

ESTIMATING TRANSITION PROBABILITIES FOR STAGE-BASED POPULATION PROJECTION MATRICES USING CAPTURE–RECAPTURE DATA¹

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Abstract. In stage-based demography, animals are often categorized into size (or mass) classes, and size-based probabilities of surviving and changing mass classes must be estimated before demographic analyses can be conducted. In this paper, we develop two procedures for the estimation of mass transition probabilities from capture–recapture data. The first approach uses a multistate capture–recapture model that is parameterized directly with the transition probabilities of interest. Maximum likelihood estimates are then obtained numerically using program SURVIV. The second approach involves a modification of Pollock's robust design. Estimation proceeds by conditioning on animals caught in a particular class at time i , and then using closed models to estimate the number of these that are alive in other classes at $i + 1$. Both methods are illustrated by application to meadow vole, *Microtus pennsylvanicus*, capture–recapture data. The two methods produced reasonable estimates that were similar. Advantages of these two approaches include the directness of estimation, the absence of need for restrictive assumptions about the independence of survival and growth, the testability of assumptions, and the testability of related hypotheses of ecological interest (e.g., the hypothesis of temporal variation in transition probabilities).

Key words: capture–recapture models; *Microtus pennsylvanicus*; multistate models; parameter estimation; Pollock's robust design; stage-based population projection matrices; stage transition probabilities.

INTRODUCTION

The Leslie Matrix approach to population analysis (Bernardelli 1941, Lewis 1942, Leslie 1945, 1948) has seen wide use in animal population ecology. In this approach, the population size at time t is characterized by a column vector, \mathbf{n}_t , containing the number of animals in each age class. The population at time $t + 1$ is then projected using a matrix, \mathbf{L} , of age-specific survival and fecundity rates:

$$\mathbf{L}\mathbf{n}_t = \mathbf{n}_{t+1}$$

During the last 15 yr many ecologists have realized that vital rates may be closely associated with organism characteristics other than age (e.g., Werner and Caswell 1979, Hughes 1984, Sauer and Slade 1987, Caswell 1989). This realization has led to the increased use of stage-based matrix models, which are similar to the

age-structured models, except that \mathbf{n}_t contains the number of animals in each stage at time t , and \mathbf{L} is a matrix of stage-specific fecundities and stage transition probabilities. There has been much work done on the analysis and asymptotic behavior of such models once a projection matrix has been specified (reviewed by Caswell 1989), but little effort has been expended on methods for estimating the component elements of the projection matrix.

Caswell (1989) described methods for estimating transition probabilities and testing hypotheses about variation among estimated projection matrices in cases where individual organisms can be identified and followed over time. These transition frequency methods should work well for sessile plants and animals, and perhaps, in some cases, for mobile animals studied in enclosures. However, these methods generally are not appropriate for use with mobile animal populations. Such populations can be sampled periodically, but individually marked animals are not captured or seen with probability 1.0 during these samples. Methods for estimating projection matrix probabilities from such populations must incorporate sampling probabilities that vary over time and stage. Estimation methods that

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do not deal properly with sampling probabilities yield biased estimates (Nichols and Pollock 1983).

Recent developments in modern band-recovery and capture-recapture models (Seber 1982, Brownie et al. 1985, Clobert et al. 1987, Pollock et al. 1990) permit estimation of age-specific survival rate, and these estimates can be used directly in age-based population projection models (Leslie 1945, Caswell 1989). However, the transition probabilities of stage-based models incorporate both the probability of surviving from one time period to the next and the conditional probability of making a transition from one stage to another between times i and $i + 1$, given that the animal is alive at $i + 1$. Estimation of transition probabilities for stage-based matrices has generally involved a two-step approach in which survival and stage transition probabilities are estimated separately and then combined. For example, Sauer and Slade (1986) used a stage-based projection matrix to model the population dynamics of *Microtus ochrogaster* based on body mass classes. Survival rate was estimated using the Jolly-Seber (Jolly 1965, Seber 1965) capture-recapture model, and growth rate was estimated using observed mass transitions. The growth and survival rate estimates were then used to estimate the matrix transition probabilities.

