2 (1, 1, 0)	0
31 Jan 1981	5	7	3 (2, 1, 0)					6 (4, 2, 0)	0
1 Mar 1981	6	20	6 (2, 4, 0)						13 (10, 1, 2)

† Some animals were experimentally removed from grid 1 during periods 4 and 5. Because of these removals, $R_h < u_h + \sum_{k=1}^{h-1} m_{kh}$ for $i = 4, 5$. If an animal was removed during the 1st d of trapping, then it was not used in the closed-model estimation.

ing algorithm of SURVIV. All computations were carried out by program RDSURVIV. In some cases, we encountered the problem that the estimated variance–covariance matrix was not positive-definite. In these cases, we did not use the computed standard errors, but instead obtained standard errors using a parametric bootstrap approach (Buckland 1980, Buckland and Garthwaite 1991), simulating data (200 simulations) based on the point estimates from the original data, and obtaining the standard errors empirically based on the replicate point estimates from the simulations.

In the case where the completely random emigration model appeared to be appropriate, we also computed estimates of temporary emigration using the ad hoc estimators of Eqs. 5 and 6. The capture probability estimates from closed and open models came from model M_t (the Lincoln–Petersen estimator, because $l = 2$; Seber 1982: 60) and the JS model, respectively.

The low-AIC models were (ϕ, p_{ij}, γ_i') and (ϕ, p_{ij}, γ_i) for grids 1 and 2, respectively (Table 5), and both models fit the data adequately (GOF $\chi^2 = 13.4$, df $= 12$, $P = 0.34$; $\chi^2 = 16.3$, df $= 15$, $P = 0.36$, respectively). The LR tests indicated rejection of the models with no temporary emigration parameters (Table 6), providing evidence that some animals were temporarily unavail-

able to capture efforts. The LR tests provided evidence of Markovian emigration on grid 1 but not grid 2 (Table 6). We are not certain whether the behaviors associated with temporary emigration were really different for the grids, but we will present estimates for grid 1 using the Markovian emigration model, and for grid 2 using the completely random emigration model as indicated by these tests and the AIC model selection criterion. There was no strong evidence of temporal variation in monthly survival on either grid (Table 6), and the low-AIC models for both grids had only single survival parameters (Table 5). However, there was evidence of temporal variation in temporary emigration probabilities, as we predicted based on the temporal variation in open-model estimates of capture probability.

Estimated probabilities of temporary emigration for grid 1 animals (Table 7) were small for sample periods 2 and 6–7 for all animals, regardless of emigration status in the previous period, under both the general Markovian model (ϕ_i, p_{ij}, γ_i') and the low-AIC model (ϕ, p_{ij}, γ_i'). These low values were expected, based on the high JS estimates of capture probability for those periods. Estimated probabilities of temporary emigration were high for periods 3–5 for animals that were temporary emigrants in the previous period under both

TABLE 5. Akaike's Information Criterion (AIC) and goodness-of-fit statistics for selected models fit to *Peromyscus leucopus* capture–recapture data, grids 1 and 2, Patuxent Wildlife Research Center, Maryland, September 1980–March 1981.

Emigration descriptor	Model	No. parameters	Grid	AIC
No temporary emigration	(ϕ, p_{ij})	20	1	145.82
			2	154.40
	(ϕ, p_{ij})	15	1	144.95
			2	149.39
Random temporary emigration	$(\phi_i, p_{ij}, \gamma_i)$	25	1	146.17
			2	143.93
	(ϕ_i, p_{ij}, γ)	21	1	144.89
			2	150.75
	(ϕ, p_{ij}, γ_i)	21	1	146.42
			2	138.96
	(ϕ, p_{ij}, γ)	16	1	144.32
			2	144.63
Markovian temporary emigration	$(\phi_i, p_{ij}, \gamma_i')$	29	1	143.04
			2	146.85
	$(\phi_i, p_{ij}, \gamma')$	22	1	146.61
			2	150.38
	$(\phi, p_{ij}, \gamma_i')$	24	1	141.39
			2	141.33
	(ϕ, p_{ij}, γ')	17	1	146.03
			2	145.09

models (Table 7). Estimates of temporary emigration for animals that were not temporary emigrants in the previous time period varied substantially over periods 3–5, but the pattern of variation was consistent for the two models (Table 7). The survival estimate under the low-AIC model (0.85) was similar to the mean of the monthly survival estimates under the more general model (0.86). Standard errors for the temporary emigration probability estimates $(\hat{\gamma}_i', \hat{\gamma}_i'')$ were large under both models. Such poor precision will likely be common for small-to-medium sample sizes, especially when time-specific parameters are needed.

