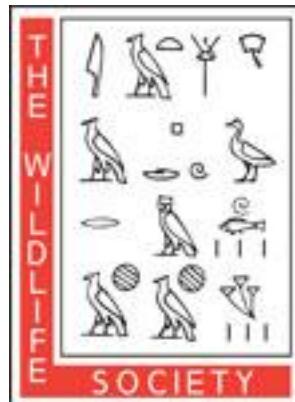


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## Problems in a Rabbit Population Study

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Source: *Wildlife Monographs*, Jun., 1963, No. 10, Problems in a Rabbit Population Study (Jun., 1963), pp. 3-51

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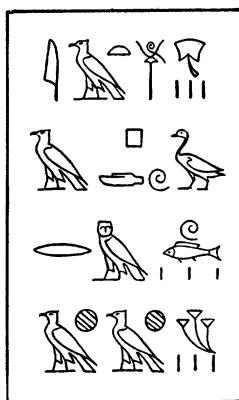


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## PROBLEMS IN A RABBIT POPULATION STUDY

by

LEE EBERHARDT, TONY J. PETERLE,  
AND RAYMOND SCHOFIELD

JUNE 1963

No. 10



**FRONTISPICE.** The elusive cottontail. Photograph by Robert Harrington, Michigan Department of Conservation.

# PROBLEMS IN A RABBIT POPULATION STUDY<sup>1</sup>

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<sup>1</sup> A Contribution from Federal Aid in Wildlife Restoration Projects Michigan W-40-R and W-96-R; Data Gathered by the Staff of the Rose Lake Wildlife Experiment Station.

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## INTRODUCTION

The primary purpose of this paper is to inform others of our findings and to assist in the guidance and planning of future research projects that involve population statistics of the cottontail rabbit (*Sylvilagus floridanus*). In an earlier paper (Peterle and Eberhardt, 1959), we outlined the basic problem that confronted us, and here we intend to suggest various approaches to the problem and what factors should be considered in the investigation of rabbit populations.

The data considered here were collected at the Rose Lake Wildlife Experiment Station from 1951 through 1957. Although we have information extending back to 1939, we began detailed analyses with the data collected in 1951 when accurate age determinations by examination of the humerus of all shot rabbits commenced. While we feel that the true age structure of the kill is important in the analysis of the problem of estimating the size of a population, all data on tagged rabbits back to 1939 were used in the section on mortality rates. As a matter of record, population estimates made in the early fall for the entire Rose Lake area from 1947 through 1957 are included (Table 1). We believe these estimates are biased, but they do give some suggestion of the densities of the rabbit population involved.

The Rose Lake Wildlife Experiment Station, established in 1938, lies in south-central Michigan approximately 12 miles northeast of Lansing. The objectives, description, and results of some projects undertaken at the station were given by Ruhl (1947) and Black (1953). Briefly, 10 per cent of the station area is in crops or hay, 14 per cent in pasture, 16 per cent in woods and brush, 39 per cent marsh and swamp, and 21 per cent in idle fields, lakes, orchards, and building sites (Fig. 1). Soils are predominantly Fox, Oshtemo, Coloma, and Plainfield sandy loams in the upland, with Houghton and Carlisle muck in the lowlands. Soil Conservation Service land capability classes range from II to VII.

The 3,040-acre area is divided into 7 sub-areas for administrative convenience (Fig. 1). All small game hunters register daily and submit all game for examination following the hunt. There are no restrictions on the number of hunters permitted on the area at any one time. Total gun pressure averaged 300 hours per 100 acres for 1951–1957. Rabbit hunting seasons began October 15 from 1938 to 1951, October 20 from 1952 to 1956, and on October 21 in 1957. The season ended December 31 from 1938 to 1951 (78 days), January 31 from 1952 to 1956 (104 days), and March 1 in 1957 (133 days). The total rabbit kill for each year is listed in Table 1.

