OPTIONAL FORM NO. 10
MAY 1962 EDITION
GSA FPMR (41 CFR) 101-11.6

UNITED STATES GOVERNMENT

Memorandum

TO : Refuge Manager, Blackwater Refuge

DATE: September 28, 1970

FROM : Assistant Regional Supervisor, Division of Refuges, Atlanta

SUBJECT: Squirrel population estimates derived from live trapping data

Attached find a reprint of an article from the Journal of Wildlife Management entitled "Estimating Squirrel Abundance from Live Trapping Data" by Nixon, Edwards and Eberhardt. The material contained in this reprint may be useful to you in carrying out the proposed wildlife management study on the Delmarva Peninsula Fox Squirrel.

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Reprinted from THE JOURNAL OF WILDLIFE MANAGEMENT
Vol. 31, No. 1, January 1967
pp. 96–101

ESTIMATING SQUIRREL ABUNDANCE FROM LIVETRAPPING DATA

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ESTIMATING SQUIRREL ABUNDANCE FROM LIVETRAPPING DATA[1]

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Abstract: Estimates of squirrel (*Sciurus carolinensis* and *S. niger*) abundance were derived from several methods of population estimation applied to data obtained by livetrapping squirrels on the Waterloo Wildlife Experiment Station in southeastern Ohio, 1962 and 1963. The frequency of capture of marked squirrels suggests that the probability of capture is not the same for all squirrels; as a result, a trapped sample typically contains a disproportionately high number of recaptures. Thus, the multiple census methods of Schnabel and of Schumacher produced estimates lower than the number of animals considered to comprise the population. Frequency of capture approximated the geometric distribution. The simplified equation for maximum likelihood estimation (MLE) for the geometric distribution, presented in 1967 by Edwards and Eberhardt, appeared useful for estimating squirrel abundance from livetrapping data, although estimates tended to be somewhat high. The intercept of a line fitted to a logarithmic plot of data on the frequency of capture, using linear regression techniques, gave what appeared to be adequate approximations of the numbers of squirrels in the zero (uncaptured) class. Although estimates derived from MLE for the geometric distribution and from linear regression are based on assumptions not strictly fulfilled by the data, these methods should prove useful until better techniques are developed. MLE for the Poisson distribution appeared to underestimate the zero class. Similarities in results of evaluations of techniques of population estimation for squirrels and rabbits suggest that further research on population estimation may provide findings applicable to a variety of species.

A primary method of estimating populations of squirrels has been the use of ratios of marked to unmarked, the well-known Petersen, or Lincoln Index method (Davis 1963:107). This method is satisfactory provided (1) that sample sizes are adequate and (2) that the samples used to estimate the marked to unmarked ratios are unbiased. The multiple censuses of Schnabel (1938), and of Schumacher (Schumacher and Eschmeyer 1943), were developed to estimate fish populations and have been used extensively in the census of small mammals. Our concern in the following analysis was the accuracy of these multiple census techniques for estimating squirrel

[1] A contribution from Federal Aid in Wildlife Restoration Project Ohio W-105-R, the U. S. Bureau of Sport Fisheries and Wildlife and the Ohio Department of Natural Resources, cooperating.

Work performed in part under contract AT(45-1)-1350 between the Atomic Energy Commission and the General Electric Company.

populations and the possible application of methods of estimation suggested for cottontails (*Sylvilagus floridanus*) by Edwards and Eberhardt (1967). Our objective was to determine an adequate estimating technique which would not require use of samples of squirrels killed by hunters or observed on transects. We wished to evaluate estimates derived from livetrapping data because livetrapping requires the activities of only one or two men for a relatively short period of time.

We wish to express our appreciation to the personnel at the Waterloo Wildlife Experiment Station who assisted in the squirrel trapping and operation of hunter checking stations, and to Mrs. Helen C. Schultz and Dr. Glen C. Sanderson of the Section of Wildlife Research, Illinois Natural History Survey, for critically reading the manuscript.

METHODS

The study area occupied 237 acres of continuous forest habitat on the 1,250-acre Waterloo Wildlife Experiment Station, Athens County, Ohio. The area is part of the low hills portion of the mixed mesophytic forest region in unglaciated southeastern Ohio. Both fox and gray squirrels occur on the area, with gray squirrels comprising about 85 percent of the squirrel population. The timber stands tend to be even aged, averaging 65 years.

