EXPERIMENTAL ASSESSMENT OF SEVERAL POPULATION ESTIMATION TECHNIQUES ON AN INTRODUCED POPULATION OF EASTERN CHIPMUNKS

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ABSTRACT.—An experimental population of eastern chipmunks (*Tamias striatus*) composed of 85 individuals of known age and sex was released on a 9.4-ha island previously devoid of chipmunks. Three commonly used mark-recapture techniques (Lincoln-Petersen, Schnabel, and Schumacher-Eschmeyer methods) and the Least Squares Removal Method were used to estimate the size of the population. With the exception of equal catchability, the experiment was designed to satisfy the assumptions of the above methods. Point estimates always underestimated the true population size, and only the confidence intervals of the Lincoln-Petersen Method consistently included the actual population value. Least squares regression analyses suggest that the experimental population is composed of two groups of animals: those easily trapped and those hesitant to enter traps. As such, all population estimation methods estimate the easily captured portion of the population and underestimate the true population size. The mathematically simple Lincoln-Petersen Method was more robust than the other methods; when unequal trappability is suspected, it is more accurate than the other methods (although some precision is sacrificed). Caution is suggested in making inter- or intraspecific statistical comparisons of population size when close adherence to the assumptions of the models utilized is not demonstrable; otherwise, statistical differences may be spurious.

Determination of the number of individuals comprising a population is one of the basic necessities in any population study, and yet one of population biology's most intractable problems. In some studies, it is possible to census animals directly because they are confined to a small area, are large and easy to see, or are gregarious and cluster together in easily censused aggregations. Generally, however, the field biologist must estimate how many organisms inhabit a particular habitat patch or geographic area. At present there are many population estimation methods available to researchers, but these often are based on assumptions that have not been tested adequately under field conditions (Petersen, 1896; Lincoln, 1930; Dice, 1938, 1941; Cahalane, 1941; Stickel, 1946, 1948; Calhoun, 1948; Hayne, 1949*a*; Zippin, 1958; Jolly, 1963; Yang et al., 1970; Seber, 1973; Smith et al., 1975; Eberhardt, 1978).

Part of the problem with methodological studies on population estimates is that it is inherently difficult to control for immigration, emigration, birth, and death in natural populations. For terrestrial vertebrates, it is only possible to control these variables under certain experimental conditions. For example, investigators have attempted to livetrap a large area heavily, and subsequently conduct snap-trapping within a small portion of the previously studied site to test the efficiency of snap traps and their effectiveness in sampling a population (Stickel, 1946, 1948; Pelikan and Zejda, 1962). Other workers have employed heroic efforts at direct censusing of a population after first trapping the area, and then compared the results from the two techniques (Edwards and Eberhardt, 1967; Strandgaard, 1967). Edwards and Eberhardt (1967) introduced a large population of cottontail rabbits into a 40-acre enclosure and then employed mark-release trapping to compare various population estimates to the known population size. Studies of this nature, however, are rare.

In this paper, we report data from a population of 85 chipmunks introduced onto an island that lacked chipmunks (*Tamias striatus*), although it appeared to offer adequate food and shelter for them. The island is one of many such islands lying within the Pymatuning Reservoir and its apparently fortuitous lack of a resident chipmunk population made it an ideal "field laboratory" for testing population estimation techniques.

Because the population of chipmunks was introduced onto an island, there was little chance of either immigration or emigration affecting the results. Few or no natural predators were seen or known to occur on that island during the period of this study, so chipmunk deaths should have been minimal. Although 19 animals were not captured during the removal phase of the experiment, we were subsequently able to remove additional chipmunks and are confident that mortality during the experiment did not affect our results. The study was conducted over a short time so that reproduction was also an unimportant factor. Finally, because the island possessed discrete boundaries, we knew exactly how large an area was being sampled and the exact density of animals in that area. Thus, the common problem of marginal residents or transients occurring within the study area was eliminated (Dice, 1938, 1941; Blair, 1940; Stickel, 1946, 1948).

We used live-trapping techniques to test some of the most popular and widely accepted mark-release population estimates—the Lincoln-Petersen Index (Lincoln, 1930), the Schumacher-Eschmeyer Technique (Schumacher and Eschmeyer, 1943), and the Schnabel Method (Schnabel, 1938). In addition, we examined the widely-used technique of removing animals from an area, calculating a regression line and estimating the total population on the area (the Removal Method, Zippin, 1958).

Study Area

Field work was conducted on Whaley Island, located in the Pymatuning Reservoir near Linesville, Pennsylvania (41°38'N. lat., 80°25'W. long.), during a 3-week period in June and July, 1978. Three distinct macrohabitats comprised the bulk of the 9.4-ha island. A planted, mature stand of evergreens consisting mainly of Norway spruce (*Picea abies*) with interspersed red pine (*Pinus resinosa*) covered 25% of the island area. The most extensive macrohabitat (~55% of the island's area) was a mature stand of deciduous trees dominated by black cherry (*Prunus serotina*), although sizable remnant populations of tamarack (*Larix laricina*), scattered maples (*Acer* spp.), and oaks (*Quercus* spp.) were also present. The remaining 20% of the island was occupied by a mixed coniferous-deciduous ecotonal zone characterized by a relatively open canopy and numerous climbing vines (*Parthenocissus quinquefolia, Vitis* spp., and *Rhus radicans*). Groundcover was well developed in the mixed vegetation zone, present but less prominent in the deciduous stand, and sparse or absent under the conifers. Finally, there was a narrow strip of thick shrubby vegetation consisting of dogwoods (*Cornus* spp.), willows (*Salix* spp.), and northern arrowwood (*Viburnum recognitum*) along the perimeter of the island.