In this paper we describe two direct approaches to estimating transition probabilities (and their sampling variances) for stage-based population projection matrices using capture-recapture data. One approach involves development of a multistate capture-recapture model, which is parameterized with the transition probabilities of interest. Estimates are obtained directly using maximum likelihood methods. This approach is similar to that used to model capture-recapture data for a population inhabiting several geographic strata (Arnason 1972, 1973, Hestbeck et al. 1991). The second approach follows the robust design of Pollock (1982). Separate transition probabilities are estimated by conditioning on animals caught in a particular class at time i , and then using closed population models (e.g., those of Otis et al. 1978) to estimate the number of these that are alive and in another class at time $i + 1$. Following the description of these methods, we present an example of their use in estimating mass transition probabilities for a *Microtus pennsylvanicus* population in Maryland.

ESTIMATION APPROACHES

Definitions and notation

Define the following statistics associated with a standard capture-recapture study on an open animal population:

n_{ij} = number of animals caught in sample period i in class (stage) j .

u_{ij} = number of unmarked (new) animals caught in sample period i in class j .

m_{ijk} = number of marked animals caught in period i in class k that were also caught in period $i - 1$ in class j .

Define the following random variable to be estimated:

M_{ijk} = number of marked animals alive and in class k in period i that were caught in class j in period $i - 1$.

Define the following model parameters:

ϕ_{ijk} = probability that an animal alive in class j in sample period i is alive and in class k in period $i + 1$.

p_{ij} = probability that an animal alive in class j at sample period i is captured at that time.

Finally, we define a capture history as a representation of the outcome of trapping for a particular animal in each time period. We will adopt the convention of writing capture histories as sequences of 0's and capital letters, where "0" indicates no capture in a particular sample period and "A" indicates capture in class or stage A . For example, *AA0B0* denotes capture in class A in periods 1 and 2, no capture in period 3, capture in class B in period 4, and no capture in period 5.

Multistate model approach

Under this approach, we condition on the u_{ij} and then model the capture histories for subsequent sample periods ($i + 1, \dots, K$) in terms of the transition (ϕ_{ijk}) and capture (p_{ij}) probabilities. Specifically, each member of u_{ij} (an animal first caught in period i in class j) is either captured or not captured in each of the periods from $i + 1$ to K . All possible capture histories can be specified, and the probability of each possible history can be written as a function of time-specific transition and capture probabilities. Consider a three-period study for a population exhibiting only two states (e.g., mass classes), A and B . Assume that transition A to B is possible, but that B to A is not possible (perhaps an animal cannot return to a small body mass class, A , after having grown into the larger mass class, B). In Table 1, we write the expected number of animals exhibiting each possible capture history under our three-period, two-class model. For example, the expected number of animals exhibiting capture history *ABB* can be written as $u_{1A}\phi_{1AB}p_{2B}\phi_{2BB}p_{3B}$. The animal must be caught in class A in period 1 (it must be a member of u_{1A}), it must survive and move to class B during the interval between periods 1 and 2 (this occurs with probability ϕ_{1AB}), it must be captured in period 2 (this occurs with probability p_{2B}), and it must survive (ϕ_{2BB}) and then be captured in period 3 (p_{3B}). Regarding estimation under this model, we note that only the product of transition and capture probability can be estimated for period $K - 1$ (i.e., we can estimate $\phi_{K-1jk} p_{Kk}$, but we cannot estimate each parameter separately).

The numbers of animals from any cohort u_{ij} experiencing different capture histories thus follow a con-

ditional multinomial distribution, conditioned on the u_{ij} . The probabilities corresponding to the different cells of the multinomial (i.e., to the different capture histories) are written as functions of ϕ_{ijk} and p_{ij} . Because the different cohorts, u_{ij} , are independent, the probability distribution for an entire K -sample study can be written as the product of the multinomial distributions for all the cohorts.

