ACTA THERIOLOGICA
Vol. 26, 31: 459—468, 1981

Comparative Accuracy of Population Estimators for Enclosed Small Mammal Populations

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Peterjohn W. T., Patterson J. L., Barrett G. W. & Farrell M. P., 1981: Comparative accuracy of population estimators for enclosed small mammal populations. Acta theriol., 26, 31: 459—468 [With 1 Table].

Density estimates for populations of *Mus musculus* and *Microtus pennsylvanicus* of known size were obtained from three perturbation studies conducted on enclosed grassland and old-field communities. The comparative accuracy of Jolly's stochastic method, a modified Schnabel census, Overton's method, the calendar-of-catches procedure, and Hayne's removal method was evaluated. Large overestimations were obtained from the Jolly procedure with mean percent errors ranging from 196 to 1245%. All other estimators produced similar mean percent errors which ranged from 12 to 46%. *Microtus* populations were underestimated by the Overton, calendar-of-catches, and Schnabel procedures in 92% of the cases. *Mus* populations were overestimated in 60% of the cases by the Schnabel and Overton methods, but were consistently underestimated by the calendar-of-catches method. Differences in catchability between species, the existence of trap-prone individuals within a species, and inherent biases of the estimators conspired to account for the inaccuracies. The estimators appear sensitive to population trends but may be inadequate for the determination of actual population size at a specific time in the total growth curve.

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I. INTRODUCTION

Selection of an appropriate technique for estimating population density is critical in most studies of population, community, or ecosystem ecology. Choice of a particular estimator has often focused on the degree of mathematical complexity or the availability of time, money, and equipment. Although statistical accuracy is of primary importance, it is frequently sacrificed for these practical considerations (Begon, 1979).

Techniques currently used for estimating the population density of small mammals consist mainly of mark-recapture and removal methods. The Schnabel estimate (Schnabel, 1938) is one of the most commonly used mark-recapture methods. The Schnabel estimator is a weighted mean of a continuous series of Lincoln indices (Petersen, 1896).

Overton's procedure (Overton, 1965), a variation of the Schnabel estimate, mathematically adjusts for known removals within the population and is, therefore, considered a more realistic model when trapping fatalities are known to occur. The calendar-of-catches method (Petrusewicz & Andrzejewski, 1962) is another recapture procedure in which a capture history ("calendar") is kept for each animal, followed by a period of intensive removal to "update the calendar" upon termination of the study. Population estimates from recapture data can also be made by Jolly's stochastic method (Jolly, 1965) in which estimates are adjusted by the probabilities associated with recapture and survival.

Hayne (1949) provided a common estimator of population size based on removal data. A plot is made of the number of animals caught per unit effort (y-axis) versus the cumulative number caught (x-axis). A least squares fit of the data is then calculated and the population size estimated by the x-intercept.

All of these methods of estimating abundance make mathematical assumptions (*e.g.*, no emigration, unaltered trapping behavior, equal probability of capture, and random sampling). These assumptions are rarely satisfied under field conditions (Krebs, 1966; Eberhardt, 1969; Smith *et al.*, 1971). Field studies have shown the influence of breeding (Ramsey & Briese, 1971), weather (Gentry *et al.*, 1966; Marten, 1973), and behavior (Crowcroft & Jeffers, 1961; Cormack, 1968) on trapping success and, therefore, on density estimates. Thus, violation of underlying assumptions often makes it impossible to correct estimates for inaccuracies.

Several studies have attempted to compare a population of known size to estimates of that population generated by various mathematical procedures (Gębczyńska, 1966; Ryszkowski *et al.*, 1966; Smith, 1968; French *et al.*, 1971; Gromadzki & Trojan, 1971, & others). However, in many of these studies the populations were not confined to enclosed ecosystems, of comparisons were not between populations living in identical community-types and experiencing similar climatic conditions. The purpose of this study was to compare the accuracy of several population estimators for small mammal populations of known densities in enclosed ecosystems replicated for community-type and season.

II. MATERIALS AND METHODS

Data on feral house mouse (*Mus musculus*) and meadow vole (*Microtus pennsylvanicus*) populations were obtained from two studies conducted in enclosed grassland and old-field communities at the Miami University Ecology Research

Center, Oxford, Ohio, U.S.A. These studies investigated the effects of fire and pesticide perturbations on structural and functional relationships among various community components, including small mammal population dynamics. Details of the procedures used and results obtained have been summarized by Crowner and Barrett (1979), Suttman and Barrett (1979), and Anderson and Barrett (in preparation). The theory and research guidelines for these investigations have been previously presented (Barrett *et al.*, 1976).