Census trapping in 1975 and 1977, and preliminary trapping in 1978 indicated that the small mammal fauna on Whaley Island was depauperate. Prior to the introduction of the experimental population of eastern chipmunks (*Tamias striatus*), the fauna was limited to red squirrels (*Tamiasciurus hudsonicus*), white-footed mice (*Peromyscus leucopus*), meadow voles (*Microtus pennsylvanicus*) and short-tailed shrews (*Blarina brevicauda*). No predators were resident on the island, although raccoons (*Procyon lotor*) may occasionally swim several hundred meters from the mainland or cross over the frozen lake in winter. Weasels (*Mustela frenata*), skunks (*Mephitis mephitis*), and foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), are also capable of crossing the lake in the winter and are common on the nearby mainland.

Methods

Experimental Animals

Chipmunks were trapped, marked by toe-clipping, and removed from three mainland deciduous forest sites. All chipmunks captured at the three sites were used in the experiment, with no attempt made to equalize age and sex categories, so that the introduced population might approximate the natural situation. Forty-eight of the 85 chipmunks trapped were from the Pymatuning Laboratory of Ecology (PLE) site, and 34 were from the Western Pennsylvania Conservancy (WPC) site. These sites correspond, respectively, to the "lab" and "farm" sites of Tryon and Snyder (1973) and are extensively described in that report. Three chipmunks were also trapped at the University of Pittsburgh housing site.

Based upon previous exposure to traps, the experimental population of 82 chipmunks consisted of two distinct subpopulations. The WPC subpopulation (14A♂♂, 12J♂♂, 9A♀♀, 12J♀♀) included chipmunks from both the WPC removal site and the University of Pittsburgh housing site, because all of these individuals had no previous exposure to traps. The PLE chipmunk subpopulation (12A♂♂, 4J♂♂, 14A♀♀, 5J♀♀) was restricted to the PLE removal site animals because these had been involved in a mark-recapture experiment and exposed to traps for at least 6 weeks. We suspected that this differential exposure to traps might cause the animals to differ in their response to traps and thus demonstrate unequal catchability. Individuals were also categorized by age and sex in order to isolate age- or sex-related trends within the subpopulations and the entire experimental population. All chipmunks were released on 28 June 1978 at the same spot on Whaley Island.

Trapping Procedures

A grid system with 20-m spacing was established to encompass the entire island. Each of the 194 trap stations had one hardware cloth live trap (Tryon and Snyder, 1973) baited with sunflower seeds. The traps were generally opened at 0800 h and checked at noon and 1600 h. Traps were not in operation on days with heavy rain in order to minimize mortality due to exposure. We utilized mark-release trapping during the first phase of the study and removal trapping during the second phase to compare these two techniques of small mammal estimation.

Mark-release.—The grid was operated for 8 days: 29 June to 1 July; 4 to 7 July; and 9 July. On 1 and 4 July the traps were checked only in the morning; on 9 July the traps were open all day, but checked only in the afternoon as this was also the first day of removal trapping.

Chipmunk number and trap location were recorded for each captured individual, followed by release at the point of capture. These data were then examined to test the assumption of equal catchability (Orians, 1958; Seber, 1973), and were also used to calculate population estimates based on the three most widely used estimation techniques: Chapman's Modified Lincoln-Petersen Estimate; the Schumacher-Eschmeyer Technique; and the Schnabel Binomial Method (Seber, 1973, pp. 59–64, 139, 140, 142). In determining confidence limits, we used the 95% limits, rather than the 90% limits recommended by Smith et al. (1975), because our study was designed to provide the best possible test of the accuracy and/or precision of the three methods by eliminating confounding natural factors.

Removal.—Trapping occurred on 5 days, 9 to 13 July. Traps were open throughout the day and checked at 1600 h. Every individual captured was removed from the island. Least squares regression lines (Zippin, 1958; Sokal and Rohlf, 1969) were then computed by plotting daily captures against cumulative captures for (1) the experimental population as a whole, (2) each of the two subpopulations defined by previous trap exposure (PLE and WPC), (3) sex and age classes without regard to subpopulation, and (4) sex and age classes within each subpopulation.

Statistical Methodology

Mark-recapture.—Numerous techniques exist for estimating the actual population size (N) of a species, but little information is available concerning recommendations for their usage under field conditions. We decided to examine the accuracy of three commonly used mark-recapture techniques under conditions where the actual population being estimated is fixed and known. The validity of population estimates generated by the Lincoln-Petersen, Schumacher-Eschmeyer, and Schnabel methods requires satisfying several basic assumptions (Seber, 1973): 1) population size must remain constant and therefore may not be affected by the natural processes of emigration, immigration, recruitment, and mortality; 2) marking may not affect catchability; 3) marks may not be lost or go unreported upon recapture; 4) individuals must be equally catchable; 5) captured animals must be a random sample of the population. A detailed mathematical description of mark-recapture techniques is presented in Seber (1973); herein, we attempt to define each technique briefly and show its derivation and relation to other methods. Those more concerned with the actual mathematical derivations should consult original sources or Seber (1973).