Rabbits to be marked for population estimates were trapped in September and October prior to the opening of the hunting season. The ordinary Biological Survey Cat Trap (pictured in Allen, 1939a), measuring  $1 \times 1 \times 2$  feet and covered with hardware cloth, was used with ear corn for bait. Ordinarily in the later years (1951–1957) we trapped the entire station area in two 11-day periods. During the first period, beginning about September 17, we trapped our "rabbit" lines along cover edges and in fields. During the second period, beginning

TABLE 1.—ESTIMATES OF SIZE AND DENSITY OF RABBIT POPULATIONS IN EARLY AUTUMN, AND NUMBERS OF RABBITS KILLED BY HUNTERS, FOR EACH OF 11 YEARS, 1947–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION. The total kill includes all rabbits shot, but a few each year were not counted because of condition at autopsy, viz., head removed, etc.

Year	Acres	Popula- tion Esti- mate	Confidence Limits 95 Per Cent Level	Rabbits per 100 Acres	Total Kill
1947	2,309	380	252–711	16.5	97
1948	2,567	1,014	696–1,865	39.5	181
1949	2,567	2,159	1,689–2,992	84.1	511
1950	2,570	1,122	891–1,516	43.7	479
1951	2,860	1,231	985–1,642	43.0	395
1952	2,860	930	746–1,232	32.5	299
1953	2,860	1,198	1,014–1,465	41.9	456
1954	2,860	956	821–1,142	33.4	443
1955	2,860	1,144	992–1,352	40.0	498
1956	2,905	1,427	1,161–1,893	49.1	463
1957	3,040	1,510	1,313–1,777	49.7	620

