USE OF TAGGED - UNTAGGED RATIOS IN ESTIMATING RABBIT POPULATIONS

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Aelred Dean Geis

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This is to certify that the

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George A Petrides
Major professor

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USE OF TAGGED-UNTAGGED RATIOS IN ESTIMATING RABBIT POPULATIONS

By

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Introduction

As a portion of a study of factors contributing to the high abundance of cottontail rabbits, Sylvilagus floridanus mearnsii (Allen), on the Kellogg Station of Michigan State College near Battle Creek, Michigan, the examination of census methods was undertaken. The circumstances under which such a study could be made were particularly favorable during the late fall and winter of 1951 when early severe winter weather concentrated the rabbit population largely between a lake and open farm land. This tended to eliminate complications of determining the size of the censused area, which would arise if the study area was part of a larger, more homogeneous plot.

The census method that at first seemed potentially most useful to wildlife biologists was based on consideration of tagged-untagged ratios in daily live trapping records. A number of workers have used live trapping figures to estimate populations by methods which assume a uniform probability of capture. These include Schnabel (1938) and Schumacher and Eschmeyer (1943) working with fish; Fisher and Ford (1947) and Jackson (1948) with insects; and Hayne (1949) with small mammals.

Chitty and Kempson (1949) demonstrated that samples from a partly marked vole (Microtus agrestis) population were not drawn at random. Young, Neess and Emlen (1952) also found that the house mouse (Mus musculus) displayed heterogeneous trap response. DeLury (1951)

recognized unrepresentative samples caused by marked fish having a different probability of capture than those that are not marked as a problem he was unable to resolve when estimating fish populations by trapping and marking experiments. When heterogeneity in trap response exists, however, population estimates based on trapping results will be in error due to biased sampling. This was suggested on the Kellogg Station when population estimates based on trapping did not agree with others. This indicated that the data which would be expected to support the assumption of homogeneous trap response should be tested so that the nature of rabbit trap response could be understood and accurate population estimates result.

Census Methods

Two ways of determining the tagged-untagged ratio in the population were used in this study. The first obtained the marked-unmarked ratio from a sample of shot animals. Allen (1938) used this method to estimate the population by the following formula:

$$\frac{\text{Total number marked}}{\text{Total population}} = \frac{\text{Number marked in kill}}{\text{Total kill}}$$

The other method, as illustrated by Hayne (1949), is similar in principal except that it is based solely on trapping results. It considers the ratio of marked to unmarked in each day's catch along with the number previously marked in a cumulative manner to arrive at a population estimate. This method is based on the assumption that a uniform probability of capture existed among all members of the population.

Obtaining a second sample by shooting had several advantages that would be expected to result in greater accuracy. If biasness exists in sampling by traps, shooting would probably produce a more representative sample since it would not involve the same bias. Also, shooting permits a more complete coverage of the study area. Evidence of the accuracy obtained by the shooting method was secured when population estimates from trapping results varied from the total population estimated by shooting to the same extent that the estimate of the population of hunter-killed rabbits by trapping data only varied from the known number killed. Therefore, it was concluded that the use of tagged-untagged ratios in the hunting kill provided a more satisfactory way of estimating cottontail populations. Many biologists will not be able to apply this method, however, because they do not have the necessary control over hunting. Hence, it was desirable to further analyze the use of trapping data alone to estimate rabbit abundance. This was done by means of a trapping experiment in late 1951.

Field Procedures

Fifty wooden traps (described by Hickie, 1940) and 27 wire mesh (size 3, Tomahawk Trap Co., Tomahawk, Wisconsin) were used. To insure complete coverage the 160 acre study area was divided in half, one trapped November 3 through 15, the other between November 20 and December 10. An irregular spacing was used because a lake in the center of the study area with two elongated, curved waterfilled swales leading from it made the operation of a grid or straight trap lines impractical.

Rabbits were marked by placing numbered tags near the center of each ear (as described by Haugen, 1940). There was no evidence of these tags being lost except that occasionally shot ripped a tag out. Trap location, age, sex and weight were recorded each time a rabbit was handled. Closely supervised hunting took place throughout the entire area between December 15, 1951 and January 10, 1952. The location at which each rabbit was shot was located on a map.

Randomness of Capture

The probability of capture on a trap line represents the average likelihood that any particular rabbit will be caught on any particular night. For example, if a probability of capture of .2 exists, the chances are 2 in 10 that a certain rabbit will be captured on any night, or in 10 nights the rabbit will be expected to be captured twice. It is computed by dividing the number of times captures are made on a trap line by the number of nights the line was operated times the population present. For example, if 200 captures were made on a line run for 10 nights with 100 rabbits in the vicinity, the probability of capture (p) would be calculated as follows:

$$p = \frac{200}{10 \times 100} = .2$$

If there is a uniform probability of capture among all members of a population or, stated another way, if each capture represents a random sample from the population, then the distribution of the number of times different members of the population are captured should agree with a poisson or binomial distribution. Snedecor (1946) and Simpson and Rowe (1939) do not give concrete rules as to when the

poisson or binomial distribution should be used. The essential difference in the two is that the poisson distribution is used where a very small probability of the occurance taking place exists. What constitutes a low probability, however, is not defined. To determine if a significant difference exists in distributions calculated by the two methods, a theoretical distribution was calculated by both methods for a probability of a magnitude commonly encountered in the data ($p = .08$). This comparison showed that the two methods gave very similar results (Table 1). Throughout this study the suggestion of Ricker (1937) has been followed that the binomial distribution be calculated when a probability of .05 or greater exists using the poisson for smaller probabilities.