The multinomial distribution of the data permits estimation using program SURVIV (White 1983). SURVIV provides maximum likelihood estimates of ϕ_{ijk} and p_{ij} and their associated variances. SURVIV also permits construction of likelihood ratio tests of constrained vs. general models that provide a convenient means of testing hypotheses about possible sources of variation in the ϕ_{ijk} and p_{ij} . For example, the null hypothesis of no temporal (period-to-period) variation in transition probabilities (ϕ_{ijk}) is very relevant to the decision about what modeling approach is most appropriate in a particular situation. The question of temporal variation can be addressed by developing a model in which the transition probabilities are constrained to be time invariant ($\phi_{ijk} = \phi_{j'k}$). The likelihood ratio test between this constrained model and the more general model (time-specific ϕ_{ijk}) then provides a formal test for temporal variation.

Robust design approach

Pollock's (1982) robust design involves a distinction between two types of sampling periods. Primary periods are those between which the sampled population is assumed to be open to changes occurring as a result of births, deaths, and movement. All of the references to sample periods (subscripted i) in the above description of the multistate model approach were to primary periods. For example, primary sampling periods might occur each month for a small-mammal study or perhaps each year for a study of migratory birds. Secondary samples occur over very short (e.g., 1-d) time intervals within each primary period, and it is hoped that the population is essentially closed to births, deaths, and movements over these secondary periods. For example, a small-mammal population might be trapped for 5 consecutive days each month (Nichols et al. 1984). The months represent the primary periods and the 5 d within each month would represent the secondary periods.

Pollock (1982) used capture history data over the secondary periods within each primary period to estimate population size with closed models such as those of Otis et al. (1978). Survival rate was estimated with the Jolly-Seber model (Jolly 1965, Seber 1965) using capture histories based on primary periods. (Capture histories simply recorded whether or not an animal was caught at least once in a primary period.) Numbers of new animals entering the population were then computed from these population size and survival rate estimates (Pollock 1982, Pollock et al. 1990).

TABLE 1. Expected numbers of animals exhibiting possible capture histories under a three-sample (1, 2, 3), two-class (A , B) model.*

u_{ij}^\dagger	Capture history	Expected number of animals
u_{1A}	AAA	$u_{1A}\phi_{1AA}p_{2A}\phi_{2AA}p_{3A}$
	AAB	$u_{1A}\phi_{1AA}p_{2A}\phi_{2AB}p_{3B}$
	AAO	$u_{1A}\phi_{1AA}p_{2A}(1 - \phi_{2AA}p_{3A} - \phi_{2AB}p_{3B})$
	ABB	$u_{1A}\phi_{1AB}p_{2B}\phi_{2BB}p_{3B}$
	ABO	$u_{1A}\phi_{1AB}p_{2B}(1 - \phi_{2BB}p_{3B})$
	AOA	$u_{1A}\phi_{1AA}(1 - p_{2A})\phi_{2AA}p_{3A}$
	AOB	$u_{1A}[\phi_{1AA}(1 - p_{2A})\phi_{2AB}p_{3B} + \phi_{1AB}(1 - p_{2B}) \cdot \phi_{2BB}p_{3B}]$
u_{1B}	A00	$u_{1A}[1 - \phi_{1AA} - \phi_{1AB} + \phi_{1AA}(1 - p_{2A}) \cdot (1 - \phi_{2AA}p_{3A} - \phi_{2AB}p_{3B}) + \phi_{1AB}(1 - p_{2B}) \cdot (1 - \phi_{2BB}p_{3B})]$
	BBB	$u_{1B}\phi_{1BB}p_{2B}\phi_{2BB}p_{3B}$
	BBO	$u_{1B}\phi_{1BB}p_{2B}(1 - \phi_{2BB}p_{3B})$
	B0B	$u_{1B}\phi_{1BB}(1 - p_{2B})\phi_{2BB}p_{3B}$
u_{2A}	B00	$u_{1B}[1 - \phi_{1BB} + \phi_{1BB}(1 - p_{2B})(1 - \phi_{2BB}p_{3B})]$
	0AA	$u_{2A}\phi_{2AA}p_{3A}$
	0AB	$u_{2A}\phi_{2AB}p_{3B}$
	0A0	$u_{2A}(1 - \phi_{2AA}p_{3A} - \phi_{2AB}p_{3B})$
u_{2B}	0BB	$u_{2B}\phi_{2BB}p_{3B}$
	0B0	$u_{2B}(1 - \phi_{2BB}p_{3B})$

* Possible transitions are class A to class A , A to B , and B to B ; B to A is not possible.

