The Use of a Robust Capture-Recapture Design in Small Mammal Population Studies A Field Example with <u>MICROTUS PENNSYLVANICUS</u>

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THE USE OF A ROBUST CAPTURE-RECAPTURE DESIGN IN SMALL MAMMAL POPULATION STUDIES: A FIELD EXAMPLE WITH *MICROTUS PENNSYLVANICUS*

Nichols and Pollock (1983) discussed estimation methodology in small mammal capture-recapture studies and recommended the use of estimators based on probabilistic models rather than direct enumeration. They suggested that the robust design of Pollock (1982) might be especially useful in small mammal studies. Briefly, this design involves K "primary" (e.g., monthly) sampling periods and ℓ "secondary" (e.g., daily) sampling periods within each of the K primary periods. Population size is estimated from capture histories within the secondary sampling periods using closed population models (see Otis et al., 1978), and survival rate is estimated from capture histories over the primary periods using open population models (e.g., Jolly, 1965, 1982; Seber, 1965; Pollock, 1981). This design thus exploits the robust nature of open model survival rate estimators (see Cormack, 1972; Carothers, 1973; Nichols et al., 1983) and the diversity of closed models that permit estimation of population size under various assumptions of unequal capture probabilities.

Recently, we tested the applicability of the robust design in a capture-recapture study of a *Microtus pennsylvanicus* population. Here we present results of that experiment in order to illustrate the robust design and demonstrate its utility in small mammal studies.

METHODS

A livetrapping grid was set out in November, 1980, by R. K. Rose in old field habitat at Patuxent Wildlife Research Center, Laurel, MD. The grid contained a 10 x 10 matrix of trapping stations spaced at 7.6 m intervals. A single modified Fitch live trap (Rose, 1973) was placed at each station. Hay and dried grass were placed in the nest box sections of the traps and whole corn was used as bait.

Primary sampling periods for the robust design experiment occurred monthly from June, 1981, until December, 1981. Within each primary period, traps were set one evening, run the following morning, locked open during the day, and reset in the evening. This procedure was repeated for 5 consecutive days within each of the 6 monthly periods. A raccoon (later captured) visited the grid and tipped over a substantial number of traps on the final 2 days of trapping for the second of the 6 monthly periods. Data from these 2 days were not used in the closed model analysis leaving only 3 trapping days in the second month.

At each capture animals were sexed and weighed and information on external reproductive characteristics obtained. Unmarked animals were tagged with numbered fingerling tags, and tag numbers of marked animals were recorded.

Subadult and adult animals ($\geq$ 22 g, Krebs et al., 1969) of both sexes were combined in our analysis. Jolly-Seber open model estimates were obtained using the bias-adjusted estimates recommended by Seber (1973:204). We report the conditional variance estimates that reflect only sampling variation or "error of estimation" (Jolly, 1965:238). Closed model estimates, fit statistics and model selection statistics were computed using the methodology and algorithm (CAPTURE) of Otis et al. (1978; also see White et al., 1978).

RESULTS

Microtus density was high throughout the experiment. We captured 312 individual animals a total of 1809 times. Primary sampling period capture histories and secondary period histories are summarized in Tables 1 and 2, respectively.

The closure test in program CAPTURE indicated rejection of the closure hypothesis for the first sampling period but not for any other periods (Table 3). This test can result in false rejection in certain situations (Otis et al., 1978:66-67), and we decided to use the closed model estimates for all periods.

Program CAPTURE includes models which permit heterogeneity of capture probabilities (variation from individual to individual), behavioral response (different capture probabilities for marked and unmarked animals), and temporal variation (from 1 day to the next), as well as all possible combinations of these sources of variation. CAPTURE also includes a discriminant function model selection procedure. This procedure chose the heterogeneity model, M_h, in all periods except month 2. However, month 2 had only 3 trapping days, and we decided to use M_h for this month also because the model selection procedure does not perform well with such a small number of sampling periods. The M_h goodness-of-fit statistics generally supported the use of this model, and the M_o vs. M_h test results provided strong evidence of heterogeneity for every month (Table 3).