Estimated probabilities of temporary emigration for grid 2 animals were relatively small for periods 2 and 6–7, and large for periods 3–5, as expected (Table 8). Estimates of temporary emigration based on the ad hoc estimators (Eqs. 5 and 6) matched estimates under the

general model $(\phi_i, p_{ij}, \gamma_i)$ fairly well. Estimated monthly survival probability (0.81) under the low-AIC model (ϕ, p_{ij}, γ_i) was very similar to the mean of the estimates under the general model (0.80). Precision of the $\hat{\gamma}_i$ appeared to be somewhat better for grid 2 than for grid 1, as expected because of the additional parameters and model complexity required by the Markovian model used for grid 1.

Microtus pennsylvanicus

Meadow voles, *Microtus pennsylvanicus*, were trapped in old-field habitat at Patuxent Wildlife Research Center, Maryland, during 1981 (Nichols et al. 1984b). The grid was a 10 × 10 square of trapping stations, with adjacent stations within each row or column separated by ≈ 7.6 m (25 feet). A single modified Fitch live trap (Rose 1973) containing hay and corn

TABLE 6. Selected likelihood-ratio test statistics for *Peromyscus leucopus* capture–recapture data, grids 1 and 2, Patuxent Wildlife Research Center, September 1980–March 1981.

Restricted model (H_0)	General model (H_a)	Grid	χ^2	df	P	Ecological hypothesis tested
(ϕ, p_{ij})	(ϕ, p_{ij}, γ_i)	1	10.5	6	0.10	No temporary emigration vs. random
		2	22.4	6	<0.01	temporary emigration
(ϕ, p_{ij})	$(\phi, p_{ij}, \gamma_i')$	1	21.6	9	0.01	No temporary emigration vs.
		2	26.1	9	<0.01	Markovian temporary emigration
(ϕ, p_{ij}, γ_i)	$(\phi, p_{ij}, \gamma_i')$	1	11.0	3	0.01	Random temporary emigration vs.
		2	3.6	3	0.31	Markovian temporary emigration
(ϕ, p_{ij}, γ')	$(\phi, p_{ij}, \gamma_i')$	1	18.6	7	<0.01	Constant temporary emigration vs.
(ϕ, p_{ij}, γ)	(ϕ, p_{ij}, γ_i)	2	15.7	5	<0.01	time-specific temporary emigration
$(\phi, p_{ij}, \gamma_i')$	$(\phi_i, p_{ij}, \gamma_i')$	1	8.4	5	0.14	Constant monthly survival vs.
(ϕ, p_{ij}, γ_i)	$(\phi_i, p_{ij}, \gamma_i)$	2	3.0	4	0.55	time-specific survival

TABLE 7. Estimated rates of survival and temporary emigration for *Peromyscus leucopus* on grid 1 under two models of Markovian emigration.

Sample period	Model $(\phi_i, p_{ij}, \gamma_i')$†						Model $(\phi_i, p_{ij}, \gamma_i')$†					
	Survival		Temporary emigration				Survival		Temporary emigration			
	$\hat{\phi}$	$\widehat{SE}(\hat{\phi})$	$\hat{\gamma}_i''$	$\widehat{SE}(\hat{\gamma}_i'')$	$\hat{\gamma}_i'$	$\widehat{SE}(\hat{\gamma}_i')$	$\hat{\phi}_i$	$\widehat{SE}(\hat{\phi}_i)$	$\hat{\gamma}_i''$	$\widehat{SE}(\hat{\gamma}_i'')$	$\hat{\gamma}_i'$	$\widehat{SE}(\hat{\gamma}_i')$
1	0.85	0.036					0.69	0.098				
2			0.03	0.094			0.62	0.179	<0.01	0.067		
3			0.76	0.138	1.00	1.036	1.00	0.087	0.68	0.170	0.55	0.256
4			<0.01	0.502	1.00	0.156	0.94	0.084	<0.01	0.324	1.00	0.243
5			0.38	0.310	1.00	0.088	0.92	0.082	0.39	0.280	1.00	0.202
6			0.14	0.104	<0.01	0.048	1.00	0.104	0.19	0.107	<0.01	0.064

† Standard errors are model-based and taken from RDSURVIV.
‡ Variance–covariance matrix as computed by RDSURVIV was not positive-definite, so standard errors were estimated using a parametric bootstrap approach (200 simulations).

was placed at each station. Traps were set one evening, run the next morning, and locked open until afternoon, when they were reset. This schedule continued for five consecutive days beginning on 27 June (period 1), 1 August (period 2), 29 August (period 3), and 3 October (period 4). Animals were weighed and marked with individually coded monel fingerling tags placed in their ears. For this example, we use only males with body mass >21 g.