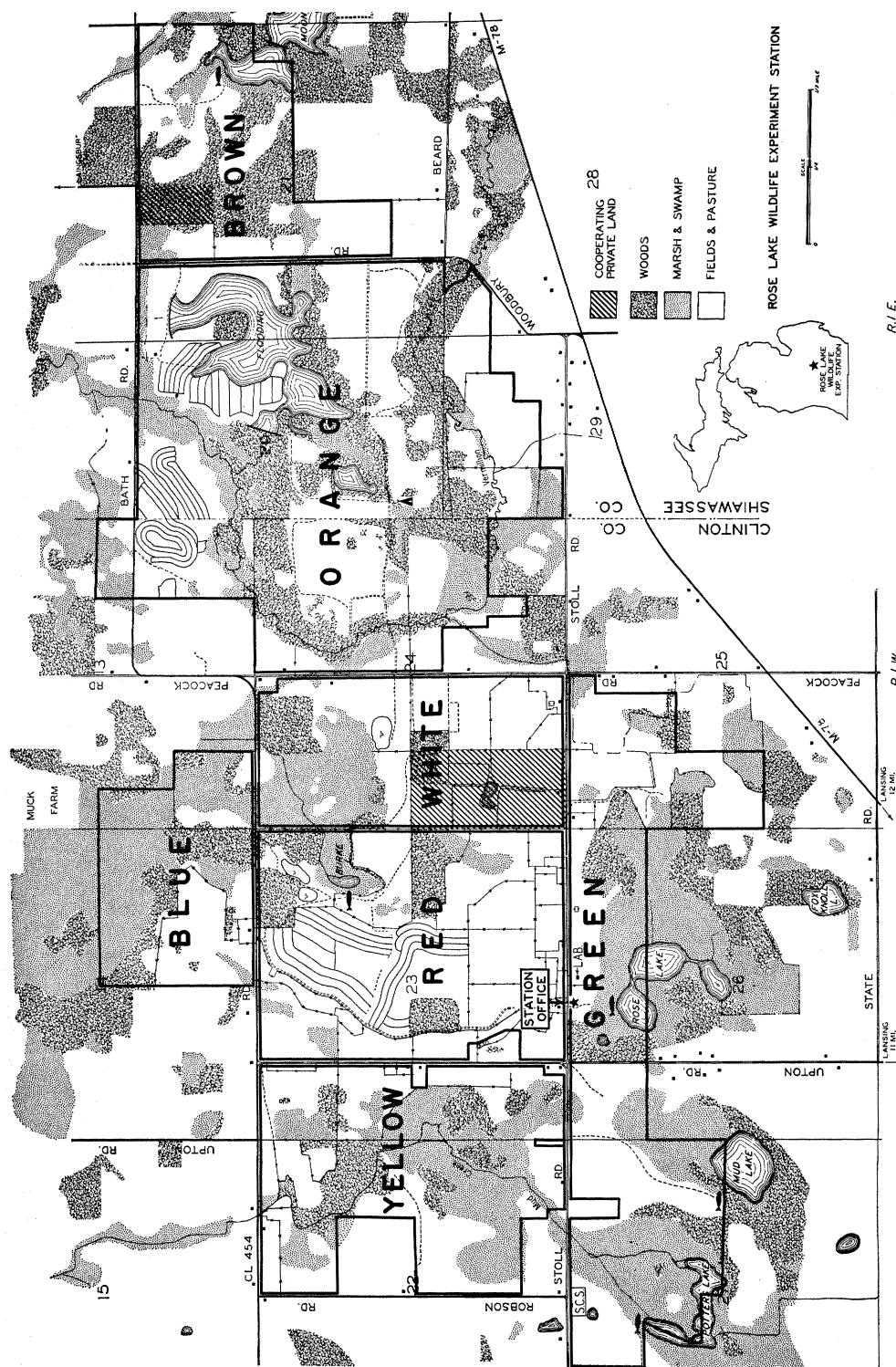


FIG. 1. Map of the Rose Lake Wildlife Experiment Station showing the distribution of the various kinds of cover, crops, and woodlands, and the locations and extents of the different hunting units.

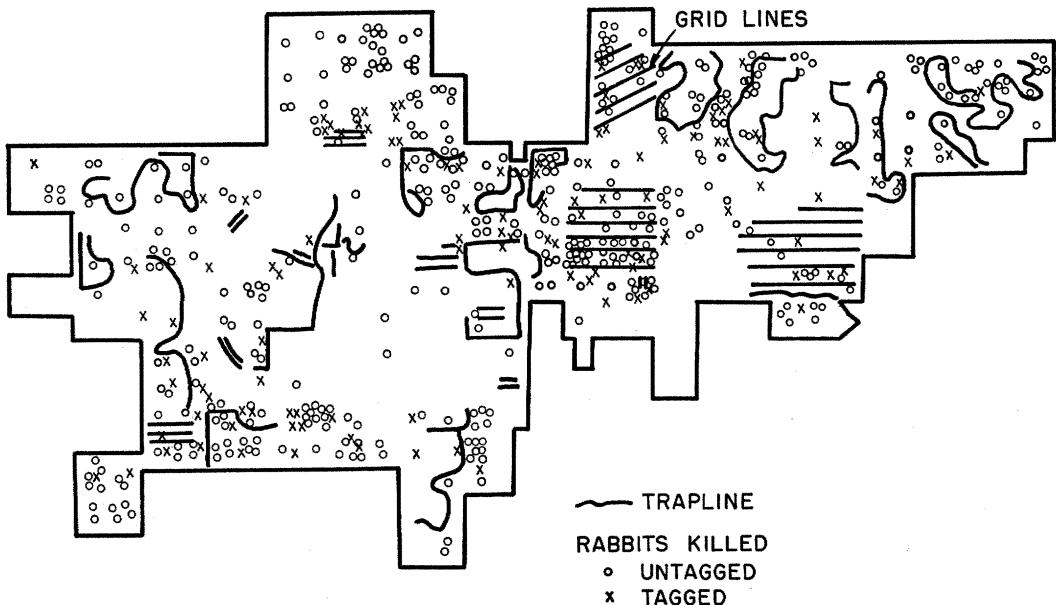


FIG. 2. Locations of traplines and points at which tagged and untagged rabbits were killed during the 1955-1956 hunting season at the Rose Lake Wildlife Experiment Station.

about October 4, trapping was essentially confined to the woodlots for tagging of fox squirrels (*Sciurus niger rufiventer*). Figures 2 and 3 indicate the placement of traplines over the area during 2 years. Over-all average trap density was 1 trap per 5.6 acres. All rabbits tagged in either period constituted the tagged segment for later population estimates. We used No. 3 (Style 4-1005 National Band and Tag Co.) mammal tags, placed in one ear only. There was no appreciable loss of tags.