The study area was gridded on a 3 × 3-chain interval, with a trap placed at the discretion of the trapper within a ⅛-acre plot surrounding each point of intersect. The resulting trap density was essentially one (0.96) trap per acre. Traps used were those described by Baumgartner (1940), modified with a galvanized metal inner lining to prevent chewing out. Traps were baited with English walnuts for 10 days before each trapping period as well as each day of trapping.

Table 1. Summary of captures for computing population estimates, using the methods of Schnabel (1938) and Schumacher and Eschmeyer (1943), from data obtained by livetrapping squirrels on the Waterloo Wildlife Experiment Station, Athens County, Ohio, 1962 and 1963.

Year	Trap Day	No. Caught C_t	Recaptures R_t	No. Marked in Population M_t
1962	1	22	0	0
	2	13	7	22
	3	15	10	28
	4	10	5	33
	5	6	5	38
	6	5	3	39
	7	15	10	41
	8	11	6	46
	9	18	8	51
	10	8	7	61
	11	16	10	62
	Totals	139	71	68
1963	1	38	0	0
	2	29	19	38
	3	31	23	48
	4	16	13	56
	5	20	19	59
	6	18	17	60
	7	17	14	61
	8	19	13	64
	9	16	14	70
	10	14	14	72
	11	5	5	72
	Totals	223	151	72

Trapping was done for 11 consecutive days in August and September, 1962 and 1963, just before the hunting season. All squirrels captured were ear-tagged and released at their points of capture. Hunters were required to check in and out of the Experiment Station, present their game for examination at the checking station, and report the locations where squirrels were bagged. Squirrels killed by the hunters on the study area provided a sample of animals for which the marked to unmarked ratio could be determined and allowed estimates to be computed using the Lincoln Index method (Davis 1963:107), which

Table 2. Frequency of capture of squirrels on the Waterloo study area in 1962, with expected values computed for several methods of estimation. Chi-square values* (in parentheses) serve as a basis for comparing the goodness of fit of the observed values with the models.

Frequency of Capture (1)	Observed (2)	Schnabel MLE (3)	Schumacher & Eschmeyer (4)	Geometric Model: Regression (5)	Geometric Model: MLE (6)	Poisson Model: MLE (7)
0	43.5†	11.7	10.3	51.1	65.1	16.1
1	33	24.1 (3.29)	22.7 (4.67)	28.8 (0.61)	33.3 (0.003)	26.6 (1.54)
2	16	22.5 (1.88)	22.4 (1.83)	16.2 (0.003)	17.0 (0.06)	22.0 (1.64)
3	10	12.8 (0.61)	13.5 (0.91)	9.1 (0.09)	8.7 (0.19)	12.1 (0.36)
4	4					
5	2	6.6 (1.75)	7.2 (0.45)	13.9 (1.73)	9.0 (0.00)	7.3 (0.40)
6	3					
$\hat{N}$	111.5±27.6	77.7	76.1	119.1	133.1	84.1

* Chi-square criteria were computed by fitting the observed values to distributions derived for the models, using the individual population estimates. Criteria were not computed for the estimated number in the zero class because suitable criteria were not available. Chi-square criteria were computed as: $(O-E)^2/E$.

† Derived using population estimate obtained using the Lincoln Index (Davis 1963:107) method based on the occurrence of marked squirrels taken by hunters.

served as a partial basis for evaluating estimates derived from data obtained by livetrapping. As with most techniques of population estimation, the accuracy of the Lincoln Index method is not above question, as its assumptions may not be fulfilled. However, estimates derived from the Lincoln Index were not subject to the bias of differential trap response.

At the time of trapping, the squirrel population contained three age cohorts: adults, early-litter juveniles, and late litter juveniles still in the nests; our estimates apply only to the first two cohorts.