The data were first analyzed using the full-likelihood approach with program RDSURVIV, using time-dependent model M_t (see Otis et al. 1978) for the closed portion of the model. We suspected that the full-likelihood models would not fit the data, because previous analyses provided strong evidence of heterogeneous capture probabilities (Nichols et al. 1984b). When the model did not fit the daily capture–recapture data ($l = 5$ d), we reduced the data to a two-sample problem ($l = 2$ d) by denoting the first 2 d of trapping as period 1 and the second 3 d of trapping as period 2 (see Menkins and Anderson 1988).

The goodness-of-fit statistics to full-likelihood models based on two secondary samples per period (Table 9) were $\chi^2 = 39.1$, df $= 9$, $P < 0.01$, for the general model with no temporary emigration (ϕ_i, p_{ij}); $\chi^2 = 39.0$, df $=$ 8, $P < 0.01$, for the general model with completely random emigration $(\phi_i, p_{ij}, \gamma_i)$; and $\chi^2 = 39.0$, df $= 7$, $P < 0.01$, for the general model with Markovian emigration $(\phi_i, p_{ij}, \gamma_i')$. Likelihood ratio tests among these three models provided no evidence ($P > 0.72$) of any need for the temporary emigration models, and the model with no temporary emigration had the lowest AIC. Estimates of temporary emigration under models $(\phi_i, p_{ij}, \gamma_i)$ and $(\phi_i, p_{ij}, \gamma_i')$ were small (<0.08; see Table 10).

Because of the lack of fit of the full-likelihood models, we hesitated to draw inferences about temporary emigration based on their associated AIC values, LR tests, and estimates. We thus computed ad hoc estimates using heterogeneity models for closed populations in conjunction with estimators in Eqs. 9 and 10. Estimates of numbers of marked animals were computed using the jackknife estimator (Burnham and Overton 1978) for model M_h for all samples except period 2, when a raccoon disturbed traps in the final 2 d of trapping (Nichols et al. 1984b), leading to small capture probabilities. We had to use model M_{th} (Chao et al. 1992) for data from primary period 2. Estimates were computed from capture frequency data (Table 9) using program CAPTURE (Rexstad and Burnham 1991). Both estimates of temporary emigration were negative,

TABLE 8. Estimated rates of survival and temporary emigration for *Peromyscus leucopus* on grid 2 under models of completely random emigration.

Sample period	Model (ϕ, p_{ij}, γ_i)†				Model $(\phi_i, p_{ij}, \gamma_i)$†				Ad hoc estimator‡	
	Survival		Temp. emigration		Survival		Temp. emigration			
	$\hat{\phi}$	$\widehat{SE}(\hat{\phi})$	$\hat{\gamma}_i$	$\widehat{SE}(\hat{\gamma}_i)$	$\hat{\phi}_i$	$\widehat{SE}(\hat{\phi}_i)$	$\hat{\gamma}_i$	$\widehat{SE}(\hat{\gamma}_i)$	$\hat{\gamma}_i$	$\widehat{SE}(\hat{\gamma}_i)$
1	0.81	0.045			0.60	0.144				
2			<0.01	0.149	0.82	0.173	<0.01	0.158	<0.01	0.313
3			0.87	0.086	0.94	0.146	0.86	0.094	0.85	0.108
4			0.85	0.162	0.75	0.172	0.71	0.261	0.88	0.090
5			0.72	0.185	0.91	0.109	0.70	0.161	0.70	0.143
6			0.16	0.110			0.18	0.112	0.18	0.112
7			0.16	0.126						

† Variance–covariance matrix, as computed by RDSURVIV, was not positive-definite, so standard errors were estimated using a parametric bootstrap approach (200 simulations).
‡ Capture probability estimates from closed (Lincoln–Petersen) and open (Jolly–Seber) models were used in conjunction with estimators Eqs. 5 and 6.

TABLE 9. Capture–recapture statistics for *Microtus pennsylvanicus* caught at Patuxent Wildlife Research Center, June 1981–October 1981. Numbers in parentheses indicate the frequencies of the three observable two-period capture histories (11, 10, 01)† within each primary sampling period, i, for new captures, u_i, and recaptures, m_{hi}. Also presented are the numbers of marked animals released at primary period h and recaptured at primary period i exactly 1, 2, ..., 5 times (these are the frequencies used to estimate $M_i^{(R_h)}$).