The Lincoln-Petersen Estimate, expressed in its most general form, is given by

$$\hat{N} = n_i M_i / m_i,$$

where n_i is the number of individuals captured in sample i; m_i is the number of marked animals captured in sample i; and M_i equals the number of marked animals in the population during sample i. When the previously mentioned underlying assumptions are satisfied, the conditional distribution of m_i, given n_i, and M_i is the hypergeometric distribution and is defined by the quantity

$$\binom{M_i}{m_i}\binom{N - M_i}{n_i - m_i}\Big/\binom{N}{n_i}.$$

Chapman (1951) shows that $\hat{N}$ (the Lincoln-Petersen population estimate) is only a good estimate of N (the actual population size) if N asymptotically approaches infinity; biases are large when n_i is small. When the sum of n_i and M_i is greater than or equal to N, which is never actually known in natural field experiments, an exactly unbiased estimate for N is given by

$$N^* = \{(M_i + 1)(n_i + 1)/(m_i + 1)\} - 1.$$

Because the sum of n_i and M_i was greater than or nearly equal to N for most samples beyond the sixth period, we chose N^* as the best estimate of N in this experiment. N^* has an asymptotically normal distribution as N approaches infinity; as such

$$N^* \pm 1.96\sqrt{V^*}$$

is an approximate 95% confidence limit for N, where V^* is the variance of the estimator N^*. Because the introduced population of chipmunks (N) was not very large, the normal approximation is not a satisfactory method for defining the confidence limits of N. Hence, we used a conservative binomial approximation in conjunction with the Clopper-Pearson charts (Pearson and Hartley, 1966) as suggested by Adams (1951) and Seber (1973). This may, on occasion, yield asymmetric confidence intervals.

The Schnabel Method (Schnabel, 1938) is conceptually a refinement of the Lincoln-Petersen Method that incorporates information from a number of consecutive samples before arriving at a population estimate. Like the Lincoln-Petersen Technique, the Schnabel Method is based upon a generalized hypergeometric model which may be approximated by the binomial distribution if the complications of sampling without replacement can be avoided. Schnabel's Binomial Estimate is nothing more than a weighted average of a number of separate Lincoln-Petersen estimates and is given by

$$N' = \sum_{i=2}^{s} n_i M_i \Big/ \left(\sum_{i=2}^{s} m_i\right),$$

where s is the total number of sampling periods. A number of methods for determining the confidence limits for this technique exist, depending upon the value of the parameters M_i, n_i, m_i, and N. We chose to define our confidence intervals based upon the sum of binomial variances (Seber, 1973) because it follows analogously from our rationale of taking a weighted average of individual Lincoln-Petersen estimates. Hence,

$$N = \left\{ \frac{\left[2\sum_{i=1}^{s} m_i + 1.96^2(1-\delta)\right] \pm \left[1.96^2(1-\delta)\left\{4\sum_{i=1}^{s} m_i + 1.96^2(1-\delta)\right\}\right]^{\frac{1}{2}}}{2\left(\sum_{i=2}^{s} m_i\right)^2} \right\} \lambda$$

where $\delta = \sum_{i=2}^{s} n_i M_i / \lambda N'$, and $\lambda = \sum_{i=2}^{s} n_i M_i$.

N′ is, however, quite sensitive to departures from underlying assumptions, especially those referring to the random behavior of marked animals. In such cases, a mean Lincoln-Petersen Estimate $[\bar{N} = \sum_{i=2}^{s} N_i^*/(S - 1)]$, whose variance is given by

$$V[\bar{N}] = \Sigma(N_i^* - \bar{N})^2/(s - 1)(s - 2),$$

is a more robust estimate of N (Seber, 1973). More refined methods exist, however, to overcome the problematic randomness assumptions.

The Schumacher-Eschmeyer Method (Schumacher and Eschmeyer, 1943) is another popular population estimation technique recommended for use when departures from randomness are probable. It is actually a least squares refinement of the binomial model used by Schnabel, where

$$\tilde{N} = \sum_{i=2}^{s} M_i^2 m_i / \sum_{i=2}^{s} m_i M_i.$$

This methodology was also popularized by Hayne (1949*b*). Following DeLury's (1947) suggestion, the 100(1 − α) confidence interval for N is given by the quantity:

$$\sum_{i=2}^{s} n_i M_i^2 / \sum_{i=2}^{s} m_i M_i \pm t_{(s-2)(\alpha/2)} \left(\tilde{\sigma}^2 \sum_{i=2}^{s} n_i M_i^2\right)^{\frac{1}{2}},$$

where $\tilde{\sigma}^2 = \left[\Sigma m_i^2/n_i - \frac{(\Sigma m_i M_i)^2}{\Sigma n_i M_i^2}\right](s - 2)^{-1}$. This model is also purported to be robust with respect to deviations from the underlying assumptions.