The 1969 fire perturbation study was conducted in two 1-acre (0.4-ha) grids planted in oats (*Avena sativa*). Twenty-nine plant species were found in each grid (Crowner & Barrett, 1979). The dominant plant species before burning were oats, giant foxtail (*Setaria faberii*), and common ragweed (*Ambrosia artemisiifolia*). It should be noted that the computations in the present study were based on only the control grid of the fire perturbation study (Crowner & Barrett, 1979) because both *Mus* and *Microtus* populations had disappeared by the time the investigation was terminated.

The 1971 pesticide (Sevin) study was conducted in eight quarter-acre (0.1-ha) grids also planted in oats. All grids were permitted to proceed into secondary succession in 1972 (Suttman & Barrett, 1979). The planted grids in 1971 were dominated by oats, common ragweed, giant foxtail, and daisy fleabane (*Erigeron annuus*). The following year the resulting vegetation was dominated by giant foxtail, horseweed fleabane (*Erigeron canadensis*), and Canada goldenrod (*Solidago canadensis*).

Population estimates were obtained using the Overton (1965) method, the calendar-of-catches (Petrusewicz & Andrzejewski, 1962) method, Jolly (1965) stochastic method, a variation of the Jolly method for enclosed populations (Seber, 1973), the Hayne (1949) removal method for 3-, 5-, and 8-day intervals, and a modified Schabel (1938) census in which the marks at risk accumulate for several trapping periods prior to the calculation of an estimate for the last day.

The calendar-of-catches estimates were made one trapping date prior to intensive removal. Both the Overton and modified Schnabel were tabulated for the same period in order to minimize time or trapping biases. Jolly estimates were calculated for the second trapping period prior to removal trapping to compensate (a) for the biases in the other mark-recapture estimates and (b) for the inherent inability of the Jolly method to estimate an end population.

Estimates were calculated separately for replicate 0.1-ha grids and then summed to yield final 0.4-ha values for each species, year, and treatment combination. Pooling these estimates was necessary to facilitate comparison between the 0.4-ha grids used in 1969 and the 0.1-ha grids used in 1971 and 1972. All population density values are expressed as actual population/0.4-ha. The actual population size was determined by removing all individuals from each grid upon termination of each study. The final removal was considered complete when no more animals could be successfully removed from each grid; the total number of animals removed was considered the actual population size for the last trapping date. These values were used to calculate the percent error (estimate-actual/actual×100) for each estimate.

III. RESULTS

Evaluations of temporal, species, treatment, and density effects on the specific estimates are presented, along with a comparison of their respective accuracies (Table 1). None of the estimates had a mean percent error less than 10% when averaged over temporal and treatment factors.

Jolly estimates (both the generalized and modified) tended to overestimate actual population size. Mean percent errors ranged from 196 to 1245%. The modified Jolly overestimated without exception, whereas the generalized formula overestimated in 78% of the cases. The mean percent error for the modified Jolly was approximately 3 times greater than the generalized estimate. No significant correlation

Table 1

Comparative accuracy of small

Species	Year	Stress (S) or Control (C)	Jolly[a] (generalized) Estimate (% Error)	Jolly[a] (modified) Estimate (% Error)	Schnabel[b] (modified) Estimate (% Error)
Mus	1969	C	246 (114)	610 (430)	104 (-10)
	1971	C	64 (49)	186 (333)	59 (37)
	1971	S	61 (-24)	163 (104)	110 (37)
	1972	C	148 (605)	402 (1814)	36 (71)
	1972	S	242 (1412)	583 (3544)	15 (-6)
	Mean % Error		441	1245	32
Microtus	1971	C	54 (-53)	194 (67)	61 (-47)
	1971	S	77 (3)	305 (307)	73 (-3)
	1972	C	17 (112)	90 (1025)	6 (-25)
	1972	S	50 (614)	81 (1057)	5 (-29)
	Mean % Error		196	614	26

[a] Estimates calculated 2 trapping periods prior to removal,
[b] Estimates calculated 1 trapping period prior to removal.
1969 — Fire perturbation, 1971 — Pesticide perturbation, 1972 — Pesticide perturbation.

was found between the percent error and actual population size for either the generalized or the modified formulas ($r=-0.57$, $p>0.2$; and $r=-0.63$, $p>0.1$, respectively). A significant correlation did exist, however, when only the values for modified *Microtus* estimates were considered ($r=-0.99$, $p<0.01$). The difference between species was apparent; the mean percent error for *M. pennsylvanicus* was approximately half the value obtained for *M. musculus*. This held true for both the modified and generalized formulas.