Observed compared to expected recapture distributions. To determine if rabbits were captured in a random manner on the study trap lines the observed distribution of the number of times individuals were captured was compared to the expected binomial distribution. The observed frequency of capture of marked rabbits was obtained from their trapping records. But, in order to determine how many rabbits were not captured it was necessary to estimate the total population from the tagged-untagged ratio in the hunting kill (Table 2). Evidence that estimates based on the kill are accurate has been already given. From the comparison of observed with expected values (Table 3 and Graphs 1 and 2) it is apparent that more rabbits were captured in the zero and in the higher categories (3 and up) than would be the case if a uniform probability of capture existed. Chi-square tests indicated that these differences were highly significant and

TABLE 1

COMPARISON OF BINOMIAL AND POISSON
DISTRIBUTIONS FOR A POPULATION OF 204 RABBITS
WITH A PROBABILITY OF CAPTURE OF .08

Times Captured	Expected Values	
	Binomial	Poisson
0	68.95	71.81
1	78.07	74.98
2	40.73	39.14
3	12.95	13.62
4	2.82	3.56
5	.44	.74
6	.05	.13
7	.00	.02
8	.00	.00
	204.01	204.01

TABLE 2

DATA NEEDED FOR A POPULATION ESTIMATE USING A SHOT SAMPLE AND TO CALCULATE PROBABILITY OF CAPTURE

	Trap Line	
	A	B
Number marked	79	89
Total number shot	71	65
Marked rabbits shot	28	23
Estimated population	200	251
Total captures	213	160
Probability of capture	.082	.053

TABLE 3

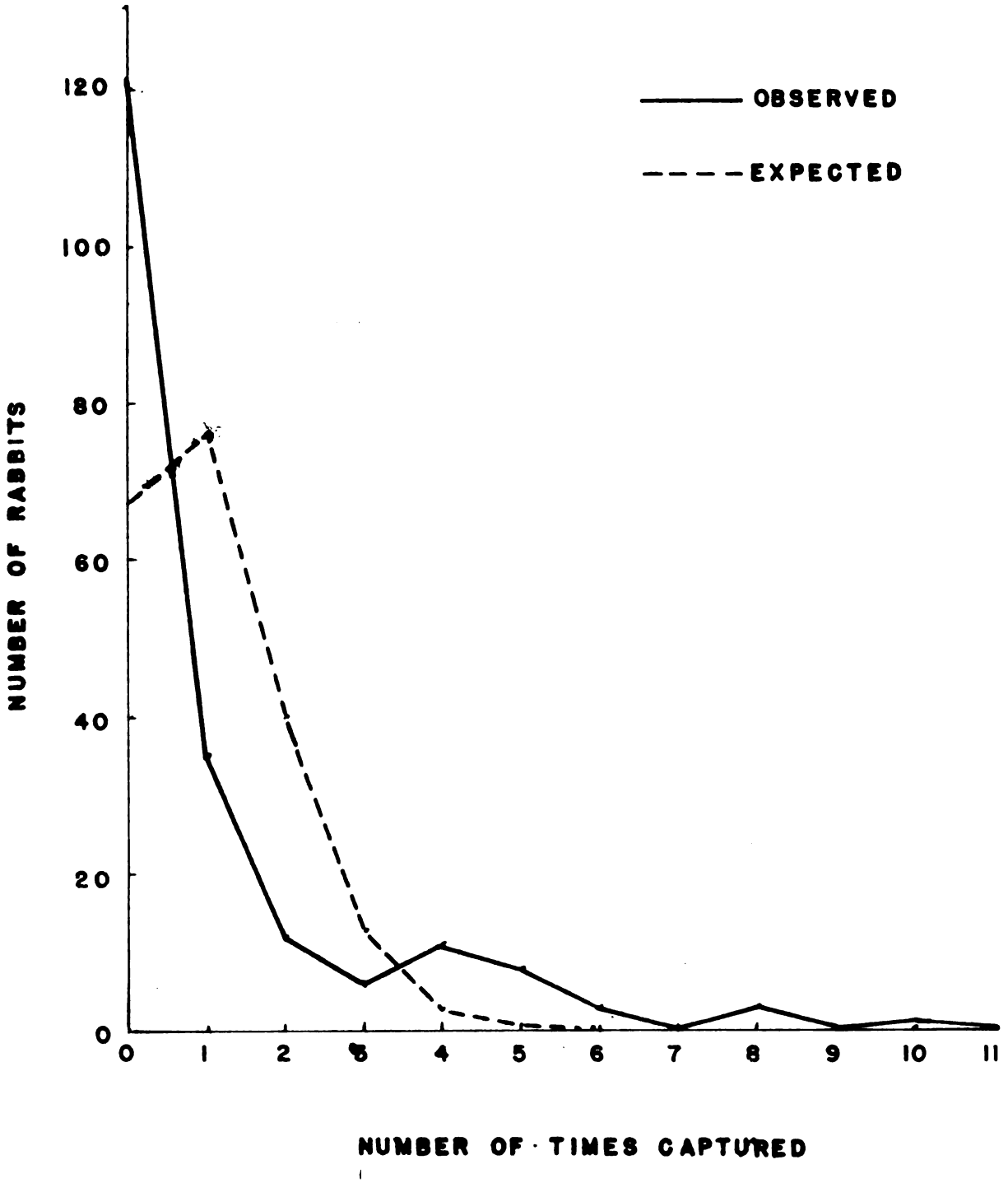
COMPARISON OF THE OBSERVED DISTRIBUTIONS OF RECAPTURES FOR TWO TRAP LINES WITH THE EXPECTED BINOMIAL DISTRIBUTIONS

Number of Captures	Trap Line A		Trap Line B	
	Observed Number	Expected Number	Observed Number	Expected Number
0	121	67.60	163	135.54
1	35	76.54	60	85.54
2	12	39.93	12	24.80
3	6	12.70	6	4.34
4	11	2.76	5	.63
5	8	.43	1	.43
6	3	.04	2	.03
7	0	.00	2	..01
8	3	.00	1	.00
9	0	.00	0	.00
10	1	.00	0	.00
	200	200.00	251	251.00

GRAPH I

Observed compared to expected binomial distribution of captures, trap line "A".