Sampling date	Sample period (h)	Number released (R_h)	Unmarked (u_h)	Number of R_h next recaptured at period i (m_{hi})			Capture frequencies used to estimate $M_i^{(R_h)}$	
				$i = 2$	3	4	$i = h + 1$	$h + 2$
27 Jun	1	49	49 (38, 4, 7)	40 (33, 7, 0)	1 (1, 0, 0)	0	(3, 14, 13, 10, 0)	(5, 2, 4, 4, 4)
1 Aug	2	67	27 (10, 6, 11)		31 (19, 7, 5)	3 (1, 2, 0)	(11, 4, 6, 5, 5)	(3, 8, 1, 5, 8)
29 Aug	3	45	13 (6, 3, 4)			29 (23, 3, 3)	(2, 7, 4, 7, 9)	
3 Oct	4		20 (5, 5, 10)					

† The five days of trapping were pooled into periods 1 (days 1–2) and 2 (days 3–5).

and the associated approximate 95% confidence intervals were large and included 0 (Table 10).

We also computed estimates based on Eqs. 11 and 12, under the assumption that the JS survival rate estimator is not badly biased by heterogeneous capture probabilities (e.g., see Carothers 1973, Pollock et al. 1990). One estimate of temporary emigration was positive, the other was negative, and both 95% confidence intervals included 0 (Table 10).

We conclude that the rate of temporary emigration was very small during the two periods for which it could be estimated, an inference that we had predicted based on the large JS estimates of capture probability for these periods: $\hat{p}_2^{js} = 0.95$, ($\widehat{\text{SE}} = 0.045$); $\hat{p}_3^{js} = 0.87$, ($\widehat{\text{SE}} = 0.068$). We also note that the estimated standard errors of Table 10 provide an indication of the loss in precision associated with the use of closed models permitting heterogeneity of capture probability (in this case, M_h and M_{th}).

DISCUSSION

We have shown that problems caused by temporary emigration for existing open-population, capture–recapture model estimators depend on the specific temporary emigration model (completely random or Markovian) and on the estimators in question. Under a

model of completely random emigration, the Jolly–Seber (JS) survival estimator is unbiased (Burnham 1993), although the precision of survival estimates is reduced. Other JS estimators ($\hat{p}_i^{js}$, $\hat{M}_i^{js}$, $\hat{N}_i^{js}$, $\hat{B}_i^{js}$) yield estimates that are biased with respect to the animals exposed to sampling efforts at period i, but unbiased with respect to the superpopulation inhabiting the general area. When the primary interest of the investigator is in survival rate or in parameters associated with the superpopulation, JS estimators can be used in the presence of completely random temporary emigration, in lieu of the estimators reported here.

When the full-likelihood approach of Kendall et al. (1995) (Eq. 2) is used to analyze capture–recapture data collected under the robust design, completely random temporary emigration will produce biased estimates, because the capture probability parameters of the closed and open portions of the likelihood no longer reflect the same underlying quantity. Capture probability estimates are negatively biased in this situation, as were survival rate estimates in our numerical examples.

When Markovian emigration occurs, where the probability of temporary emigration in period i depends on emigration status in period $i - 1$, both JS and full-likelihood estimates based on Eq. 2 are biased. When the probability of being a temporary emigrant in sam-

TABLE 10. Estimated rates of survival and temporary emigration for *Microtus pennsylvanicus* caught at Patuxent Wildlife Research Center, June–October 1981, under a general model of completely random emigration.

Sample period	Model (ϕ_i, p_{ij}, γ_i)†				Ad hoc estimators‡			
	Survival		Temp. emigration		Eqs. 8–9		Eqs. 10–11	
	$\hat{\phi}_i$	$\widehat{\text{SE}}(\hat{\phi}_i)$	$\hat{\gamma}_i$	$\widehat{\text{SE}}(\hat{\gamma}_i)$	$\hat{\gamma}_i$	$\widehat{\text{SE}}(\hat{\gamma}_i)$	$\hat{\gamma}_i$	$\widehat{\text{SE}}(\hat{\gamma}_i)$
1	0.86	0.058						
2	0.53	0.066	<0.01	0.052	<0.01	0.280	0.02	0.077
3			0.06	0.080	<0.01	0.216	<0.01	0.242

† Model goodness-of-fit statistic: $\chi^2 = 39.0$, df $= 8$, $P < 0.01$.