The mean percent error for the Schnabel estimate was similar to the 8-day removal method for *M. musculus* (32 and 33, respectively). Similar mean percent error were determined for the Schnabel (26), the Overton (34), the calendar-of-catches (27), and the 5-day removal (25) methods for *M. pennsylvanicus*. The Schnabel method underestimated *M. pennsylvanicus* populations in all cases and was more nearly accurate for intermediate densities (75 mice/0.4-ha) than for extremes in density (116 and 7 mice/0.4-ha). The inverse of the relationship was true for *M. musculus,* with greater accuracy being achieved for extremes in densities (115 and 16 mice/0.4-ha) than for intermediate densities (80, 43, and 21 mice/0.4-ha). No significant correlation between population size and percent error was found for *Microtus* ($r = -0.26$, $p > 0.1$) or for *Mus* ($r = -0.36$, $p > 0.1$).

The mean percent error for Overton's method (12) was comparable to the calendar-of-catches method (19) for *M. musculus.* For *M. pennsylvanicus,* the mean percent error of Overton's method (34) was similar to that of the Schnabel (26), calendar-of-catches (27), 3-day removal (41), and the 5-day removal (25) methods. *Microtus* populations were underestimated in all cases and accuracy was approximately 3 times greater for *Mus* populations than for *Microtus* populations. No significant density effect was observed for either *Mus* or *Microtus* populations ($r = 0.16$, $p > 0.1$; $r = 0.85$; $p > 0.2$, respectively).

mammal population estimates.

Overton[b] Estimate (% Error)	Calendar-of-[b] Catches Estimate (% Error)	Removal 3 days Estimate (% Error)	Removal 5 days Estimate (% Error)	Removal 8 days Estimate (% Error)	Actual Density (No./0.4-ha)
108 (-6)	99 (-14)	120 (4)	113 (-2)	110 (-4)	115
56 (30)	34 (-21)	85 (98)	62 (44)	61 (42)	43
96 (20)	52 (-35)	154 (92)	104 (30)	122 (52)	80
20 (-5)	18 (-14)	21 (0)	18 (-14)	—	21
16 (0)	14 (-12)	22 (38)	—	—	16
12	19	46	23	33	
54 (-53)	67 (-42)	52 (-55)	64 (-45)	89 (-23)	116
53 (-29)	48 (-36)	127 (69)	53 (-29)	76 (1)	75
6 (-25)	8 (0)	9 (12)	8 (0)	—	8
5 (-29)	5 (-29)	5 (-29)	—	—	7
34	27	41	25	12	

The calendar-of-catches method underestimated the actual population size in 89% of the cases. Greater accuracy was obtained for extremes in *Mus* density (116 and 16 mice/0.4-ha) when compared to intermediate densities (80, 43, and 21 mice/0.4-ha). For *Microtus,* no significant correlation was found between population size and percent error ($r = 0.77$, $p > 0.1$). This was also true when all estimates were considered ($r = 0.56$, $p > 0.2$).

Results indicate that the removal method is more nearly accurate at extremes in density for both *Mus* and *Microtus* populations. No apparent difference in the mean percent errors between species existed, except for the 8-day removal, when a difference of 20.6% was observed. Extension of the removal period to 3, 5, and 8 days increased the accuracy of the estimates for *Microtus* populations, but not for *Mus*.

IV. DISCUSSION

Carothers (1973) recognized that bias in estimates of population density arises from failure of one or more of the underlying assumptions (*e.g.*, small sample size). Violation of assumptions commonly occurs in field studies employing mark-recapture methods (Young *et al.*, 1952; Crowcroft & Jeffers, 1961; Gentry *et al.*, 1966; French *et al.*, 1971; Summerlin & Wolfe, 1973). Computer simulations have also been employed to observe the effects of violating various assumptions (Manly, 1970; Carothers, 1973) and the intrinsic bias of the estimator when all assumptions are met (Gilbert, 1973). This study, using data generated for 2 small mammal species in enclosed systems replicated for season and community-type, allowed the evaluation of various estimates under the constraints of field conditions.