Each rabbit in the hunter's bag was examined and the following data recorded: number of tag, sex, age (the humerus was examined and forepaws collected for X-ray), weight, location shot, date and time shot, external parasites or abnormalities, collector's name, and the name of the examiner. We excluded from our calculations all rabbits with heads damaged or removed.

We present this paper in seven sections. These are not wholly and logically separate divisions, but offer a basis for separating various aspects of a number of problems that stand in the way of any attempt to

obtain accurate vital statistics on a rabbit population. Much of the work at Rose Lake and elsewhere has been concerned with the effect of habitat manipulation on rabbit populations. While there is little doubt that habitat management can produce appreciable changes in rabbit numbers, we are far from having a clear idea just what and how much management is most satisfactory for the purpose, nor do we know whether such management is economically feasible. Many, if not most, of these answers await a truly reliable picture of the statistics and dynamics of wild rabbit populations. In our attempt to compile some data collected at Rose Lake, we find that many of the vital statistics are either not reliable by virtue of uncertainty about the assumptions under which they were collected, or are contradicted by other information. Until we find ways of meeting the necessary assumptions and reconcile the differences in the several approaches, we do not feel that there is much point in attempting detailed analysis of population dynamics or fluctuations. We do not, as a matter of fact, actually have

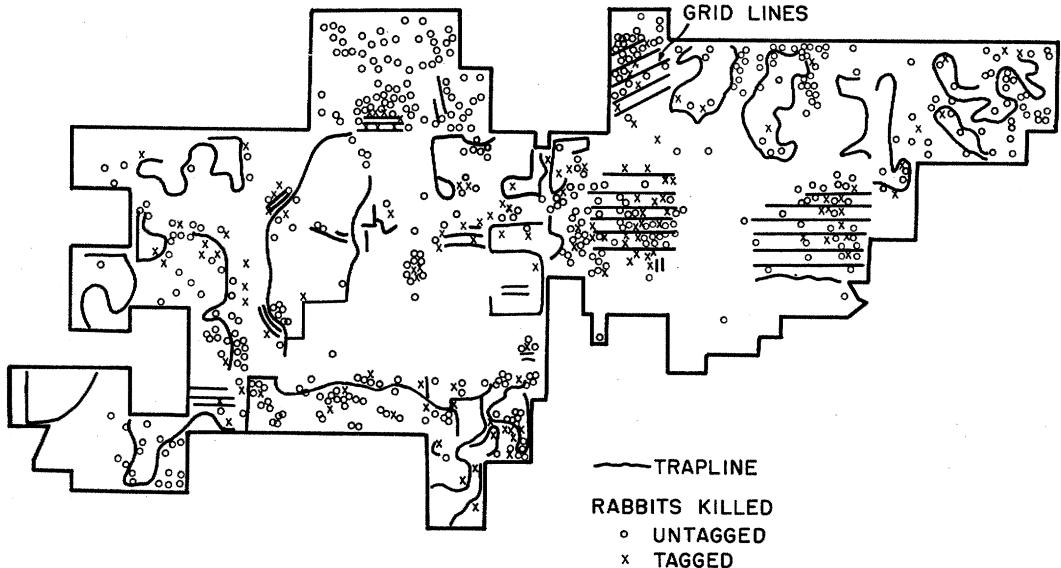


FIG. 3. Locations of traplines and points at which tagged and untagged rabbits were killed during the 1957-1958 hunting season at the Rose Lake Wildlife Experiment Station.

evidence that populations as a whole have fluctuated very much in the seven years studied here. We will treat, then, problems mainly associated with attempts to compile certain vital statistics. This study is incomplete as far as we are concerned, so our conclusions are mainly related to the beginning of research on several aspects. For this we make no apology to the "practical" man—we suggest only that he look back over the data on which his present course of activity is based to see whether the same flaws we describe are present.

We owe certain apologies to the theoretically inclined person, since much we present here is unsatisfactory in several respects, and we pay very little attention to statistical tests in some places where they might add to the significance of our discussions. Our defense on this score is that the problem at hand calls for a great deal of statistics, and a little might do rather more harm than good. We feel that one of the immediate necessities is to make the material available to others in sufficient detail for treatment of some of the more interesting statistical aspects. One of our strongest reasons for not doing some of the

simpler tests, Chi-square and the like, in several places, is that the elementary application of these tests may indicate only rejection of the hypothesis at the stated level of significance, but tell us nothing about the probability of failure to reject a false hypothesis because of inadequate sampling.