‡ Estimates computed using the following closed- and open-model estimates (standard errors): $\hat{M}_2^{(R_1)} = 41$ (1.71); $\hat{M}_3^{(R_1)} = 21$ (3.17); $\hat{M}_3^{(R_2)} = 44$ (6.68); $\hat{M}_4^{(R_2)} = 27$ (2.35); $\hat{M}_4^{(R_3)} = 32$ (2.07); $\hat{\phi}_1^{js} = 0.86$ (0.058); $\hat{\phi}_2^{js} = 0.53$ (0.066).

pling period i was higher for animals that were emigrants in period $i - 1$ than for animals that were in the sampled area in period $i - 1$, then survival and capture probability estimates in our numerical examples were negatively biased for both JS and full-likelihood estimators. We expect this pattern of Markovian dependence ($\gamma_i'' < \gamma_i'$) to be most common. Under the opposite pattern ($\gamma_i'' > \gamma_i'$), JS capture probability estimates were negatively biased, but survival estimates were positively biased.

Thus, temporary emigration causes problems in the analysis of capture–recapture data, leading to biased estimates of most quantities of interest. We recommend use of the models developed here as a reasonable method to test for the presence of temporary emigration, to distinguish between completely random and Markovian models of temporary emigration, and to estimate probabilities of capture, survival, and temporary emigration under these models. Even in the absence of temporary emigration, the full-likelihood approach leads to efficient estimation of survival and capture probabilities using robust design data (Kendall et al. 1995). We further recommend the use of program RDSURVIV to analyze capture–recapture data collected under the robust design.

A full-likelihood approach to estimation is not currently possible for situations in which animals exhibit sufficient heterogeneity in capture probabilities that closed-population models incorporating such heterogeneity (e.g., Otis et al. 1978) are needed to adequately model the data. For such situations, the probability of temporary emigration can be estimated under the completely random emigration model using the ad hoc estimators presented in Eqs. 9–12. We have not studied the detailed properties of these two ad hoc estimators. We suspect that Eq. 11 may exhibit larger bias, but speculate that it will typically have a smaller mean squared error than Eq. 9. We have not yet been able to develop any ad hoc estimators for the situation of heterogeneous capture probabilities under a Markovian model.

Our approaches to estimating temporary emigration require two assumptions that deserve emphasis. First, the studied population must be closed to gains and losses (including emigration) over the secondary periods within each primary period. Any movement in or out of the study area is assumed to occur only between primary sampling periods. It should be possible to relax this assumption somewhat by permitting certain forms of trap response during secondary sampling periods and using a trap-response full-likelihood approach to estimate conditional (on presence in the study area) first-capture probabilities, p_i^*. Second, we assume equal survival probabilities for animals that are in and out of the study area during any primary period. Certainly, we can envision ecologically plausible scenarios under which animals in and out of the sampled area would be exposed to different mortality sources and exhibit different survival probabilities. This assumption could be tested directly with a multistate modeling approach (Brownie et al. 1993), but such a test would require sampling efforts outside the primary sam-

ple area. The effects of violations of this assumption merit further attention.

There is an additional implicit assumption when estimating N_i or B_i under model (ϕ_i, p_{ij}, γ_i), or N_i^0 or B_i^0 under the JS model. Recruits that enter the superpopulation between periods are assumed to be present in the sampled area with the same probability as the rest of the superpopulation, $1 - \gamma_i$ (Barker 1997).

A limitation of our general model of Markovian emigration ($\phi_i, p_{ij}, \gamma_i'$) is that all parameters are not identifiable. Instead, constraints are required in order to use this model for estimation. Natural constraints involve assuming constancy of some parameters over time (e.g., Sandland and Kirkwood 1981). We believe that a very general and reasonable constraint that permits identifiability is to set the probabilities for the penultimate and final sampling periods equal ($\gamma_{k-1}' = \gamma_k'$ and $\gamma_{k-1}'' = \gamma_k''$).

Our examples provided some insight into the potential utility of these models, and results of these analyses merit some discussion. We would not characterize the *Peromyscus leucopus* data as "good" from the perspective of capture–recapture analysis (i.e., numbers of captures and recaptures were not large and there were only two secondary capture periods per primary period). Nevertheless, we selected these data because we had a priori reason to suspect the presence of temporary emigration during certain sampling periods.

Even with these sparse data, the tests for temporary emigration provided clear evidence of its existence. The test for Markovian dependence of temporary emigration probabilities provided strong evidence of such dependence for grid 1, but no evidence for grid 2. The estimates of temporary emigration probabilities for grid 1 were imprecise, but were generally high for the cold-weather sample periods and low for the other periods. The estimated probability of being a temporary emigrant in period i was very high for all animals that were temporary emigrants in period $i - 1$, for all cold-sample periods ($i = 3$–5). Estimates of temporary emigration probabilities on grid 2 were also high ($\hat{\gamma}_i > 0.70$) for periods 3–5. The ad hoc estimator of Eqs. 5 and 6 provided estimates of temporary emigration that were generally similar to those based on the full-likelihood approach.