Population size estimates were computed using both the Jolly-Seber open model and the closed model, M_h (Table 4). Jolly-Seber estimates can be computed for months 2-5, while closed model estimates can be computed for each period, 1-6. The Jolly-Seber estimates of capture probability are very high (mean, $\hat{p} = 0.91$) and the Jolly-Seber population size estimates, $\hat{N}_i$, are thus very precise (small standard errors). Jolly-Seber $\hat{N}_i$ are negatively biased in the presence of heterogeneity, but bias should be relatively small when capture probability is high (Carothers, 1973; Gilbert, 1973). Nevertheless, in every month for which a comparison is possible, the population estimate based on M_h is higher than the Jolly-Seber estimate (Table 4). Thus, despite the greater precision of the Jolly-Seber estimates, we prefer the M_h estimates which should exhibit lower bias. We also note that Jolly-Seber capture probabilities would be lower with the 2- or 3-day trapping periods characteristic of most small mammal studies. This would produce less precision and more bias in the Jolly-Seber $\hat{N}_i$.

The Jolly-Seber survival rate estimator $\hat{\phi}_i$, is robust to heterogeneity of capture probability (Carothers, 1973) and is not biased by permanent trap response (Nichols et al., 1983). We thus believe that our survival estimates should exhibit very little bias (Table 5). Because of our high capture probabilities, these estimates are very precise (Table 5).

Recruitment, B_i, or the number of individuals entering the population between times i and i+1, and present at time i+1, is estimated as:

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i (\hat{N}_i - n_i + R_i) \qquad (1)$$

where n_i and R_i are the numbers of animals caught and released, respectively, at period i. Jolly-Seber $\hat{B}_i$ are estimated by using Jolly-Seber $\hat{N}_i$ in (1), while the robust design uses $\hat{N}_i$ from the closed models (e.g., M_h). An estimate of B_1 is possible with the robust design but not with the Jolly-Seber model. For the 3 periods in which a comparison is possible, the robust design yields higher estimates of B_i in 2 periods while the Jolly-Seber $\hat{B}_i$ is higher in 1 period (Table 5). Jolly-Seber $\hat{B}_i$ are more precise than the robust $\hat{B}_i$, but the latter should exhibit less bias.

DISCUSSION

This example illustrates well the potential importance of the robust design to small mammal capture-recapture studies. The design produced very precise estimates of survival rate, population size and recruitment which would permit powerful tests of hypotheses dealing with small mammal population ecology. The closed model tests (Table 3) strongly indicated heterogeneity of capture probabilities, and model M_h permits robust estimation of population size in this situation. Since heterogeneity is believed to be common among small mammals (see Smith et al., 1975) we believe the robust design will often be preferable to the Jolly-Seber methodology.

Although the robust design was developed to permit robust parameter estimation, we note here that it also has advantages in certain inference procedures. A problem in many important small mammal studies during the last 2 decades involves the use of estimators having a non-negligible sampling correlation to draw inferences about underlying parameters. For example, a number of papers have addressed questions about the relationship between population size and other parameters such as survival rate. Such questions are typically addressed using estimates of population size and survival rate which have a built-in sampling correlation and which would thus tend to indicate a particular type of relationship even in the absence of a relationship between the true underlying parameters. Another common practice in small mammal population studies is to treat population size or rate of increase (ratio of 2 successive population sizes) as the dependent variable in a multiple regression analysis and quantities such as survival rate as independent variables. Naturally, when correlated estimates are used in such analyses they may produce misleading results. Enumeration estimates have been used in most analyses of this type, and a sampling correlation does exist between the population size and survival rate estimates. Although Jolly-Seber estimates have been recommended for future small mammal work (Nichols and Pollock, 1983), we note that Jolly-Seber estimates of survival rate and poulation size also exhibit a sampling correlation. By using different types of data to estimate N_i and ϕ_i, the robust design yields independent estimates of these parameters which can be used to address questions about true functional relationships.