One other note of theoretical interest is that we have used either discrete or continuous models as a matter of convenience for the purpose at hand, without much attempt at justification. This is again a matter of our interest being principally in future research aimed at explaining some of the contradictions noted here. We wish only to sketch out some of the possibilities and not to attempt to exhibit precise relationships. Very likely the only worthwhile models for much of the population behavior described here will be probabilistic. We feel that attempting such representations will be worthwhile only after some of the conflicting aspects of our data have been straightened out. Again, we are not attempting here to describe population dynamics, but rather vital statistics.

### ACKNOWLEDGMENTS

This is a contribution from Federal Aid in Wildlife Restoration Projects Michigan W-40-R and W-96-R.

The considerable volume of data contained in this paper is the result of years of work by many biologists and employees associated, at one time or another, with the Rose Lake Wildlife Experiment Station since its inception in 1938. The authors extend their sincerest thanks to all those who took part in the collection, tabulation, and interpretation of the data contained in this paper. We are grateful for editorial assistance from Drs. C. T. Black and D. W. Douglass.

Contributions and responsibilities of the authors are as follows: Eberhardt prepared the gross organization of the paper, determined and performed the statistical treatment, and wrote most of the narrative. Peterle participated in and supervised most of the exploratory and basic computations and graphing of data. Schofield's thesis in partial fulfillment of requirements for the Master of Science degree in the Department of Fisheries and Wildlife at Michigan State University, is the basis for the section concerning mortality rates. Also, R. G. Heath, formerly of the Rose Lake Wildlife Experiment Station initiated analysis of the multiple catch information, and did some of the computing.

### THE LINCOLN INDEX

As discussed in an earlier paper (Peterle and Eberhardt, 1959), the Lincoln Index (Lincoln, 1930) is apparently invalid for estimating rabbit populations at Rose Lake, since it does not meet one of the assumptions necessary to unbiased use of the method. We refer to the premise that tagged and untagged rabbits have the same probability of capture in hunting. The ratios of tagged to untagged rabbits in the kill for recent hunting seasons, with weekly and cumulative values are shown graphically in Figure 4. In each year there seems to be a definite decline in the proportion of marked animals as the total kill increases. Such a

situation can arise in several ways, principally from hunters inadvertently selecting tagged animals, and from tagged animals leaving the area, and from untagged individuals entering the area from outside. Results of Chi-square tests of homogeneity for these data are listed in Table 2.

"Selection" of tagged animals by hunters means that those rabbits are in some way more vulnerable to hunting, either inherently or geographically. In inherently greater vulnerability, one might speculate that such individuals are also more readily tagged, and possibly also more susceptible to other causes of death. We have some evidence that vulnerability to tagging does not follow that of hunting, but this will be discussed later. Such as it is, our evidence points towards geography as a cause. We have concentrated our trapping on presumably better habitat of cover "edges" and suspect that hunters also concentrate their efforts on these same areas. On occasion we have deliberately set traps in areas of high kill to tag a segment of that population. We suspect that rabbits tend to stay in the same area or the same type of area throughout their lives, and, consequently, tagged animals may be subjected to much higher gun pressure than untagged animals (assuming, of course, that the untagged animals are less accessible to traps). The literature frequently mentions small home ranges for rabbits, although, as with

TABLE 2.—CHI-SQUARE VALUES OF HOMOGENEITY FOR RATIOS OF TAGGED TO UNTAGGED RABBITS FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AND FOR THE 7 YEARS COMBINED, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Year	Chi-square	Degrees of Freedom	Significance
1951	11.29	5	$0.025 < P < 0.05$
1952	3.66	5	$0.50 < P < 0.60$
1953	15.74	8	$0.025 < P < 0.05$
1954	15.36	10	$0.10 < P < 0.20$
1955	8.16	11	$0.60 < P < 0.70$
1956	16.94	7	$0.01 < P < 0.025$
1957	28.52	11	$0.001 < P < 0.005$
Combined	99.67	—	$P = 0.0005$