The *Microtus pennsylvanicus* trapping was carried out using the robust design on a dense population, producing a good data set from the perspective of a capture–recapture analyst. Analysis using the full-likelihood models of RDSURVIV provided no evidence of temporary emigration, and indicated that model (ϕ_i, p_{ij}) of Kendall et al. (1995) was the most appropriate of the three general models tested. However, all three models fit these data poorly, so we were not confident in the results. The two ad hoc estimators computed using estimates from the heterogeneity models of program CAPTURE produced small estimates of temporary emigration with approximate 95% confidence intervals covering 0, a result consistent with the model-based inferences.

The ad hoc estimates of temporary emigration were negative in some cases, and we suspect that this will be common in situations where the true probability of temporary emigration approaches 0, due to sampling variation. Negative estimates can also occur if the closure assumption is violated within primary periods, where there is an influx of animals between subsamples (i.e., between secondary periods).

The absence of evidence of temporary emigration for this *M. pennsylvanicus* population is not surprising, especially considering the very high capture probability estimates based on open models. High capture probability estimates from open models simply do not admit the possibility of much temporary emigration. Indeed, in cases where open models fit capture–recapture data adequately, the maximum possible probability of temporary emigration can be approximated as $1 - \hat{p}_i$.

For *M. pennsylvanicus,* the phenomenon of temporary emigration is interpreted strictly in terms of local movement. For *P. leucopus,* we interpret temporary emigration not as two-dimensional movement off the trapping grid, but as movement below ground (into burrows and dens) and as inactivity (perhaps including torpor). The association of this temporary emigration with cold temperatures permits specific modeling of this relationship (e.g., using ultrastructural models; Lebreton et al. 1992), and we plan to model γ_t for these populations as a function of covariates such as temperature.

Both of these examples involved small mammals trapped with relatively short intervals between primary trapping sessions. We also believe that the ability to estimate temporary emigration will be useful in studies of breeding populations in which primary periods are separated by 1 yr. For example, it is thought to be fairly common in bird populations for individuals to return to specific breeding grounds if they are breeders in a particular year, but to go elsewhere if they do not breed. Indeed, this scenario forms the ecological basis for recent work on estimating age-specific breeding probabilities (Clobert et al. 1990, 1994). We believe that the models presented here can be useful in estimating breeding probabilities for bird species in which these probabilities are thought to vary from year to year, even among adults.

Capture–recapture studies of amphibians at breeding ponds have also been used to draw inferences about breeding probabilities and skipped breeding attempts (Husting 1965, Gill 1985, 1987). The test of Balser (1981) could be used to detect temporary emigration (skipped breeding attempts) (Nichols et al. 1987) occurring under the Markovian model, but not under the completely random emigration model. We recommend use of the robust design for such amphibian studies and suggest that the models proposed here will be useful for testing hypotheses about skipped breeding and estimating breeding probabilities.

We view these temporary emigration models as com-

plementing multistate capture–recapture models (Brownie et al. 1993) as a means of studying breeding probabilities and costs of reproduction. Multistate models are useful in situations where (1) both breeding and nonbreeding animals are available for capture/observation on the same study area (e.g., on the breeding grounds), and (2) each captured/observed animal can be designated as a breeder or nonbreeder. Multistate models permit estimation of the proportion of animals in each of the two reproductive states, as well as state-specific survival probabilities and probabilities of breeding the next season (Nichols et al. 1994, Nichols and Kendall 1995). Temporary emigration models will be useful in situations where animals in one of the reproductive states (typically nonbreeders) are unavailable for capture/observation. Temporary emigration models offer the potential to model breeding probabilities using environmental covariates with ultrastructural models. When viewed in the context of breeding probabilities, the test of Markovian vs. completely random temporary emigration is directly relevant to hypotheses about reproductive costs (e.g., does breeding in year i reduce the probability of breeding in year i + 1). However, the hypothesis of a reproductive cost in survival cannot be addressed using temporary emigration models, which require the assumption of equal survival of breeding and nonbreeding animals. When robust design data are not available for species that cannot be captured/observed as nonbreeders, then the approaches of Clobert et al. (1990, 1994) and Viallefont et al. (1995) to estimating breeding probabilities and testing hypotheses about reproductive costs should be considered.

Finally, we emphasize that we have used single-age, single-state models to illustrate our approach, but that there should be no limitation (other than adequate data) to such a simple situation. The models we describe can be generalized to situations where temporary emigration probabilities vary by state variables that are static (e.g., sex), deterministically variable (e.g., age), or stochastically variable (e.g., body size).