FINDINGS

Livetrapping from August 28 through September 7, 1962, resulted in the capture and marking of 68 squirrels. Trapping from August 2[illegible] through September 3, 1963, resulted in the tagging of 72 squirrels. In 1962, 41 squirrels, including 25 marked, were shot on the study area. In 1963, only 30 squirrels, 17 marked, were taken. Using these data, the Lincoln Index method (Davis 1963:107) yielded estimates, with 95 percent confidence limits, of 112 ± 28 and 127 ± 41 squirrels on the study area in 1962 and 1963, respectively. Unfortunately, the sample of squirrels taken by hunters was too small to provide estimates of high precision for either 1962 or 1963.

The Schnabel (1938 *in* Ricker 1958:101; [3.13], [3.14]) method used on data obtained during livetrapping (Table 1), provided estimates of 70 and 69 squirrels respectively, in 1962 and 1963. Because Schnabel's method only approximates the MLE of the population (N), DeLury's iterative solution (1951 *in* Ricker 1958:101; [3.15], [3.16]) of the true maximum likelihood equation for Schnabel's method, which consists of adjusting by a series of weights, was used to obtain estimates of 78 and 73 squirrels for the two years, respectively (Tables 2 and 3). Estimates obtained using Ricker's (1958:101) modification of the Schumacher method were 76 and 71 squirrels in 1962 and 1963, respectively (Tables 1, 2, and 3).

It is our opinion that the multiple censuses of Schnabel and Schumacher when applied to our data provided estimates lower than the actual number of squirrels in the pop-

Table 3. Frequency of capture of squirrels on the Waterloo study area in 1963, with expected values computed for several methods of estimation. Chi-square values* (in parentheses) serve as a basis for comparing the goodness of fit of the observed values with the models.

FREQUENCY OF CAPTURE (1)	OBSERVED (2)	SCHNABEL MLE (3)	SCHUMACHER & ESCHMEYER (4)	GEOMETRIC MODEL Regression (5)	GEOMETRIC MODEL MLE (6)	POISSON MODEL MLE (7)
0	55.1†	1.9	1.7	25.4	34.4	4.0
1	23	8.7 (23.50)	7.5 (32.03)	19.2 (0.75)	23.3 (0.004)	11.9 (10.35)
2	14	16.6 (0.41)	15.3 (0.11)	14.6 (0.02)	15.8 (0.21)	17.4 (0.66)
3	9	19.1 (5.34)	18.4 (4.80)	11.0 (0.36)	10.7 (0.27)	17.2 (3.91)
4	6	14.7 (5.15)	14.7 (5.15)	8.3 (0.64)	7.2 (0.20)	12.6 (3.46)
5	8	7.9 (0.001)	8.4 (0.02)	6.3 (0.46)	4.9 (1.96)	7.4 (0.05)
6	7					
7	3	4.1 (15.22)	4.6 (11.90)	12.6 (0.03)	10.1 (0.36)	5.5 (7.68)
8	0					
9	2					
$\hat{N}$	127.1±40.6	73.0	70.6	97.4	106.4	76.0

* Chi-square criteria were computed by fitting the observed values to distributions derived for the models, using the individual population estimates. Criteria were not computed for the estimated numbers in the zero class because suitable criteria were not available. Chi-square criteria were computed as: $(O-E)^2/E$.

† Derived using population estimate obtained using the Lincoln Index (Davis 1963:107) method based on the occurrence of marked squirrels taken by hunters.

ulation in both 1962 and 1963. In support of this position we note that (1) multiple census estimates were considerably less than those obtained using the Lincoln Index method, and (2) there was a generally poor fit of the observed values for frequency of capture to the expected values (Tables 2 and 3). Apparently a differential probability of capture existed among squirrels, which resulted in a disproportionately high number of recaptures; thus, the populations were underestimated. This is in agreement with Flyger (1959:221), who reported considerably lower estimates using Schnabel's method than were derived from sight records of color-marked squirrels, and it also agrees with the data obtained on cottontails by Edwards and Eberhardt (1967).

Provided probability of capture is relatively small (usually $p < 0.10$) and the same for all members of the population, frequency of capture should approximate the Poisson. Although probability of capture was in the range of 0.10 to 0.20 per squirrel per day, we proceeded to compute estimates using Hartley's (1958:174) method of MLE for the Poisson distribution with missing data; respective values for 1962 and 1963 were 84 and 76 (Tables 2 and 3).