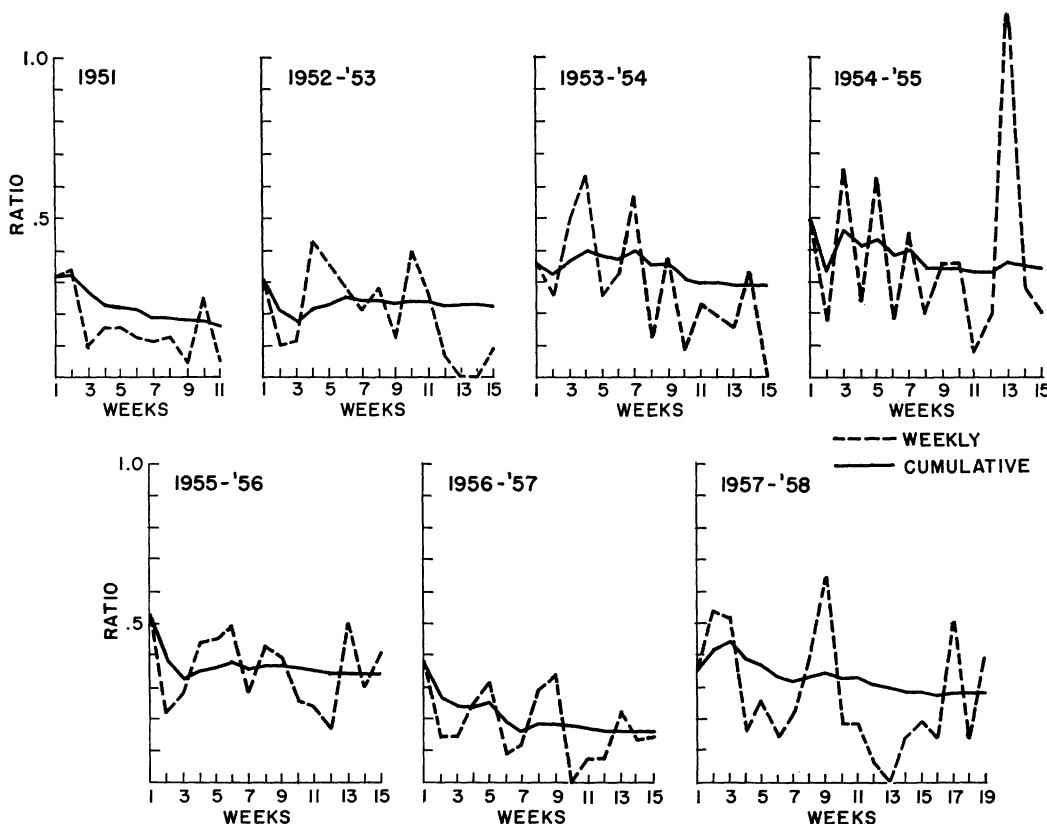


FIG. 4. Ratios of tagged to untagged rabbits in the hunting kill by week and by season for each year of the study period at the Rose Lake Wildlife Experiment Station.

any wild animal, it is difficult to confirm. Movement undoubtedly does occur and must have some effect on the proportion tagged, inasmuch as we can scarcely conceive of a unidirectional movement being a regular thing. That is, we expect some degree of movement in any animal population, with its extent and magnitude dependent on "home range" or "territoriality," along with various seasonal aspects (sexual activity, cover changes, hunting, etc.). If the study area is sufficiently small compared to the magnitude of the movements, then we can expect some tagged animals eventually to drift off the area. If a proportionate number of untagged animals also moves away from the scope of recovery, then the proportion of tagged animals in the population remaining should not be affected. However, we should ordinarily ex-

pect a similar drift from the untagged population outside the area and this, of course, will affect the proportion tagged. Two factors might accelerate such movements at Rose Lake. Hunting pressure there is much greater than in surrounding areas so that rabbits in favorable habitat on the area may be reduced in number (shot) much sooner, and the vacated habitat might consequently "draw in" untagged animals from surrounding areas, thus decreasing the proportion tagged as the hunting season progresses. This does not seem in accord with the known tendency of rabbits to stay very close to home throughout most of the year. The second and possibly more likely factor is that because the areas immediately adjacent to Rose Lake have fair summer cover but less winter cover, rabbits born outside the area may tend to move into the area