† Unmarked animals caught in period i .

The estimation of transition probabilities using the robust design approach involves conditioning on the group of animals caught in a particular class at a particular primary sample period (n_{ij}). Note that here we do not restrict this initial group of animals to unmarked animals but use all marked and unmarked animals of the specified stage or class caught in the specified period. We then select the animals from this group that are captured in a specified class in the next primary period, m_{i+1jk} , and use their capture history data over the secondary periods (say 5 d within primary period $i + 1$) to estimate M_{i+1jk} using models developed for closed-population capture-recapture studies (Otis et al. 1978). The transition probability of interest and its corresponding variance are then estimated as:

$$\hat{\phi}_{ijk} = \hat{M}_{i+1jk}/n_{ij}, \tag{1}$$

$$\widehat{\text{var}}(\hat{\phi}_{ijk}) = [\widehat{\text{var}}(\hat{M}_{i+1jk})]/(n_{ij})^2. \tag{2}$$

AN EXAMPLE

Here we use both estimation approaches to estimate mass class transition probabilities for *Microtus pennsylvanicus* captured at Patuxent Wildlife Research Center, Laurel, Maryland during 1981–1982. The primary periods of interest were roughly 1 mo apart. Primary period 1 involved five secondary periods (days) of trapping from 3 to 7 October 1981, period 2 was from 31 October to 4 November 1981, and period 3 was from 4 to 8 December 1981. We were interested in esti-

TABLE 2. Numbers of *Microtus pennsylvanicus* exhibiting each mass-based capture history (sequence of mass classes A, B, etc.).*

Number of animals in cohort	Capture history	Number of animals
$\mu_{1A} = 28$	ABB1	10
	ABB0	4
	AB01	1
	AB00	3
	A0B1	2
	A0C1	2
	A000	6
$\mu_{1B} = 15$	BBB1	1
	BCC1	2
	BCC0	1
	BC01	1
	BC00	1
	B000	9
$\mu_{1C} = 39$	CDC1	3
	C0D0	1
	C0C1	1
	CC00	2
	CCC1	12
	CCC0	5
	CCD1	1
	C001	1
	C000	13
$\mu_{1D} = 45$	DDD0	3
	DDD1	12
	DDC0	1
	DDC1	5
	DD00	2
	D0D0	1
	D0C0	1
	DCD1	1
	DCC0	2
	DC00	2
	D000	15
μ_{2A}	OAB1	21
	OAB0	4
	OAO1	1
	OAO0	4
$\mu_{2B} = 19$	0BB1	10
	0BC1	5
	0BC0	1
	0B01	1
	0B00	2
$\mu_{2C} = 4$	0CC1	1
	0CC0	1
	0C00	2
$\mu_{3A} = 4$	00A1	2
	00A0	2
$\mu_{3B} = 24$	00B1	18
	00B0	6
$\mu_{3C} = 6$	00C1	1
	00C0	5
$\mu_{3D} = 1$	00D1	1

* Capture histories reflect the four primary periods and are used in estimation via the multistate model approach. Unobserved capture histories do not appear here.

mating the transition probabilities between periods 1 and 2 and periods 2 and 3. However, the multistate model estimation approach required that we have an

additional sampling period. We designated all sampling periods after period 3 (the next sample period occurred in early January 1982, and we also used all subsequent periods in 1982) as “period” 4. Period 4 contributed only recaptures to the data needed for estimation, and we maximized our number of recaptures by combining all periods after period 3. Because of our use of all subsequent recaptures, we did not assign period 4 animals to mass class, but simply recorded whether or not the animal was caught (1 indicating capture, 0 indicating no capture).