Removal method.—The Removal Method is a population estimation technique based on the assumption that the size of a sample (n_i) from a population is proportional to the amount of effort put into taking the sample (Seber, 1973). In other words, a fixed trapping regime is assumed to catch a fixed proportion of the population, regardless of the size of the population. If trapping and removal is done in a sequential fashion, the yield per trap period should decrease in a linear fashion but the rate of removal should remain constant. Hjort and Ottestad (1933) first used this technique to estimate bear populations in Norway in 1914. Our study was designed to ensure a fixed trapping regime: the total number of traps and the amount of time traps remained open per trapping period remained constant throughout the removal phase.

Hayne (1949*b*) elaborated upon the model and has shown that if the probability of capture ($\bar{p}$) remains constant, then the expected value of n_i, given that x_i individuals were previously removed from the population, is given by

$$n_i = \bar{p}\,(N - x_i).$$

As a result, plots of n_i versus x_i should be linear, and the x intercept provides a graphical estimate of N. Least squares linear regression techniques yield estimates for both $\bar{p}$ (probability of capture or removal rate) and N, and are given by:

$$\bar{p} = -\Sigma n_i(x_i - \bar{x})/\Sigma(x_i - \bar{x})^2$$

and

$$\tilde{N} = \bar{x} + (\bar{n}/\bar{p}).$$

These population estimates derived from the Least Squares Linear Regression Method should be accurate if three basic conditions are met: 1) population size is not modified by emigration, immigration, recruitment, or mortality during the removal period; 2) each individual is equally catchable during the same period; 3) the probability of capture is constant between sampling periods. This experiment was designed to satisfy the first condition while the properties of the regression line indicate whether or not the third condition has been met. Least squares regression fits a line to the data points such that a maximum amount of variance is explained by the equation of the straight line. The correlation coefficient (r) indicates a good fit (a value of 1.00 is a perfect fit) while the coefficient of determination (r^2) measures the percent of variation in the dependent variable explained by variation in the independent variable. When regression analyses are performed rather than correlations, analysis of variance may be used to determine the statistical significance of the regression (i.e., tests the null hypothesis that the slope of the regression line is equal to 0). If the F ratio in the test is significant, and r^2 is high, then it is safe to assume that the individuals being captured are being removed from the population at an equal rate estimated by the slope of the line. The validity of the second assumption can only be ascertained if the actual population size is known; this is rare in natural systems but an a priori fact in this experiment.

The unit of effort expended in obtaining n_i individuals in each sample was constant, hence, if the n_is approach a normal distribution, then one can obtain 100(1 − α) percent confidence intervals for N ($\bar{x} + d_1 \geq N \geq \bar{x} + d_2$) by solving for the real roots of the quadratic equation:

TABLE 1.—*Trapping data and population estimates for a population of 82 chipmunks.*

Sampling period (i)	n_i[a]	m_i[b]	M_i[c]	N^*[d]	N'[e]	$\tilde{N}$[f]
1	11	0	—	—	—	—
2	4	1	11	29.00	44.00	44.00
3	20	3	14	77.75	81.00	83.09
4	15	6	31	72.14	78.90	78.74
5	5	2	40	81.00	82.42	84.07
6	19	12	43	66.69	75.25	74.19
7	23	16	50	71.00	73.90	73.06
8	19	15	57	71.50	73.44	72.76
9	23	21	61	66.64	71.61	70.74
10	11	11	63	63.00	70.52	69.54
11	23	21	63	68.82	70.22	69.42
12	22	18	65	78.89	71.54	71.10
13	37	34	69	75.00	72.29	72.11

[a] n_i = number of individuals captured in sample i;. [b] m_i = number of marked individuals captured in sample i; [c] M_i = number of marked individuals in the population during sample i; [d] N^* = Chapman's Modified Lincoln-Petersen Estimate = $\{[(n_i + 1)(M_i + 1)/(m_i + 1)] - 1\}$; [e] N' = Schnabel Binomial Estimate = $\sum_{i=2}^{s} (n_iM_i)/\sum_{i=2}^{s} m_i$; [f] $\tilde{N}$ = Schumacher-Eschmeyer Estimate = $\sum_{i=2}^{s} M_i^2n_i/\sum m_iM_i$.

$$d^2\left(\bar{p}^2 - \frac{\sigma^2 t^2_{s-2(\alpha/2)}}{\Sigma(x_i - \bar{x})^2}\right) - 2d\bar{n}\bar{p} + \left(\bar{n}^2 - \frac{\sigma^2 t^2_{s-2(\alpha/2)}}{s}\right) = 0,$$

where

$$\sigma^2 = \Sigma(n_i - \bar{n})^2 - [\Sigma n_i(x_i - \bar{x})]^2/[\Sigma(x_i - \bar{x})^2\{s - 2\}].$$

More detailed treatments are available in Leslie and Davis (1939), DeLury (1947), Chapman (1954), and Seber (1973).

RESULTS

Mark-recapture.—Seventy-five of the 85 chipmunks released on Whaley Island were captured at least once during the mark-recapture phase; a total of 232 captures was recorded (Table 1). Three chipmunks died or were removed from the island during the study; these individuals are not included in Table 1 and were not considered in the calculations of population estimates.