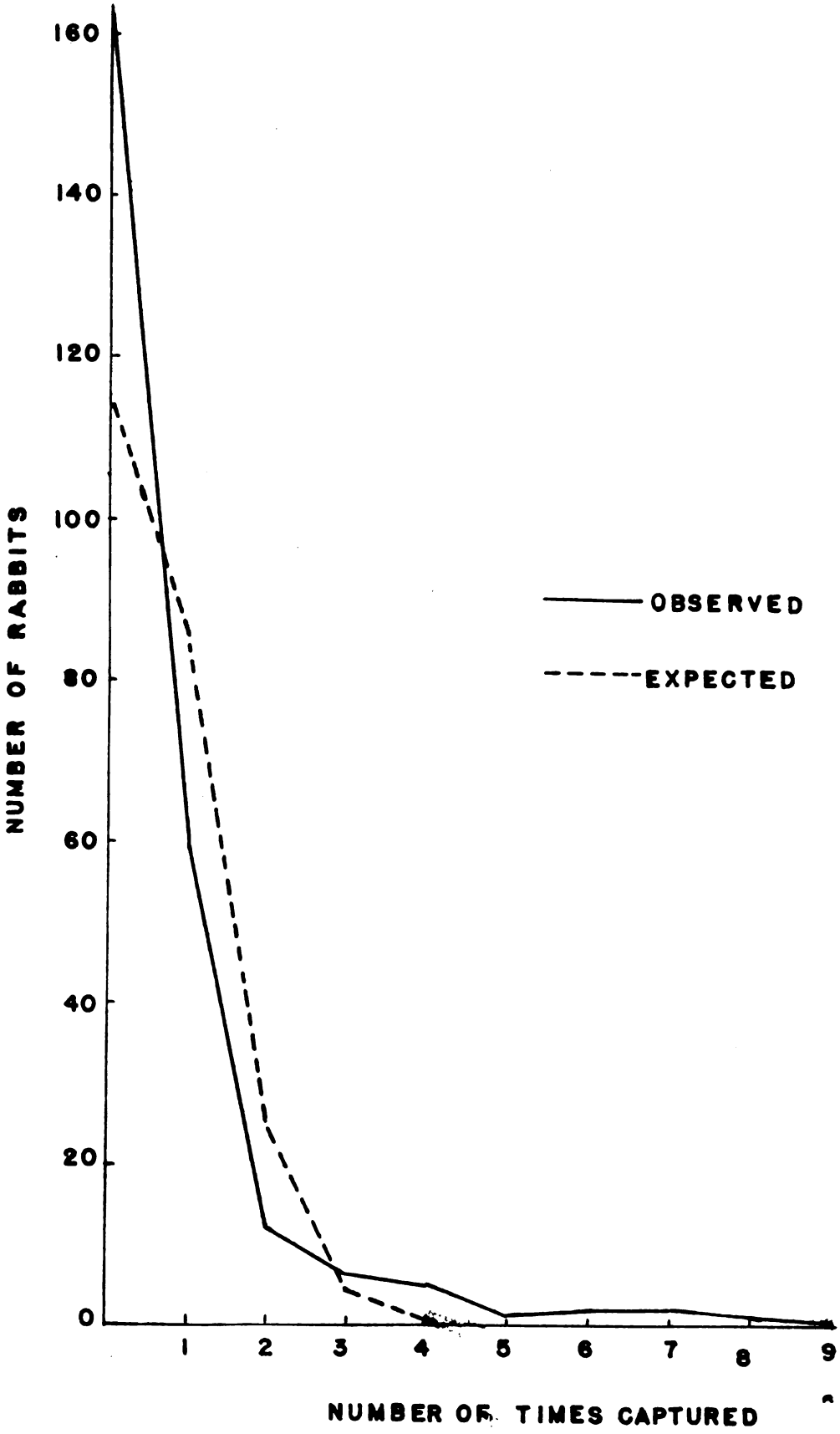
GRAPH I


OBSERVED
EXPECTED
NUMBER OF RABBITS
120
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
9
10
11
NUMBER OF TIMES CAPTURED

GRAPH II

Observed compared to expected binomial distribution of captures, trap line "B".

GRAPH II


160
140
120
100
80
60
40
20
0
NUMBER OF RABBITS
OBSERVED
EXPECTED
1
2
3
4
5
6
7
8
9
NUMBER OF TIMES CAPTURED

that the distribution of captures were not at random. Hence, the assumption basic to current census methods using only trapping data, that a uniform probability of capture exists, has been shown not to apply to Kellogg Station rabbits.

Influence of sex, age and previous trap experience. In further analysis to understand and possibly correct for this variance, the data for three trap lines were broken into 16 identifiable elements as to sex, age and previous trap experience. The probability of capture was calculated for each to determine if the different population elements consistently had different probabilities of capture of the same direction and magnitude. Table 4 shows that differences did exist between categories but they were not consistent except in regards to trap experience. Once a rabbit was captured it was more likely to be recaptured than a rabbit which had not been taken.