We used a 10 × 10 livetrapping grid with trap stations placed at 7.6-m intervals, and we baited with whole corn. Voles were ear-tagged with serially numbered fingerling tags, and animals were weighed at each capture (see Nichols et al. 1984 for additional description of field methods). For this exercise we used four mass classes: A, <22 g (defined as juveniles by Krebs et al. 1969); B, 22–33 g (subadults of Krebs et al. 1969); C, 34–45 g; and D, >45 g. Mass class was assigned based on mass at first capture within a primary period. We combined sexes for our analyses in order to obtain good sample sizes.

Mass class capture history data are presented for all observed histories in Table 2. Rather than try to estimate transition probability for very unlikely monthly transitions, we omitted all transitions that were not observed. The following transitions were thus included in our model: AB, BB, BC, CC, CD, DC, and DD. The four-period capture history data of Table 2 permitted separate estimation of specific transition probabilities for periods 1 and 2, so we parameterized our general model (denoted model I) with ϕ_{1jk} and ϕ_{2jk} . We also developed a reduced-parameter model (denoted II) in which specific transition probabilities for periods 1 and 2 were constrained to be equal, $\phi_{1jk} = \phi_{2jk} = \phi_{jk}$.

Estimates of transition probabilities based on the multistate model approach and computed using program SURVIV are presented in Table 3. Model I provided estimates for each of the estimable time periods, 1 and 2, whereas model II provided a single estimate for each transition probability under the hypothesis of no temporal variation. The point estimates for periods 1 and 2 under model I differ substantially in some cases (e.g., BB, DC). The goodness-of-fit test statistic for

TABLE 3. *Microtus pennsylvanicus* transition probability estimates based on the multistate model approach.

Mass transition	Model I				Model II	
	$\hat{\phi}_{1jk}$	SE	$\hat{\phi}_{2jk}$	SE	$\hat{\phi}_{jk}$	SE
AB	0.81	0.08	0.88	0.06	0.87	0.05
BB	0.07	0.07	0.68	0.08	0.51	0.06
BC	0.34	0.13	0.21	0.07	0.24	0.06
CC	0.59	0.08	0.75	0.08	0.66	0.05
CD	0.09	0.05	0.07	0.04	0.08	0.03
DC	0.12	0.05	0.35	0.10	0.22	0.05
DD	0.55	0.08	0.58	0.10	0.56	0.06

TABLE 4. Goodness-of-fit (GOF) and between-model likelihood ratio (LR) tests for the two mass transition models, I and II.

Test	χ^2	df	P
Model I (GOF)	70.7	56	.09
Model II (GOF)	99.1	64	<.01
Model II vs. I (LR)	28.4	8	<.01

model I indicated marginal fit, whereas the statistic for model II indicated rejection of the model for this data set (Table 4). The likelihood ratio test between models II and I also provided evidence that the time-specific transition parameters of model I were needed to model these data adequately (Table 4).

We also used the robust design approach to estimate the transition probabilities for period 2 to 3, ϕ_{2jk} . Table 5 contains the resulting estimates and designates the closed population model on which each \hat{M}_{ijk} was based. We used the discriminant function model selection procedure of program CAPTURE (Otis et al. 1978) in selecting a model for each data set. Model M_0 , which assumes that capture probability is constant over both time (secondary trapping periods) and individuals (Otis et al. 1978), was used for most transitions, whereas M_H , a model permitting variation in capture probability among individuals but not over time (Burnham and Overton 1978), was required in two cases (Table 5). Data were insufficient to obtain estimates for the CD transition.

Comparison of estimates of ϕ_{2jk} obtained using the two different approaches (Tables 3 and 5) indicates that they are similar. Standard errors tended to be smaller for the estimates obtained using the robust design approach. We believe that this resulted primarily from the small standard errors for \hat{M}_{3jk} based on model M_0 of Otis et al. (1978). These small standard errors may be misleading, as they result from a model with very restrictive assumptions, violation of which can cause serious bias (Otis et al. 1978). Certainly, program CAPTURE provides goodness-of-fit and between-model test statistics for use in model selection, but these tests tend to have low power when used with sample sizes such as those we used. The robust design did not permit estimation of the transition probability for CD. This is not surprising because this probability was low ($\hat{\phi}_{2CD} = 0.07$, Table 3), and sample size (m_{3CD}) was thus too small for reasonable use of the Otis et al. (1978) models.