The experimental design satisfied or closely approximated the first three previously-mentioned assumptions necessary for the proper application of mark-release techniques; catchability however, is a property of individual chipmunks and is impossible to control in natural populations. Leslie's test for equal catchability (Orians, 1958) was utilized to determine whether or not individuals demonstrated differential trap response (Table 2). As suspected, the experimental population was composed of animals exhibiting heterogeneous catchability ($x^2 = 159.43$; d.f. = 81; $P \ll .005$).

The point estimates and 95% confidence intervals for each mark-recapture population estimation method during all sample periods are shown in Fig. 1. For any mark-recapture technique, successive estimates of population size from period 2 to period 13 are correlated. This serial correlation is not a problem in an experimental analysis such as this because we wish to show the precision and accuracy of each period as if it were an isolated analysis. The temporal sequence is important, however, when one wishes to know how intense a sampling regime should be before estimating population size. In general, point estimates were similar within a sample period and confidence intervals were large during early samples. The large initial confidence intervals may be attributed in part to small sample size and low initial recapture rates.

Point estimates of population size determined by the Schnabel Method consistently

TABLE 2.—*The observed frequency distribution of recaptures for the experimental eastern chipmunk population.**

Number of captures (x)	Observed number of individuals (fx)	xfx
0	10	0
1	14	14
2	13	26
3	18	54
4	12	48
5	7	35
6	5	30
7	1	7
8	1	8
9	0	0
10	1	10
11	0	0
12	0	0
13	0	0
Total (Σ)	82	232

* Leslie's Test for Equal Catchability (Orians, 1958): $\bar{x} = 2.83$; $\sigma^2 = 2.08$; $\chi^2 = \Sigma(x - \bar{x})^2/\sigma^2 = 159.43$, degrees of freedom:$(\Sigma fx) - 1 = 81$, $P \ll .005$.

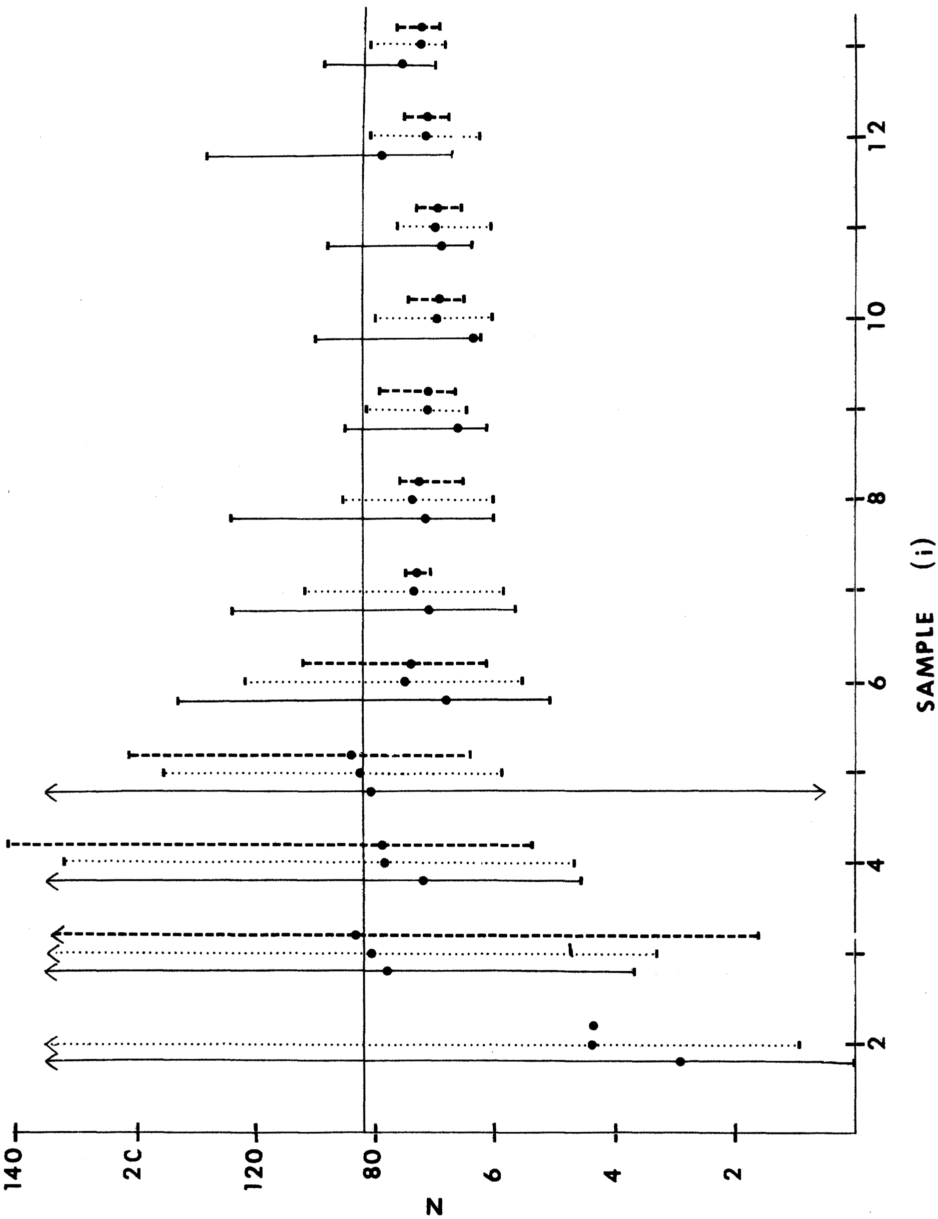
underestimated the true population density of chipmunks on Whaley Island. The precision of the confidence intervals for these estimates increased with sample interval, although the last five intervals (9 through 13) failed to include the true population size.