LITERATURE CITED

Arnason, A. N., and K. H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly–Seber estimates for mark–recapture experiments. Canadian Journal of Fisheries and Aquatic Science **38**:1077–1095.

Balser, J. P. 1981. Confidence interval estimation and tests for temporary outmigration in tag–recapture studies. Dissertation. Cornell University, Ithaca, New York, USA.

Barker, R. J. 1997. Joint modeling of live–recapture, tag–resight, and tag–recovery data. Biometrics, *in press.*

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for mul-

tiple strata including non-Markovian transitions. Biometrics **49**:1173–1187.

Buckland, S. T. 1980. A modified analysis of the Jolly–Seber capture–recapture model. Biometrics **36**:419–435.

Buckland, S. T., and P. H. Garthwaite. 1991. Quantifying precision of mark–recapture estimates using the bootstrap and related methods. Biometrics **47**:255–268.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–214 *in* J.-D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhäuser-Verlag, Basel, Switzerland.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16–30 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph **5**. Bethesda, Maryland, USA.

Burnham, K. P., and W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika **65**:625–633.

Carothers, A. D. 1973. The effects of unequal catchability on Jolly–Seber estimates. Biometrics **29**:79–100.

Chao, A. 1988. Estimating animal abundance with capture frequency data. Journal of Wildlife Management **52**:295–300.

———. 1989. Estimating population size for sparse data in capture–recapture experiments. Biometrics **45**:427–438.

Chao, A., S.-M. Lee, and S.-L. Jeng. 1992. Estimating population size for capture–recapture data when capture probabilities vary by time and individual animal. Biometrics **48**:201–216.

Clobert, J., J.-D. Lebreton, D. Allaine, and J. M. Gaillard. 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. Biometrics **50**:375–387.

Clobert, J., J.-D. Lebreton, and G. Marzolin. 1990. The estimation of local immature survival rate and of age-specific proportions of breeders in bird populations. Pages 199–213 *in* J. Blondel, A. Gosler, J.-D. Lebreton, and R. McCleery, editors. Population biology of passerine birds: an integrated approach. NATO ASI Series, Volume G24, Springer-Verlag, Berlin, Germany.

Gill, D. E. 1985. Interpreting breeding patterns from census data: a solution to the Husting dilemma. Ecology **66**:344–354.

———. 1987. Reply to Nichols et al. Ecology **68**:217–220.

Hestbeck, J. B., Nichols, J. D., and Malecki, R. A. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada Geese. Ecology **72**:523–533.

Hill, R. W. 1983. Thermal physiology and energetics of *Peromyscus;* ontogeny, body temperature, metabolism, insulation, and microclimatology. Journal of Mammalogy **64**:19–37.

Husting, E. L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum.* Copeia **1965**:352–362.

Hwang, W.-D., and A. Chao. 1995. Quantifying the effects of unequal catchabilities on Jolly–Seber estimators via sample coverage. Biometrics **51**:128–141.

Kendall, W. L., and K. H. Pollock. 1992. The robust design in capture–recapture studies: a review and evaluation by Monte Carlo simulation. Pages 31–43 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier, London, UK.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A

likelihood-based approach to capture–recapture estimation of demographic parameters under the robust design. Biometrics **51**:293–308.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs **62**:67–118.

Lebreton, J.-D., G. Hemery, J. Clobert, and H. Coquillart. 1990. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. I. Transversal models. Biometrics **46**:609–622.

Lee, S.-M. and A. Chao. 1994. Estimating population size via sample coverage for closed capture–recapture models. Biometrics **50**:88–97.

Menkins, G. E., Jr., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology **69**:1952–1959.

Nichols, J. D., G. R. Hepp, K. H. Pollock, and J. E. Hines. 1987. The Husting dilemma: a methodological note. Ecology **68**:213–217.

Nichols, J. D., J. E. Hines, and K. H. Pollock. 1984*a*. Effects of permanent trap response in capture probability on Jolly–Seber capture–recapture model estimates. Journal of Wildlife Management **48**:289–294.

Nichols, J. D., J. E. Hines, K. H. Pollock, R. L. Hinz, and W. A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. Ecology **75**:2052–2065.

Nichols, J. D., and W. L. Kendall. 1995. The use of multistate models to address questions in evolutionary ecology. Journal of Applied Statistics **22**:835–846.

Nichols, J. D., K. H. Pollock, and J. E. Hines. 1984*b*. The use of a robust capture–recapture design in small-mammal population studies: a field example with *Microtus pennsylvanicus.* Acta Theriologica **29**:357–365.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference for capture data on closed animal populations. Wildlife Monographs, Number **62**.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management **46**:757–760.