DISCUSSION

We believe that the estimation approaches described above should generally be preferable to the two-step approaches (estimate survival rate and growth rate or other conditional stage transition probability, and then combine these estimates to estimate the unconditional stage transition probability) used previously to esti-

mate the entries in stage-based population projection matrices for mobile animal populations. We estimate both the transition probabilities and their variances directly. Although we have never seen sampling variances computed by those following a two-step approach, we suspect that variances computed by combining variances for estimated growth and survival rates will tend to be larger than those we obtain via direct estimation.

Direct estimation of transition probabilities also requires fewer restrictive assumptions than two-step estimation. For example, some applications of the two-step approach in mass-based work have assumed that survival rate is independent of mass. Thus, the only variation in transition probabilities is induced by variation in growth rate. It would be possible to estimate survival rate over an interval for each mass class at the beginning of that interval. However, even this approach requires the assumption that survival from i to $i + 1$ is independent of the mass transition made during that interval. Although we have no evidence that such an assumption is unreasonable, it would be difficult to test, and our approaches bypass the problem altogether.

Another advantage of both of our recommended approaches involves the ability to test assumptions. Goodness-of-fit tests and between-model tests are computed for the closed capture-recapture models used to estimate M_{ijk} (Otis et al. 1978). Goodness-of-fit tests and between-model likelihood ratio tests also can be used to test assumptions of our multistate models. The between-model tests can be used to test hypotheses of biological interest (e.g., temporal variation in transition probabilities) that are important in selection of an appropriate modeling approach for projecting population size through time.

We have not conducted a formal comparison of our two approaches for estimating stage transition probabilities, but we suspect that the multistate model approach will tend to be more useful in most applications. The robust design approach, with its use of closed population models, has the potential to provide a better way of handling different sources of variation in capture probability (e.g., the ability of model M_H to esti-

TABLE 5. *Microtus pennsylvanicus* transition probability estimates, ϕ_{2jk} , based on the robust design approach.

Mass transition jk	n_{2j}	Model	\hat{M}_{3jk}	\hat{SE}	$\hat{\phi}_{2jk}$	\hat{SE}
AB	30	M_H	29	2.54	0.97	0.08
BB	38	M_0	26	1.49	0.68	0.04
BC	38	M_0	6	0.84	0.16	0.02
CC	34	M_H	28	2.48	0.82	0.07
CD*
DC	28	M_0	9	0.03	0.32	0.001
DD	28	M_0	17	0.14	0.61	0.005

* Data were too few to obtain these estimates.

mate M_{ijk} in the presence of heterogeneous capture probabilities). However, the model selection procedure used to identify the important sources of variation in capture probability for a particular data set, and thus to select the appropriate estimation model, requires large data sets in order to perform well (Otis et al. 1978). The subsetting of data required for the robust design approach (i.e., the estimation of each M_{ijk} using data from a specific group of marked animals, m_{ijk}) will frequently result in data sets that are too small to provide adequate information for selecting the most appropriate closed model.

The multistate model approach does not appear to require as much data as the robust design approach (e.g., ϕ_{2CD} , representing a low-probability transition, could be estimated using the multistate approach but not the robust design). The survival rate estimates based on the Jolly-Seber model tend to be robust to heterogeneous capture probabilities (Carothers 1973, 1979, Pollock et al. 1990), and some initial simulation work by us indicates that the multistate model $\hat{\phi}_{ijk}$ are similarly robust to heterogeneous capture probabilities. An additional advantage of the model-based approach is the ability to directly test hypotheses about sources of variation in ϕ_{ijk} using alternative models and between-model tests (e.g., as in Table 4). Such hypotheses can also be tested using estimates from the robust design approach in conjunction with the methods of Sauer and Williams (1989), but such tests are not always as powerful as the between-model tests of the multistate approach.