In all but two cases (samples 3 and 5), the Schumacher-Eschmeyer point estimates were also less than the population's true size. The precision of these estimates increased from sample 3 to 7, after which they remained more or less constant in magnitude. The confidence interval for the estimate associated with sample 2 is mathematically undefined and not included in the analysis. The last seven confidence intervals (samples 7 to 13) did not include the population's true density, and in fact, deviated from it more than the other two methods.

The Lincoln-Petersen procedure, like the previous two methods, produced point estimates below the true population value. The confidence intervals were large for the estimates from early samples (samples 2 to 5) and leveled off appreciably thereafter. In all cases, the Lincoln-Petersen Method had larger confidence intervals than the other methods; more importantly, however, its confidence intervals included the true population value of 82 individuals.

The mean Lincoln-Petersen estimate was determined by first utilizing all sampling periods, and then by only utilizing periods with five or more captures (periods 3 through 13). In the first case, the 95% confidence interval for population size is given by 68 ± 8.6 individuals, while in the latter case, it is given by 72.0 ± 3.8. Clearly, neither point estimate is an improvement over estimates of the other methods. In both cases, the confidence intervals fail to include the true population value and as such appear to be less robust than the Lincoln-Petersen Method.

Removal method.—Sixty-three of the 82 chipmunks on Whaley Island were captured during 5 days of removal trapping (Table 3). The population estimate determined by the Least Squares Linear Regression Method considerably underestimated the actual population size and consistently underestimated the numbers of chipmunks in both the WPC and PLE subpopulations and in the various sex and age classes (Table 4). Underestimation was not a function of removal rate because the removal rates (actually rates of population change are reported, hence the negative slope) ranged from −0.682 for juveniles (e.g., juveniles were removed at a 68% rate each



140
2C
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80
6
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4
6
8
10
12
SAMPLE (i)

TABLE 3.—*Removal-trapping data for eastern chipmunks on Whaley Island by site, sex, and age.*

	WPC site*				PLE site				
	Males		Females		Males		Females		
Day	Adults	Juv.	Adults	Juv.	Adults	Juv.	Adults	Juv.	Total
1	3	1	5	2	5	7	5	9	37
2	3	0	3	0	3	2	1	2	14
3	1	0	1	1	1	2	0	0	6
4	1	0	1	1	2	0	0	0	5
5	0	0	0	1	0	0	0	0	1
Total	8	1	10	5	11	11	6	11	63

* See Methods for details on sources of the animals placed in the experimental population.

period) to −0.426 for the WPC subpopulation, but percent underestimations were similar for both groups (17–27%). The age and sex classes within the WPC subpopulation had similar removal rates, ranging from −0.419 to −0.440, and the percent underestimations ranged from 17.1 to 39.4% (Table 5); the two most underestimated classes were also the smallest. The PLE subpopulation had highly variable removal rates among the different age and sex categories (−0.523 to −0.821), although the percent underestimations were generally lower than those in the equivalent WPC classes (Table 5).

The high values for the correlation coefficient within each group (Tables 4 and 5) indicate that the individuals within those categories were removed from the population at approximately equal rates throughout the removal period. However, the removal rates varied greatly between groups (0.421 to 0.821), but not enough to produce a low correlation coefficient for data from the entire population.

The 95% confidence intervals for N were determined only for the entire population, and are given by $61.02 \leq N \leq 65.76$, with a point estimate of 63.30 individuals.

Within any natural population, there probably exists a continuum of degrees of catchability. However, within the bounds of this study, there appears to be two biostatistically important groups. Chipmunks that were captured more frequently during the mark-recapture phase were also, on the average, removed earlier during the removal phase (37 individuals removed on day one had an average of 4.03 previous captures; 14 individuals removed on day two had an average of 2.43 previous captures; 6 individuals removed on day three had an average of 2.67 previous captures; 5 individuals removed on day four had an average of 1.80 previous captures; 1 individual removed on day five was never previously captured). It therefore appears that the chipmunk population contained two types of animals—those that were relatively easy to capture (and contribute to the high r^2 in regression analysis), and others that rarely entered traps. The removal rates referred to in Tables 4 and 5, then, are the removal rates for that group of chipmunks within each category that is relatively easy to trap; hence, the removal method underestimates the size of the various subpopulations as well as the population as a whole. Five days of removal trapping were apparently

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FIG. 1.—Point population estimates and 95% confidence intervals for the Lincoln-Petersen (solid line), Schnabel (dotted line), and Schumacher-Eschmeyer (dashed line) methods. The actual population size (82 individuals) is indicated by a solid horizontal line. In general, confidence limits decrease with increased sampling; only the confidence intervals generated by the Lincoln-Petersen Method consistently include the actual population size.