However, differences in other categories did exist and it is possible that the distribution of recaptures in a sample made up by pooling trapping data from several population elements with different probabilities of capture will not correspond to a binomial distribution even though the sampling within each population element has been at random. In order to determine if the discrepency between expected and observed values was due to the various combinations of ages and sexes having different probabilities of capture, the following analysis was made. For each age and sex combination the theoretical expected fraction of the sample for each capture category was calculated (Table 5). These were then combined in the same ratio as the numbers of

TABLE 4

PROBABILITIES OF CAPTURE OF VARIOUS
POPULATION ELEMENTS ON THREE TRAP LINES

Population Element	A Nov.	B Dec.	C March
Combined	.082	.053	.046
All males	.084	.037	.048
All females	.079	.062	.045
All adults	.111	.050	*
All juveniles	.077	.052	
Adult males	.084	.044	
Juvenile males	.084	.037	
Adult females	.131	.052	
Juvenile females	.071	.064	
All after first capture	.141	.072	.070
Males after first capture	.177	.067	.076
Females after first capture	.116	.075	.065
Adults after first capture	.131	.017	*
Juveniles after first capture	.141	.091	
Captured first on a previous line	.133	.039	
Not captured on a previous line	.062	.060	

* In March all are considered to be adults.

individuals in the various age and sex combinations. These weighted mean values (Table 5, line 5) were then compared with those obtained by calculating the expected binomially distributed fractions directly from the probability of capture for the entire population where the different ages and sexes were not considered separately (Table 5, line 6). There was not a large enough difference between the two series of values to account for the large differences previously noted. This indicates that the discrepencies were not due to age and sex differences.

Further evidence that the discrepency is not due to a random distribution of captures within each age and sex combination having a different probability of capture is shown in Table 6. There the observed distribution of captures within each age and sex group and of rabbits after they have been captured once is compared with what would be expected if the distribution was at random. These comparisons also are displayed in Graph 3. Chi-square tests revealed that significant differences occurred in each instance. As with the combined data, there were too many individuals in the no- and many-capture categories. This rather conclusively demonstrates that combining data from rabbits' different ages, sexes and trap experience was not the cause of the variance between the observed and expected values. Trap addiction or avoidance apparently is an attribute of the individual rabbit which results in non-random selection of animals by traps.

Nature of heterogeneous trap response. The above discussion demonstrated the existance of heterogeneous trap response, but it gave no indication

TABLE 5

COMPARISON TO SHOW THE EFFECT OF COMBINING DATA
FROM THE FOUR AGE AND SEX COMBINATIONS

Sex and Age	Number Captured	Probabilities of Capture	Fraction of the Population expected in each capture category						
			0	1	2	3	4	5	6
Adult ♂	5	.084	.320	.381	.210	.070	.016	.003	.000
Adult ♀	9	.131	.161	.315	.286	.158	.060	.016	.005
Juvenile ♂	28	.084	.320	.381	.210	.070	.016	.003	.000
Juvenile ♀	37	.071	.384	.381	.175	.049	.009	.001	.000
Combined 5:9:28:37		.082	.331	.373	.202	.070	.018	.003	.000
Binomial distribution		.082	.329	.386	.204	.064	.015	.002	.000

TABLE 6

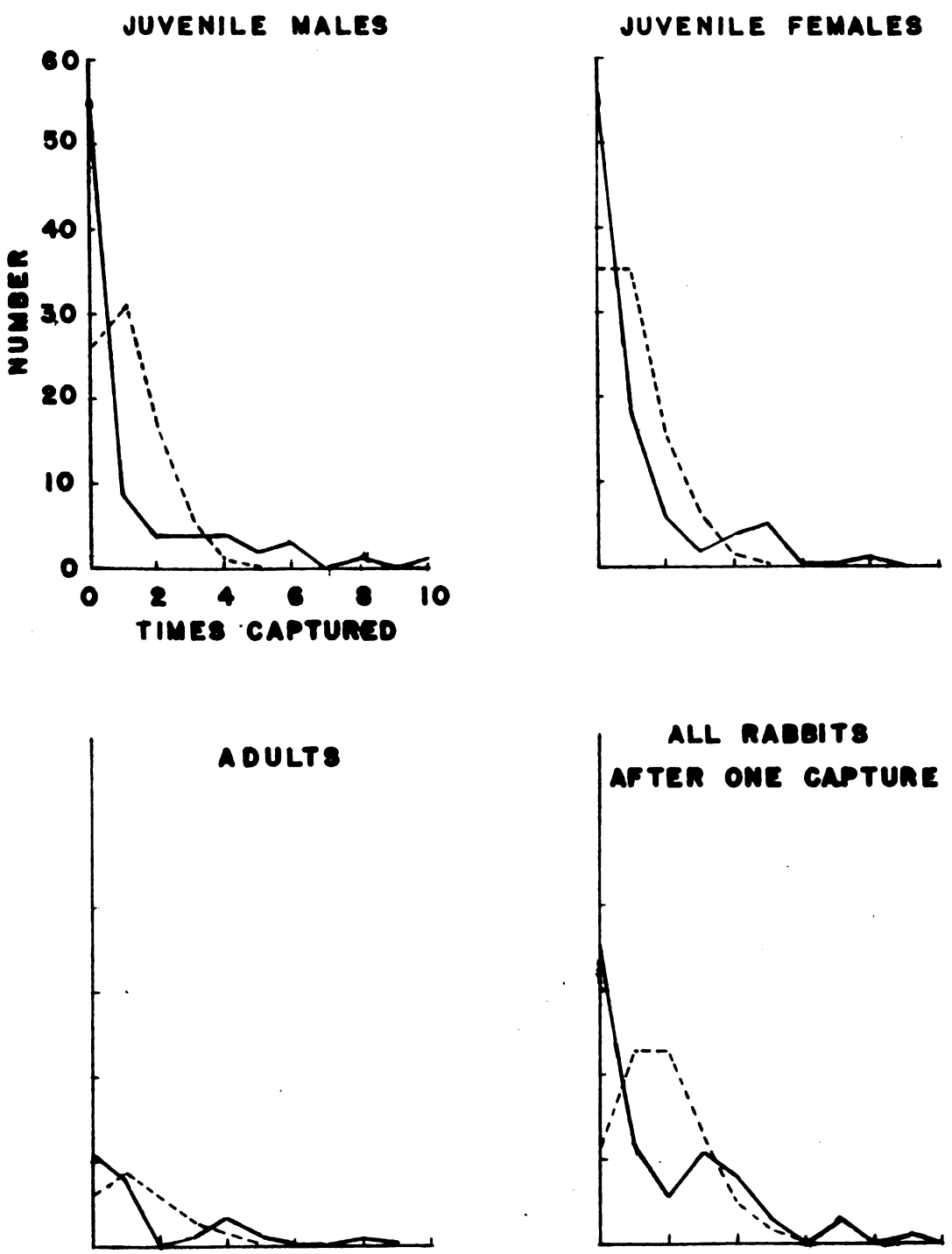
OBSERVED RECAPTURE DISTRIBUTION COMPARED TO THOSE EXPECTED FOR RABBITS OF VARIOUS SEXES, AGES AND WITH TRAP EXPERIENCE