Results demonstrated dramatic discrepancy between the Jolly stochastic method and all others. This is inconsistent with French *et al.* (1971), who found Jolly's method to be superior for estimating rodent population size. The reasons for the large overestimation may be twofold. First, estimates were determined at the farthest point from the mid-trap day, which is felt to be the day giving the most nearly accurate population estimate (Cormack, 1972; Gilbert, 1973). The second possible explanation would be the existence of a "small sample" bias which often causes an overestimation of actual population size (Carothers, 1973). This might result from an insufficient number of traps being set or by a small population size. Indications that such a bias was incurred were given by the strong negative correlation between the percent error of the modified estimates and the actual population size for *Microtus* and by the reduced accuracy for both estimators during 1972 when the lowest population sizes existed for both species. The Jolly method apparently requires a large sample size for accurate estimates (Manly, 1970), which may present a serious problem in the study of fluctuating natural populations where it is often impossible to maintain sample sizes above a predetermined level. Results from the modified formula were less accurate than the generalized form. Cormack (1968) stated that the generalized form is preferable.

The Schnabel, Overton, and calendar-of-catches methods had mean percent errors of similar magnitude. The consistent underestimation of *Microtus* populations by the Overton and Schnabel methods was probably due to the greater difficulty in trapping *Microtus* (Beacham & Krebs, 1980) and/or the existence of a trap-prone segment of the population (Cormack, 1972).

The calendar-of-catches method consistently underestimated both *Mus* and *Microtus* populations, which was attributable to the fact that some animals were never captured during the study, although their presence became known after intensive removal was initiated. Underestimates might also be caused by offspring reaching catchable age between the time of estimation and the initiation of the removal period. Furthermore, estimates were made from data recorded in December or January. Although *M. musculus* may breed during the winter (Pomeroy & Barrett, 1975; Crowner & Barrett, 1979), increased breeding normally occurs between March and October (Lidicker, 1966). Therefore, it is doubtful that many animals reached a trappable age during the 1 to 2 weeks between trapping periods.

Gentry *et al.* (1968) evaluated the accuracy of removal estimates for various trapping intervals. They concluded that at least 9 days of trapping are necessary for accurate population density estimates and that the length of the trapping period appears to be species dependent. Our data tend to support their conclusions.

It appears that community-type (*e.g.*, agriculture vs. old-field) caused a direct effect on actual population size and, thus, on the accuracy of the estimators. For example, both *Mus* and *Microtus* population densities were greatly reduced in the 1972 old-field community as compared to the agricultural grids. This relationship appeared to cause a significant increase in the percent error for the generalized and modified Jolly estimators.

The development of various new estimators and modifications of existing ones will, we hope, increase the accuracy of population estimates. This accuracy appears to be dependent on the behavior of each species. On the basis of this study, it appears that current methods of estimating small mammal populations are sensitive to population fluctuations, but may inadequately support studies where extremely accurate population estimates are needed. Critical population comparisons between different species must be evaluated in terms of such factors as species behavior, population size, and community-type.

Acknowledgements: This study was partially supported by NSF Grant 20975 awarded to Barrett. We thank the cadre at the Miami University Ecology Research Center for field assistance and Mrs. Ruth McLeod for manuscript preparation.

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Accepted, May 15, 1981.

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PORÓWNANIE DOKŁADNOŚCI OCEN ZAGĘSZCZENIA ZAMKNIĘTYCH POPULACJI MAŁYCH SSAKÓW

Streszczenie

Oceny zagęszczenia znanych populacji *Mus musculus i Microtus pennsylvanicus* uzyskano w eksperymentach nad wpływem pożaru i pestycydów na biocenozy na ogrodzonej łące i ugorze porolnym. Ocenę względnej dokładności przeprowadzono stosując stochastyczną metodę Jolly'ego, zmodyfikowany wzór Schnabela, metodę

Overtona, kalendarz złowień i metodę wyłowu Hayne'go. Stosując metodę Jolly'ego uzyskano największe przeceniane zagęszczenia, przy czym średni procent błędu sięgał od 196 do 1245% (Tabela 1). Wszystkie pozostałe metody dają podobny średni procent błędu wynoszący od 12 do 46%. Populacje *Microtus* były niedodoszacowane metodą Overtona, kalendarzem złowień i metodą Schnabela, w 92% przypadków. Ocena liczebności w populacjach myszy była zawyżana w 60% przypadków przez metody Schnabela i Overtona, lecz zaniżana przy użyciu kalendarza złowień (Tabela 1). Błędy w oznaczeniach liczebności wynikają, jak można sądzić, z różnic w łowności obu gatunków, jak i zróżnicowanej reakcji na pułapkę między poszczególnymi osobnikami danego gatunku.