TABLE 4.—*Least squares linear regression analyses for the entire eastern chipmunk population and its constituent classes.*

	Entire population	Site		Sex		Age	
		PLE	WPC	Male	Female	Adult	Juv.
Correlation coefficient	−0.997	−0.999	−0.993	−0.996	−0.996	−0.989	−0.992
Removal rate (slope)	−0.576	−0.662	−0.426	−0.496	−0.660	−0.504	−0.682
Population estimate	63.26	38.99	25.48	32.31	31.29	36.28	27.22
Actual population size	82	47	35	42	40	49	33
Percent underestimate	22.9	17.0	27.2	23.1	21.8	26.0	17.5

adequate to remove the easily trapped animals from the island. The tendency to underestimate the number of chipmunks in each group occurred because 5 days of removal trapping were insufficient to trap significant numbers of individuals from the hard-to-capture portion of the population. The inability of the removal method to define accurately the true population size is not so much attributable to sex, age, or site differences among the component individuals in the experimental population as it is to the fact that all categories contain difficult-to-trap animals; this deflates the final estimate in the removal method.

DISCUSSION

All of the mark-release population estimates utilized in this study possess the property of having smaller confidence limits with increasing sample size. Thus, the precision of the estimate increases with increasing trapping effort, although this does not necessarily mean that the accuracy of the various techniques increases in like manner. In fact, all of the point estimates calculated during the later phases of the study for the three methods were within 25% of the actual population size. Nevertheless, there are important differences among the techniques. Our data allow us to compare their accuracy and precision and to make recommendations as to which method is the most desirable.

The Schumacher-Eschmeyer Method yielded point estimates comparable to those of the other techniques, but because it is the most mathematically elaborate of the three, its confidence intervals are the narrowest and tended not to include the known population size at the 95% level. The Schnabel Binomial Technique, intermediate in mathematical sophistication between the other two methods, also possessed 95% con-

TABLE 5.—*Least squares linear regression for WPC and PLE subpopulations of the eastern chipmunk by sex and age.*

	WPC site				PLE site			
	Sex		Age		Sex		Age	
	Males	Females	Adult	Juv.	Males	Females	Adult	Juv.
Correlation coefficient	−0.976	−0.976	−0.976	−0.732	−0.995	−0.999	−0.990	−0.999
Removal rate (slope)	−0.440	−0.419	−0.440	−0.429	−0.523	−0.821	−0.582	−0.721
Population estimate	9.69	15.75	19.38	5.8	22.62	17.14	17.04	22.10
Actual population size	16	19	26	9	26	21	23	24
Percent underestimate	39.4	17.1	25.5	35.6	13.0	18.4	25.9	7.9

fidence limits of intermediate width, but they too generally excluded the actual population size. All three mark-release point estimates tended to underestimate the known population size by about 15% in the later stages of the study, and only the Lincoln-Petersen Estimate (mathematically the least complicated of the three methods) always included the actual population size within its broader 95% confidence limits.

Examination of Fig. 1 in some detail yields a number of points. At the sixth sampling period, the Lincoln-Petersen Index gave a point estimate of 68 chipmunks, with the 95% confidence interval spanning 41 to 113 animals. By the thirteenth sampling period, the point estimate had risen to 75 chipmunks, with confidence limits ranging from 70 to 88. This last estimate is exceedingly accurate and precise, but it should be noted that there is daily variation in both the point estimates and their confidence limits. Thus, the Lincoln-Petersen estimate for the twelfth sampling period was 79 chipmunks, with the 95% confidence limits ranging from 68 to 108 animals. This estimate is only marginally superior to that obtained as early as the sixth sampling period. Nonetheless, it is evident that, on the average, confidence limits for the Lincoln-Petersen Index were narrower during the later sampling periods, while point estimates approximated the known population size.

Of the three techniques we examined, the Chapman Modification of the Lincoln-Petersen Index was the best technique to estimate the known population size of chipmunks. It is also the simplest estimate to calculate and requires the fewest assumptions about the organisms in question. We feel that it is precisely this lack of biological and mathematical complexity that makes this technique the most robust. In our experimental design we were able to control for immigration, emigration, reproduction, and death; we also were able to eliminate edge effects from animals in other habitats and neighboring populations. However, we were not able to control for catchability, and, indeed, we determined that our experimental population was composed of individuals that were differentially trappable. Further, this unequal catchability was apparently not related to previous exposure to traps, but rather seemed to be an individual trait appearing throughout the population. It appears then that the assumption of equal catchability, which is a prerequisite of most mark-release techniques, would seldom if ever be met in a large population. Even with this assumption being violated, however, the Lincoln-Petersen Index was still able to provide an acceptable estimate of the actual population size.

Of the various assumptions necessary in mark-release studies, we would suppose that immigration and emigration would be fairly well balanced over a short time period. Similarly, the processes of birth and death should be negligible over such time periods. The two remaining critical assumptions are catchability and random sampling of the population. Obviously these assumptions are not independent and a violation of one perforce indicates a violation of the other. Our field experience with many species of small mammals leads us to suggest that differential trappability is probably widespread in nature, and there is some support for this idea in the literature (Geis, 1955; Eberhardt et al., 1963; Edwards and Eberhardt, 1967; Nixon et al., 1967; Strandgaard, 1967; Gliwicz, 1970; Andrzejewski and Rajska, 1972; Perry et al., 1977; and others). Thus, this may be an important factor that is overlooked in many population studies; because of this, population estimation techniques whose precision is generated by rigorous adherence to assumptions of randomness of capture are doomed to yield results whose apparent precision is illusory.