Number of Captures	Adults		Juvenile Males		Juvenile Females		After One Capture	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
0	11	5.42	55	26.56	56	35.73	35	10.98
1	8	8.80	9	31.62	19	35.45	12	23.30
2	0	6.58	4	17.43	6	16.29	6	23.07
3	1	3.00	4	5.81	2	4.57	11	13.82
4	3	.95	4	1.33	4	.85	8	5.69
5	1	.20	2	.25	5	.10	3	1.66
6	0	.02	3	.00	0	.00	0	.40
7	0	.00	0	.00	0	.00	3	.08
8	1	.00	1	.00	1	.00	0	.00
9	0	.00	0	.00	0	.00	1	.00
10	0	.00	1	.00	0	.00	0	.00

GRAPH III

Observed compared to expected binomial distribution of captures for several population elements.

GRAPH III


JUVENILE MALES
JUVENILE FEMALES
NUMBER
60
50
40
30
20
10
0
0
2
4
6
8
10
TIMES CAPTURED
ADULTS
ALL RABBITS
AFTER ONE CAPTURE

as to the extent to which the probabilities of capture varied or the relative numbers of individuals with different probabilities of capture. An examination of the distribution of recaptures on a trap line suggested that they might be divided so as to fall into three groups with different probabilities of capture. One hundred and sixty-eight rabbits were caught 0-2 times, 25 were captured 3-5 times, and 7 were taken 6-10 times. The probabilities of capture of these groups were .027, .314 and .571, respectively. However, for the above classification to be valid the expected binomial distribution of captures for each of these trap vulnerability categories when added together must closely approximate that observed from actual trapping records. To test this the expected number of individuals in each capture category i.e., caught 0 times, 1 times, 2 times, etc., was calculated for each trap vulnerability classification (Table 7, columns 1, 2 and 3). Then the expected values in each capture category for each trap vulnerability classification were added to obtain the number of individuals in each capture category for the entire population made up of representatives from three elements with different probabilities of capture (Table 7, column 4). There was no significant difference between this distribution and the one based on the actual trapping records. Also, as before there was a highly significant difference between this distribution and that obtained by assuming that the population was made up of individuals having an equal probability of capture. The relationship between these three distributions is shown in Graph 4. This analysis indicates that the reaction of the rabbit population to traps can be explained by recognizing that