Pollock, K. H., J. D. Nichols, J. E. Hines, and C. Brownie. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs, Number **107**.

Pollock, K. H., and M. C. Otto. 1983. Robust estimation of population size in closed animal populations from capture–recapture experiments. Biometrics **39**:1035–1049.

Rexstad, E., and K. P. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, USA.

Rose, R. K. 1973. A small-mammal live trap. Transactions of the Kansas Academy of Science **76**:14–17.

Sandland, R. L., and G. P. Kirkwood. 1981. Estimation of survival in marked populations with possibly dependent sighting probabilities. Biometrika **68**:531–541.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Spendelow, J. A., and J. D. Nichols. 1989. Annual survival rates of breeding adult Roseate Terns (*Sterna dougalii*). Auk **106**:367–374.

Viallefont, A., E. G. Cooch, and F. Cooke. 1995. Estimation of trade-offs with capture–recapture models: a case study on the Lesser Snow Goose. Journal of Applied Statistics **22**:847–861.

White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. Journal of Wildlife Management **47**:716–728.

Whitehead, H. 1990. Mark–recapture estimates with emigration and re-immigration. Biometrics **46**:473–479.

APPENDIX

The capture process across primary periods under the Markovian temporary emigration model, and hence the likelihood that describes it (L_{1b}), is complex. However, matrix notation makes it more tractable. In describing the capture process from release in primary period h to recapture in primary period s, let

$\mathbf{f}_{h+1}$ = a 1×2 vector of probabilities of not being captured during first primary period after release, given that an animal survives from primary period h to $h + 1$ and is in the superpopulation at $h + 1$,

$$= \begin{bmatrix} \gamma''_{h+1} \\ (1 - \gamma''_{h+1})q^*_{h+1} \end{bmatrix}^T,$$

$\mathbf{G}_i$ = a 2×2 transition matrix of probabilities that an animal is outside the study area (column 1) or inside the study area but not captured (column 2) in primary period i ($i = h + 2, h + 3, \ldots, s - 1$), given that it is outside (row 1) or inside (row 2) the study area in primary period $i - 1$, survives to period i, and is in the superpopulation in both periods,

$$= \begin{bmatrix} \gamma'_i & (1 - \gamma'_i)q^*_i \\ \gamma''_i & (1 - \gamma''_i)q^*_i \end{bmatrix}, \quad \text{and}$$

$\mathbf{d}_s$ = a 2×1 vector of probabilities of being in the study area in primary period s, given that an animal is in and out of the study area in primary period $s - 1$ and survives to period s,

$$= \begin{bmatrix} (1 - \gamma'_s) \\ (1 - \gamma''_s) \end{bmatrix}.$$

Note that we can then describe the probabilities of any multinomial cell from L_{1b}, as in Tables A1 and A2. Describing the model in this fashion makes it easier to compute parameter estimates using program SURVIV (White 1983). SURVIV requires specification of each cell probability as a function of the estimable parameters. We wrote a program (RDSURVIV, available from J. E. Hines) that exploits the matrix notation described here in building these cell probabilities for SURVIV automatically for an arbitrary number of primary and secondary periods. See Brownie et al. (1993) for a similar development for multistate capture–recapture models.

TABLE A1. Recapture array (m_{ha}).

Year of release	Number released	Year of recapture			
		2	3	4	5
1	R_1	m_{12}	m_{13}	m_{14}	m_{15}
2	R_2		m_{23}	m_{24}	m_{25}
3	R_3			m_{34}	m_{35}
4	R_4				m_{45}

TABLE A2. Multinomial cell probabilities.

Year of release	Year of recapture			
	2	3	4	5
1	$\phi_1(1 - \gamma''_2)p^*_2$	$\phi_1\mathbf{f}_2\phi_2\mathbf{d}_3p^*_3$	$\phi_1\mathbf{f}_2\phi_2\mathbf{G}_3\phi_3\mathbf{d}_4p^*_4$	$\phi_1\mathbf{f}_2\phi_2\mathbf{G}_3\phi_3\mathbf{G}_4\phi_4\mathbf{d}_5p^*_5$
2		$\phi_2(1 - \gamma''_3)p^*_3$	$\phi_2\mathbf{f}_3\phi_3\mathbf{d}_4p^*_4$	$\phi_2\mathbf{f}_3\phi_3\mathbf{G}_4\phi_3\mathbf{G}_4\mathbf{d}_4p^*_5$
3			$\phi_3(1 - \gamma''_4)p^*_4$	$\phi_3\mathbf{f}_4\phi_4\mathbf{d}_5p^*_5$
4				$\phi_4(1 - \gamma''_5)p^*_5$