As noted by Pollock (1982), the major problem asociated with the robust design is the large trapping effort required. Otis et al. (1978) recommend a minimum of 5 days of trapping for good performance of their closed population models, and this represents a substantial effort to be expended at each primary trapping period. However, many small mammal studies involve 2-3 days every 2 weeks. Redistribution of sampling to 5 days every month would represent similar effort and would produce the advantages of robust and precise estimation of population size, survival rate, and recruitment. We therefore recommend this design for future small mammal capture-recapture studies aimed at estimating demographic parameters.

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Table 1. Capture history data over primary sampling periods summarized in Leslie Method B Table (Leslie 1952) format.

Period last captured (dates)	Period captured					
	1	2	3	4	5	6
1 (6/27-7/1)	-	85	5	0	0	0
2 (8/1-8/5)		-	68	7	0	1
3 (8/29-9/2)			-	66	2	0
4 (10/3-10/7)				-	60	4
5 (10/31-11/4)					-	84
6 (12/4-12/8)						-
Marked animals caught	0	85	73	73	62	89
Unmarked animals caught	109	43	29	31	40	60
Total animals caught	109	128	102	104	102	149
Total animals released	104	121	101	103	100	148

Table 2. Capture frequency data for the secondary sampling periods within each primary period.

Primary period (month)	Statistic[a]	Secondary period (day) 1	2	3	4	5
1	Animals caught	63	71	74	64	63
	Frequency	20	14	21	21	28
2	Animals caught	66	81	82	–[b]	–[b]
	Frequency	35	37	40	–[b]	–[b]
3	Animals caught	53	54	46	47	43
	Frequency	37	23	16	13	12
4	Animals caught	61	63	61	52	69
	Frequency	29	15	16	16	27
5	Animals caught	60	67	65	56	64
	Frequency	19	19	19	17	26
6	Animals caught	87	89	79	85	64
	Frequency	40	28	32	28	20

[a] Animals caught denotes the number of animals caught on each day of trapping. Frequency denotes the number of animals caught on 1, 2, 3, 4, and 5 occasions.

[b] A raccoon tipped over traps on the final 2 days of the second primary period, and these data were omitted from the analysis.

Table 3. Test statistics for population closure and M_h goodness-of-fit based on data in Table 2.

Primary period (month)	Closure test		M_h goodness-of-fit			M_o vs. M_h[a]		
	z	P	χ^2	df	P	χ^2	df	P
1	-1.94	0.03	5.7	4	0.23	74.7	3	0.00
2	-1.16	0.12	6.7	2	0.04	8.1	1	0.00
3	0.59	0.72	4.1	4	0.39	67.6	3	0.00
4	0.83	0.80	8.1	4	0.09	118.5	3	0.00
5	-0.52	0.30	4.2	4	0.39	66.9	3	0.00
6	-1.13	0.13	12.9	4	0.01	62.8	3	0.00

[a] M_o vs. M_h essentially tests for heterogeneity of capture probabilities.

Table 4. Comparison of *Microtus* population size estimates using closed population model M_h (robust procedure) and using the Jolly-Seber model. Standard errors are given in parentheses

Primary	M_h		Jolly-Seber Model	
1	125	(5.3)	-	
2	145	(6.9)	139	(4.3)
3	141	(10.0)	118	(4.5)
4	142	(11.3)	110	(3.1)
5	115	(4.7)	111	(3.2)
6	189	(10.3)	-	

[a] Trap losses in each month of 5, 7, 1, 1, 2, 1 were added to the M_h estimates.

Table 5. Survival rates and then birth numbers using both the robust procedure and the Jolly-Seber model. Standard errors are given in parentheses.

Primary period	Survival rates (Jolly-Seber)	Birth numbers (Robust)	Birth numbers (Jolly-Seber)
1	0.89 (0.022)	38 (8.8)	-
2	0.66 (0.023)	50 (11.4)	31 (3.6)
3	0.69 (0.022)	45 (13.6)	30 (2.9)
4	0.63 (0.014)	26 (8.8)	42 (3.0)
5	-	-	-