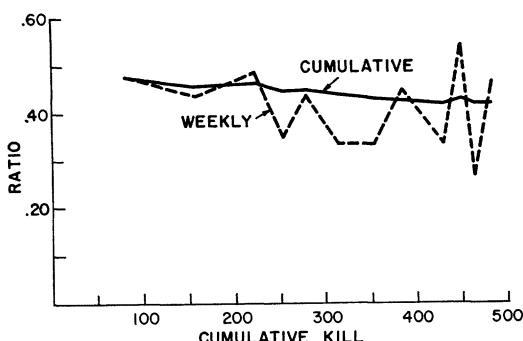


FIG. 5. Ratios of tagged to untagged rabbits compared with the cumulative hunting kill along grid traplines for the entire study period at the Rose Lake Wildlife Experiment Station.

in the fall. We believe such movements ordinarily would take place after live-trapping, but before intensive rabbit hunting begins (late November).

If, as we assume, the observed decline in ratio or proportion of tagged animals is a consequence of hunters concentrating on trapline areas (cover edges), or the placement of traps where hunters hunt, then movements on a much smaller scale may be important. Rabbits may either move into the trapline areas, or hunters later in the season may move out of the traplines as hunting becomes less rewarding there.

More concrete evidence in support of our idea that movement of untagged rabbits onto the Rose Lake area is not a major factor, is discussed in the section on Movements. However, there is one item bearing directly on the problem presented here.

Four of the 36 rabbit traplines now operated at Rose Lake form systematic or "grid" patterns, covering some 200 acres. If our notion of hunters concentrating on traplines along cover edges is valid, then the grid traplines should not show a decline in proportion tagged since traps in these 4 areas are in a regular pattern and many traps are in places where we would not expect them to have the best chance to catch a rabbit. The grid lines (Fig. 2) did not take enough rabbits in any one year to show anything except an erratic pattern, but the combined data for 7 years from those 4 lines show a very small decline in the ratio of tagged to untagged rabbits (Fig. 5). We believe this occurs because trap density in those lines is just about double that of surrounding areas. Any exchange of animals from inside and outside the area during the hunting season should result in a decline of the proportion bearing tags among those shot on the grid areas.

Differences in vulnerability to hunting and trapping between age classes are described in further sections of this paper. We note here, however, that the decline in proportion tagged seems apparent in all age classes, for example, the data for 3 years for juvenile males, juvenile females, and adults (Fig. 6). (Numbers are too few to separate adults by sex. Separate inspection does not show any persistent tendency for adult males and females to differ, however.)

We do not wish to suggest here that "tagged" and "untagged," or "trapped" and

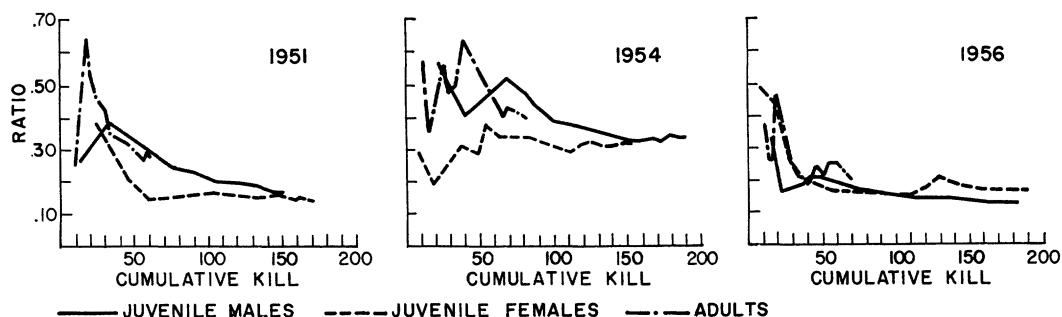


FIG. 6. Ratios of tagged to untagged rabbits of 3 classes, juvenile males, juvenile females, and adults, in the hunting kill during 3 years at the Rose Lake Wildlife Experiment Station.