Considering that the estimates from MLE for the Poisson distribution were well below Lincoln Index estimates and that the observed values gave a generally poor fit to the Poisson distribution, we conclude that MLE for the Poisson did not produce satisfactory estimates from these data.

Eberhardt et al. (1963) proposed that populations of small mammals be estimated from the frequency of capture of individual animals (as opposed to methods based on marked to unmarked ratios) during live-trapping. Techniques for estimating cottontail populations are demonstrated by Edwards and Eberhardt (1967). The principle is that a trapped population contains animals captured 0, 1, 2, 3, . . . *n* times, and that these data follow a distribution which can be adequately approximated by a theoretical frequency distribution. Because the numbers of animals captured 1, 2, 3, . . .

n times are known, the problem is to find a model which provides the best estimate of the number in the zero class (those not captured) whose probability of capture is essentially not zero.

Edwards and Eberhardt (1967) point out that logarithmic plots of the frequency of capture of cottontails frequently exhibit linearity and that the zero intercept of a line fit to these data appeared to provide an adequate approximation of the animals not captured; summing the observed and estimated values gives an estimate of population size. They caution that the linear relationship is not always to be expected but, when approximated, may be utilized to provide reasonably satisfactory estimates.

The frequencies of capture of squirrels trapped in 1962 and 1963 were plotted on semilog paper and straight lines fitted by least squares (linear regression). Estimates from linear regression were 119 and 97, respectively, for 1962 and 1963 (Tables 2 and 3). These estimates were closer to the estimates obtained using the Lincoln Index than were the estimates derived from the multiple censuses of Schnabel (1938) and Schumacher (Schumacher and Eschmeyer 1943). Thus, it appears that, as Edwards and Eberhardt (1967) observed with cottontails, when data on the frequency of capture of squirrels during livetrapping approximated linearity, the regression techniques produced better estimates than those produced by the multiple census methods.

The simplified derivation of the MLE for the geometric distribution, which Edwards and Eberhardt presented, produced estimates of 133 and 106 in 1962 and 1963, respectively (Tables 2 and 3). Tests for goodness of fit of capture frequency data to the geometric distribution for 1962 and 1963 indicated that the observed values did not differ significantly from those expected.

DISCUSSION

The observed values suggest that probability of capture is not the same for all individuals. While this may have been the result of trap placement or density, we can not rule out differences in the behavior of individual squirrels or the possible role of capture in altering the probability for additional captures. A population may even contain cohorts having a zero probability of capture. The possible effects of factors such as age, sex, and reproductive status should be primary considerations in future studies. The problems of population estimation and trap response are of sufficient magnitude to justify continued research. Future research will probably result in findings applicable to a variety of species.

In this presentation we have endeavored to proceed with caution on the basis of limited and incomplete data and yet provide hypotheses which may result in improved estimates of squirrel populations by using livetrapping data. We have proceeded on the assumption that a mathematical function represents the frequency of capture. The true situation is no doubt much more complex than a simple frequency distribution such as the geometric or Poisson. On the basis of the demonstrated fit of the MLE for the geometric distribution, and of estimates from linear regression, it seems logical to use these methods to obtain indices of squirrel abundance until such time as new or more refined estimating techniques are developed.

Edwards and Eberhardt (1967) made the empirical suggestion that linear regression and MLE for the geometric distribution appeared to give useful estimates when about 50 percent of the population had been captured at least once and the total number of captures was 1½–2 times the number of individuals captured. As shown in Tables 2 and 3, data obtained by livetrapping squirrels apparently satisfied these criteria during both years. We feel that for the present, at least, workers who would use these methods for estimating squirrel abundance should see that their data conform to these criteria.

We caution that the data on which our opinions are based are restricted in that we could not compare our estimates with the actual numbers of squirrels in the populations. For those who would argue that differences between the Lincoln Index and the multiple census estimates may be the result of immigration we can only reply that we do not feel that dispersal was a major factor, because of (1) an absence of recoveries of tagged squirrels from areas of the experiment station other than the study area, (2) the close agreement of our observations with those of Flyger (1959), and (3) the similarities of our data with those reported by Edwards and Eberhardt.

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Received for publication January 20, 1966.