Finally, we note that our treatment here has emphasized estimation of transition probabilities for stage-based population projection matrices. However, our approach can also be useful in estimating and testing hypotheses about the two separate components of these transition probabilities. Survival rate for a particular mass class is obtained by summing all the corresponding transition probabilities. If we make the assumption that survival probability depends only on mass at the beginning of the interval over which it is estimated, then we can also estimate the conditional growth transition probabilities. Let s_{ij} denote the probability that an animal in class j at time i survives until time $i + 1$. Let r_{ijk} denote the probability that an animal in class j at time i is in class k at time $i + 1$, given that it is alive at $i + 1$. Then we can estimate these quantities as follows:

$$\hat{s}_{ij} = \sum_k \hat{\phi}_{ijk}, \quad (3)$$

$$\hat{r}_{ijk} = \hat{\phi}_{ijk} / \hat{s}_{ij}. \quad (4)$$

Variances of these quantities can be easily estimated (see Hestbeck et al. 1991).

A more direct approach to estimating s_{ij} and r_{ijk} when survival probability depends only on mass at the beginning of the interval of interest is to parameterize

our model with these parameters rather than with ϕ_{ijk} . All parameters are identifiable (hence estimation is possible) because of the constraint $\sum_k r_{ijk} = 1$ (i.e., all

animals must be in 1 of the possible mass classes at time $i + 1$). This direct parameterization also permits the testing of interesting hypotheses about mass-specific survival and growth rates using constrained models.

Even if we cannot make the assumption that survival probability depends only on mass at the beginning of an interval, the estimators in Eqs. 3 and 4 still estimate interesting quantities. For example, even if the survival probability over the interval i to $i + 1$ depends on the particular mass transition made during the interval (i.e., $s_{ijk} \neq s_{ijk'}$), the estimator in Eq. 3 still estimates average survival probability for marked animals alive at time i in mass class j . For this general case, \hat{r}_{ijk} in Eq. 4 estimates the probability of having made a particular transition (j to k) conditional on having survived the interval, or, expressed differently, the proportion of survivors that made a particular transition.

We believe that the ability to estimate class-specific survival rates (as in Eq. 3) may prove to be very useful. Currently, we address questions about the influence of individual attributes such as body mass on survival by stratifying the marked sample into mass categories and then using methods such as those of Burnham et al. (1987) to test for survival differences between strata (e.g., Krementz et al. 1989). J. R. Skalski (*personal communication*) has developed an approach in which stratification is unnecessary and survival is actually modeled as a function of continuous variables such as body mass. Under both the stratification and continuous variable modeling approaches, however, the individual variable (e.g., body mass) is typically measured at one point in time (generally on initial capture), and that measurement is assumed to characterize the animal throughout the capture-recapture study. For many variables this approach is certainly appropriate, but other variables such as body mass would be expected to change over the course of a capture-recapture study. The estimation approach we describe would be well suited for use with such variables, as it permits estimation of class-specific survival rate in the situation where animals can change classes from one period to the next.

Although our purpose here has been to describe and illustrate a methodology, we believe that results from our example analysis merit brief mention. The evidence of temporal variation in the ϕ_{ijk} led us to examine the point estimates for the two time periods, and two tendencies were observed. First, the point estimates of survival rate (computed using Eq. 3, but not shown; note that the complement of survival includes both death and permanent emigration) were lower for period 1 (early October to early November) than for period 2 (early November to early December) for all four mass

classes. We are not aware of previous analyses of seasonal variation in survival rates of *Microtus pennsylvanicus* that are based on reliable estimation methods, so we do not know how typical this result might be. Second, the conditional transition probability estimates (\hat{f}_{ijk} , computed using Eq. 4, but not shown) associated with growth (B to C , C to D) and, in the high mass category, maintenance (D to D), tended to be higher for period 1 than period 2. These estimates are thus consistent with the tendency of *Microtus pennsylvanicus* to gain mass during summer but to stop growth and even lose mass during late fall and winter (Brown 1973, Iverson and Turner 1974).

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