TABLE 7

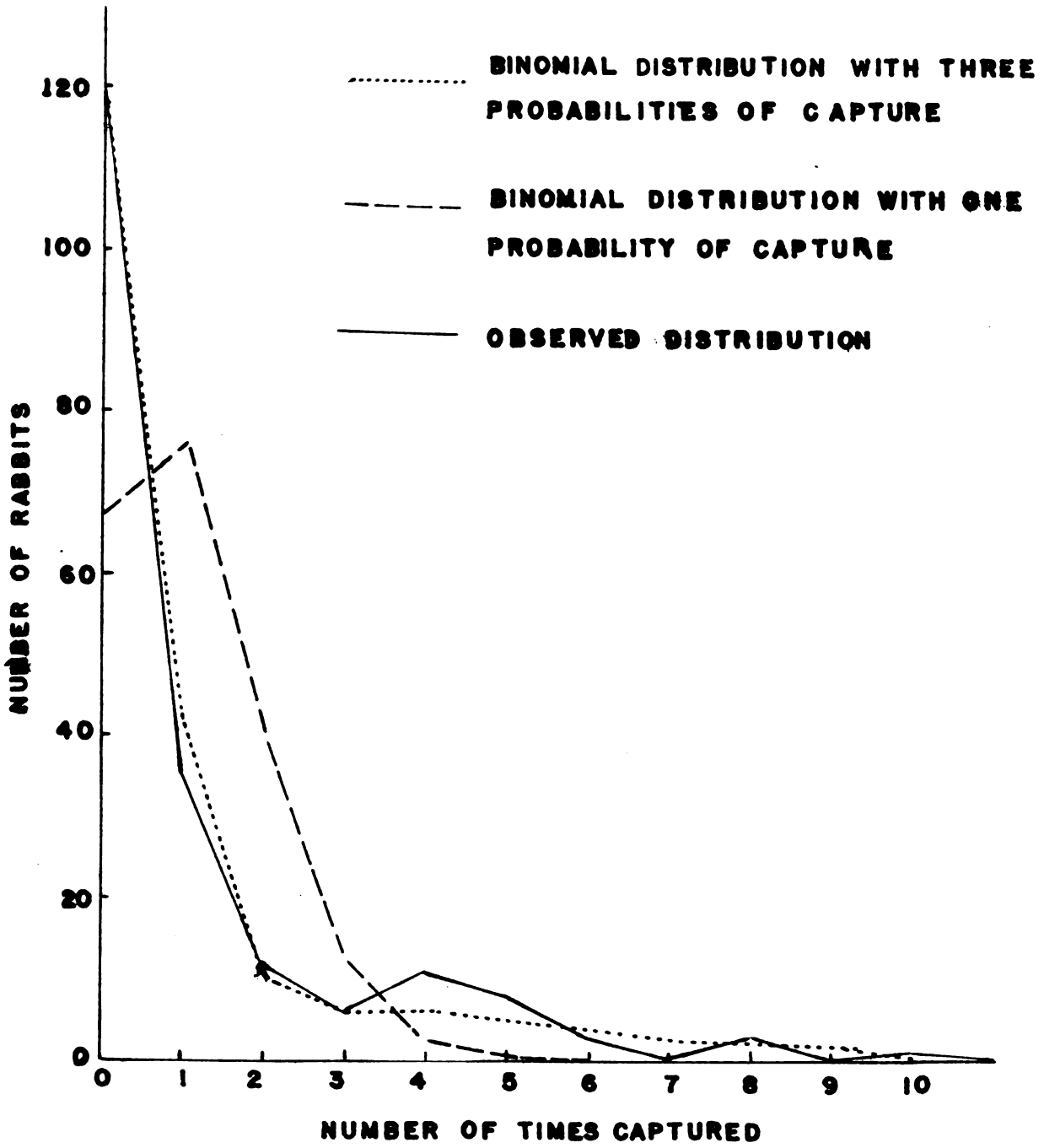
EXPECTED DISTRIBUTION OF RECAPTURES FOR A POPULATION MADE UP OF ELEMENTS WITH THREE DIFFERENT PROBABILITIES OF CAPTURE COMPARED TO THAT OBSERVED AND THE BINOMIAL FOR A SINGLE PROBABILITY OF CAPTURE

Times Captured	Expected Distributions of Rabbits Observed to be Captured			Sum of 1, 2 and 3 p = .082	Observed in Data p = .082	Binomial p = .082
	(1) 0-2 Times p = .027	(2) 3-5 Times p = .314	(3) 6-10 Times p = .571			
0	118.2	.2		118.4	121	65.8
1	41.5	1.1		42.6	35	77.2
2	7.3	3.0		10.3	12	40.8
3	.8	5.1	.1	6.0	6	12.8
4	.2	5.8	.2	6.2	11	3.0
5		4.8	.6	5.4	8	.4
6		2.9	1.1	4.0	3	
7		1.4	1.5	2.9	0	
8		.6	1.5	2.1	3	
9		.1	1.1	1.2	0	
10			.6	.6	1	
11			.2	.2		
12			.1	.1		
	168.0	25.0	7.0	200.0	200	200.0

GRAPH IV

Expected distribution of captures for a population having three probabilities of capture compared to the observed distribution and the binomial distribution for a single mean probability of capture.

GRAPH IV


BINOMIAL DISTRIBUTION WITH THREE PROBABILITIES OF CAPTURE
BINOMIAL DISTRIBUTION WITH ONE PROBABILITY OF CAPTURE
OBSERVED DISTRIBUTION
NUMBER OF RABBITS
120
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10
NUMBER OF TIMES CAPTURED

the population is made up of individuals with varying probabilities of capture. Some have a high probability and a relatively large number have a low probability. Other individuals have an intermediate position.

The question may be raised as to whether those animals caught many times were trap-addicted i.e., had something in their nature which caused them to readily enter traps, or whether they merely had a small range near a trap and consequently were captured frequently. Table 8 sheds light on this question. It shows that the frequently captured rabbits had been caught in a number of different locations. This suggests that these rabbits had an inclination to enter traps. Possibly they had a particular liking for the corn used as bait, or perhaps merely a curiosity about traps, and consequently entered them whenever they were encountered. Other evidence of the addiction towards traps was shown in tracks in the snow of rabbits walking around sprung traps after the trapping period had been completed, apparently trying to enter them. It is not believed rabbits sought traps for cover because they apparently entered open wire mesh traps as readily as solid wooden ones.

Effect of heterogeneous trap response on population estimates. The above consideration indicates that any census method based on trapping records which assume a uniform probability of capture will lead to inaccurate rabbit population estimates. Also, these estimates will always be lower than the actual population because:

TABLE 8

NUMBER OF LOCATIONS AT WHICH FREQUENTLY HANDLED COTTONTAILS WERE TRAPPED

Rabbit	Times Captured	Number of Trap Locations
A	10	5
B	8	7
C	8	6
D	6	5
E	6	3
F	5	4

1. The members of the population which have a high probability of capture tend to cause a high previously-captured fraction in each catch and hence depresses the population estimate.
2. The largest part of the population is not captured during the trapping period and consequently is not given due consideration.