It is particularly important to recognize the unrefined nature of population estimation techniques that utilize mark-release data when population sizes are compared over time. For example, using the Lincoln-Petersen Technique in the current investigation, we were 95% certain that the actual population size for the twelfth sampling period lay somewhere between 68 and 108 chipmunks. Given this broad range of possibilities, it would be exceedingly difficult to discern trends of population change with any statistical reliability. Unfortunately, statistical comparisons of population sizes are probably often based upon estimates whose underlying assumptions have been violated, thus invalidating any further analyses of these estimates. We suppose there is a tendency to choose a particular population estimation technique because it seems to yield answers of great precision which then lend themselves to further statistical comparison with estimations obtained for other populations. However, the use of such estimates could lead to incorrect conclusions regarding the actual population sizes in two or more areas or in different time periods. The great precision of the Schumacher-Eschmeyer Method, for example, could result in estimates suggesting significant differences between population sizes when, in fact, the populations do not differ in size. Utilizing the Lincoln-Petersen Index with its broader confidence limits would be more conservative, tending to make the detection of subtle differences in population size difficult.

Because of the great probability of violating one or more of the underlying assumptions that are necessary for an accurate determination of population size, we suggest that broader confidence limits are the only means of ensuring an acceptable concordance between the estimate and the actual population size. While this implies that small differences among estimates will be undetectable, this fact appears to be unavoidable in studies whose accuracy depends upon numerous uncontrolled variables and unrealistic assumptions. We believe that the tenuous nature of population estimates must be taken into account by any investigator attempting to compare population sizes or to explain apparent, but perhaps not real, differences.

Edwards and Eberhardt (1967) found that the Lincoln-Petersen Method was the most accurate estimation of a known population of cottontail rabbits, while both the Schnabel and Schumacher-Eschmeyer methods "grossly underestimated" the sample population; neither of the latter two methods included the actual population size within their 95% confidence limits. Strandgaard (1967) suggested that it was necessary to mark at least 66% of a population of roe-deer before the Lincoln-Petersen Method yielded a reliable estimate of population size. In this study, we had captured 77% of the chipmunks by the ninth sampling period, whereas 88% of the population had been captured by the end of the study. Relatively good estimates were obtained by the Lincoln-Petersen Technique for all of the later periods. The percentages of animals caught during sampling periods 6, 7, and 8 were 61, 70, and 74, respectively. Although the point estimate during each of these periods was comparable to that obtained during later periods, the precision of the technique at this time was low because the confidence limits were large. Thus we did not begin to get a relatively accurate and precise estimate of the population size until about 75% of the animals had been captured at least once. This fact supports the suggestion of Strandgaard (1967) that it is necessary to capture a large portion of the population under study in order to arrive at a realistic assessment of its actual size. This result also points out the need for avoiding sampling periods of very short duration during which only a small percentage of the entire population can be captured. In populations composed largely of individuals that are difficult to trap, it may not be possible to obtain a precise or accurate estimate of the population size via mark-release techniques. The length of the trapping period must be increased in order to capture a larger percentage of animals; this causes the probability of violating one or more of the assumptions regarding mortality, natality, immigration, or emigration to increase. Given such a population, other techniques of population estimation might have to be developed or employed.

Because of differences in the trappability of chipmunks within the experimental population, the Removal Method of sampling was the least accurate technique we examined. The readily-trapped animals were removed early in the study, and the remaining fraction, largely composed of hard-to-catch individuals, only gradually appeared in the later trapping periods. Thus regression lines based on these data tended to underestimate the population. More importantly, this method yielded small confidence intervals because the readily-trapped animals were equally easily captured (i.e., there was small deviation from the calculated regression line). This resulted in the most inaccurate estimate of all the methods examined, one whose ostensive precision was meaningless.

In conclusion, our results suggest the following points. (1) The Removal Method of population estimation should be avoided because its results are inaccurate and misleadingly precise. (2) The Schumacher-Eschmeyer Technique should not be used for populations of small mammals whose homogeneity of capture response is undefined. Great caution should be exercised in making statistical comparisons of population estimates determined by this method because its precision may mask its lack of accuracy. (3) The Schnabel Technique suffers from the same limitations as the Schumacher-Eschmeyer Method and should not be used for any species that must be enticed into entering traps. (4) The Lincoln-Petersen Index was the easiest and most accurate method of population estimation in this study. The unrefined nature of this technique contributes to its accuracy but precludes the detection of subtle differences between estimates. (5) The estimation of abundance in natural populations is subject to great inaccuracy because of the failure of mathematical assumptions to account adequately for the dynamic variability characteristic of animal populations. The approximate nature of most estimates should be recognized by investigators, and great care exercised in drawing conclusions whose validity is based on the necessity of obtaining a determination of abundance that is both accurate and precise. (6) Estimation techniques that incorporate variable trap response by animals need to be developed before one can compare population estimates with confidence.

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