Trapping records are commonly used in three ways to obtain population estimates. One way is to consider the marked-unmarked ratios during parts of a continuous sampling period. There are several modifications of this method, but all assume random sampling. If this exists then the previously marked fraction in each day's catch should represent the true marked fraction in the population. The extent to which heterogeneity of trap response distorts the previously marked fraction in each day's catch from the correct value is shown in Table 9 and Graph 4. The end result of this discrepency is shown when the estimated population from trapping data by the method proposed by Hayne (1949) is compared with that obtained from the marked-unmarked ratio in the hunting kill. The latter method avoids the bias in sampling present in the first method based solely on trapping. Trap line "A" had a population estimate from trapping data which was 40% of the much more accurate estimate from shot animals. Trap line "B" had an estimate which was 47% of the number arrived at from the tagged-untagged ratio in the hunting kill. Probably a more accurate way of determining the extent to which the population estimate

TABLE 9

PROPORTION OF THE DAILY CATCH PREVIOUSLY MARKED COMPARED TO THE TRUE FRACTION OF THE POPULATION PREVIOUSLY MARKED

TRAP LINE A

Date	Handled for First Time	Recaptures	Total Catch for Day	Total Number Previously Handled	Proportion of Catch Previously Handled	Proportion of Population Previously Handled
Nov. 3	8	0	8	0	.000	.000
" 4	2	1	3	8	.333	.040
" 5	2	1	3	10	.333	.050
" 6	12	3	15	12	.200	.060
" 7	5	4	9	24	.444	.120
" 8	6	5	11	29	.454	.145
" 9	7	14	21	35	.667	.175
" 10	10	17	27	42	.630	.210
" 11	10	16	26	52	.615	.260
" 12	6	21	27	62	.778	.310
" 13	5	14	19	68	.737	.340
" 14	4	18	22	73	.818	.365
" 15	2	20	22	77	.909	.385

TABLE 9 Continued

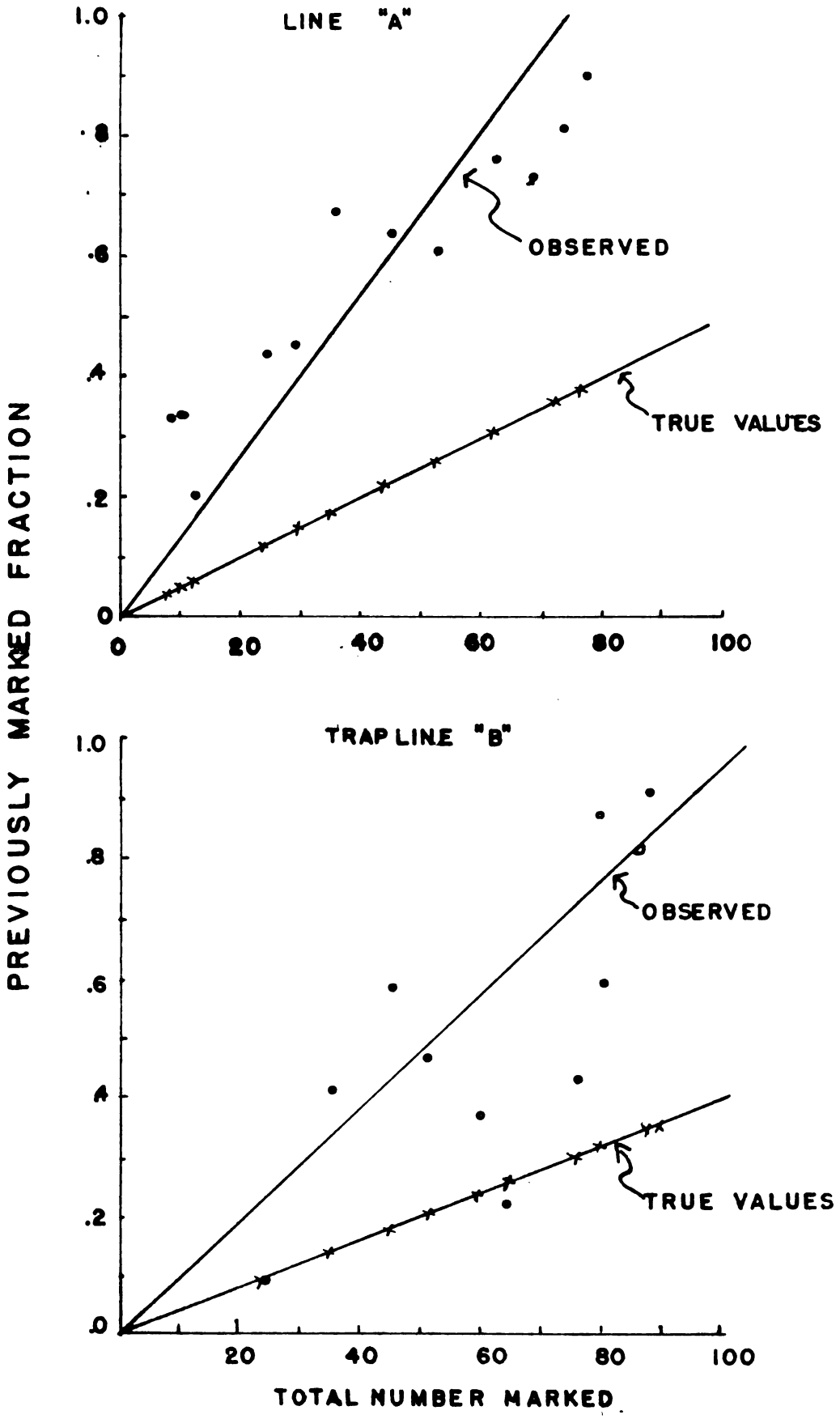
TRAP LINE B

Date	New	Recaptures	Total Catch for Day	Total Number Previously Handled	Proportion of Catch Previously Handled	Proportion of Population Previously Handled
Nov. 20	24	0	24	0	.000	.000
" 21	11	1	12	24	.083	.095
" 27	10	7	17	35	.412	.139
" 28	6	7	12	45	.583	.179
" 29	8	7	15	51	.467	.203
Dec. 4	5	3	8	60	.375	.239
" 5	11	3	14	65	.214	.259
" 6	4	3	7	76	.428	.303
" 7	1	7	8	80	.875	.318
" 8	5	7	12	81	.583	.323
" 9	2	9	11	86	.818	.343
" 10	1	10	11	88	.909	.350

GRAPH V

Observed compared to the true previously marked fraction in each day's catch on two trap lines.

GRAPH V


LINE "A"
1.0
.8
.6
.4
.2
0
OBSERVED
TRUE VALUES
0
20
40
60
80
100
PREVIOUSLY MARKED FRACTION
TRAP LINE "B"
1.0
.8
.6
.4
.2
0
OBSERVED
TRUE VALUES
20
40
60
80
100
TOTAL NUMBER MARKED

was distorted due to heterogeneous trap response is shown by estimating the population of shot rabbits from their trapping record. In other words, a population estimate for the number killed was made from the trapping records of a known number of shot cottontails. These turned out to be 43% and 42% of the number shot in the vicinity of trap lines "A" and "B", respectively. This not only shows the inaccuracy of the estimates based solely on trapping data but also indicates that the estimates of the total population based on the tagged-untagged ratio in the hunting kill were probably quite accurate. Data from the Kellogg Forest, although not collected with the same precision as that at the Kellogg Bird Sanctuary and Farm, indicate that estimates based on trapping results also ran about 40% of the number present.

Haugen (1940) estimated rabbit populations by trapping until previously marked animals predominated in each day's catch. He then considered the number that had been marked as the total resident population. Later captures of unmarked rabbits were described as being transients which were not part of the resident population. When Haugen's method was applied to data collected in this study, the population estimates were only 28.5% and 39.5% of the estimates obtained from the tagged-untagged ratio in the hunting kill.

Green and Evans (1940) with snowshoe hares and Southern (1940) with the European wild rabbit used the tagged-untagged ratio in a second trapping period only to estimate the number present. For use with the cottontail this practice yields estimates that are far too low. This is illustrated by estimating a population using the average

marked fraction for the last two days of trapping to represent the fraction of the population that had been previously marked. This estimate can then be compared with that obtained by trapping, then shooting (Table 10). Once again the estimated number was only about 40% of the actual number present. It is apparent that population estimates which depend upon a second large sample by trapping are just as inaccurate as those in which each day's catch is given consideration in making the estimate.

Correction of biased trap response. Because population estimates by the method described by Hayne (1949) consistently ran about .40 of the number present it seems justifiable to use the reciprocal of .40 or 2.5 as a correction factor for population estimates based solely on trapping results. The spring 1951 breeding adult population of the Kellogg Bird Sanctuary and Farm based on trapping results was 75, an obviously low value. If that number is corrected by multiplying by 2.5 the estimate would be 188, a much more reasonable number judging from the previous spring's population and field observations.

Although the above correction factor appears to hold at the Kellogg Station thus far, it should be tested more widely. The influence of the time of year, various trap spacings and different population densities should also be evaluated. How constant the correction factor remains under different conditions depends on how constantly the probabilities of capture within the population vary to the same relative extent.

TABLE 10

"LINCOLN INDEX" POPULATION ESTIMATES BASED ON A FINAL SAMPLE TAKEN IN TRAPS COMPARED TO THOSE OBTAINED WHEN THE SECOND SAMPLE IS SHOT

	Trap Line A	Trap Line B
Number marked up to last two days	73.	86.
Average marked fraction last two days	.863	.863
Estimate population		
final sample by trapping	84.6	99.7
" " " shooting	200.	251.

Area Censused

In order to determine population densities it is necessary to know the area over which animals are being censused. This problem was simplified in present study because the population was largely concentrated in winter cover which lay between open farm land and a lake; and the locations of marked shot rabbits known. By marking the locations on a map where tagged rabbits were shot, it was possible to see at a glance the area over which marked rabbits ranged. Unfortunately other workers may not enjoy these benefits and consequently determining the area censused may be a very complex problem. Several mammalogists (Dice, 1938; Stickle, 1946; MacLulich, 1951) working with small rodents have offered solutions to this problem based on capture locations. Unfortunately, the assumptions basic to these methods are questionable when working with rabbits. The rabbit research project at the Kellogg Station has not yet developed a method of estimating the census area based solely on trapping records; however, the subject is being investigated.

Summary

Rabbits were not live-trapped in a random manner. This was not due to age or sex. The inclination to enter or avoid traps apparently was a quality of the individual rabbit. The nature and extent of variation in trap response was demonstrated.

The error in several current census methods caused by heterogeneous trap response was shown and a method of correction for it suggested. Evidence was presented which indicated that population estimates based on the tagged-untagged ratio in the hunting kill were accurate.

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