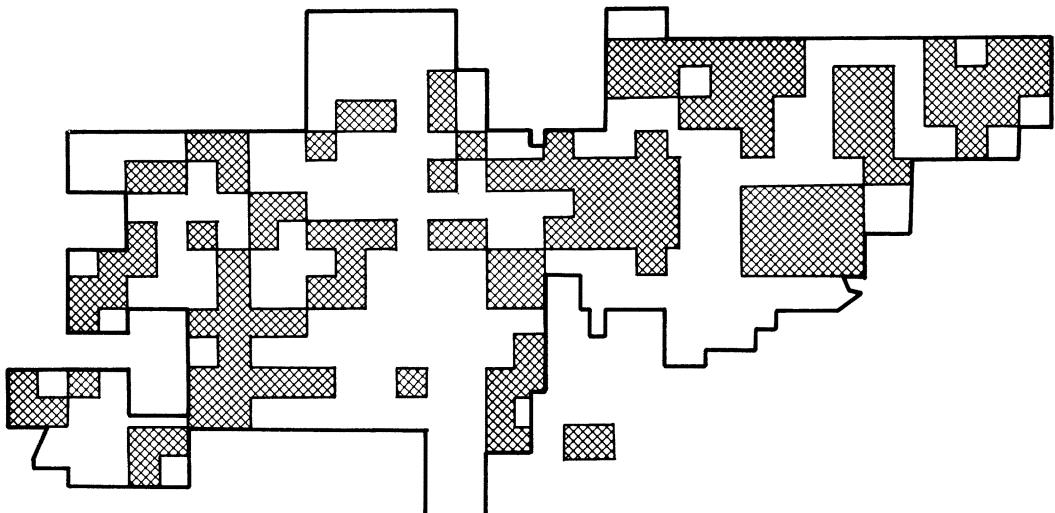


FIG. 7. Locations of 10-acre blocks of land containing one or more live traps at the Rose Lake Wildlife Experiment Station during 1957. The shaded areas contain traps, the clear areas do not.

"untrapped" animals are separate and discrete classes in a spatial sense. Differences proposed are most likely best described as "on the average" and are no doubt the result of gradual changes. As pictorial evidence of this supposition, Figures 2 and 3 depict schematic representations of trap-lines and the location of all rabbits shot in the 1955–1956 and 1957–1958 seasons. Accuracy of locations where animals were killed depends heavily on individual rabbit hunters, and at least a few hunters have rather vague ideas of where they hunted in spite of the many landmarks and system of colored signs delimiting hunting units. In any case, there seems to be a tendency for hunters to bag tagged rabbits close to traplines, and in fact, to bag most rabbits near traplines. In some degree this is a function of cover; some areas are croplands and probably do not support appreciable rabbit populations in midwinter. Also, in recent years we located additional rabbit traplines in areas of consistently high rabbit kill.

The relationship between tagged rabbits in the bag and traplines has been studied in another manner. For purposes of location, the Rose Lake area has been arbitrarily gridded into square 10-acre blocks. If these

blocks are classified by presence or absence of traps, there is an arrangement of "trapped" and "untrapped" areas of sorts (Fig. 7). As illustrated in Figure 3, the kill in the "trapped" blocks has the higher proportion of tagged animals, but both "trapped" and "untrapped" blocks show a decline in proportion tagged. Figure 2 shows that much of the "untrapped" area does not include any rabbit kills (but this does not, of course, imply that rabbits are absent from these areas). We do not see any effective way of sorting out trapped and untrapped areas on a geographic or ecologic basis. This is largely another way of saying we suppose the changes and differences operating here are gradual.

We do have records of hunting effort for major segments of the area, but not in sufficient detail to permit study of differences in intensity of hunting between trapline and non-trapline areas. In the absence of such data we do not see that it will be possible to correct such a bias in our Lincoln Index estimates without introducing unsupported assumptions.

Either intuitively or on the basis of simple mathematical models described later in this paper, it seems evident to us that if our thesis of differential hunting effort is

correct, then the Lincoln Index estimate of population size will be too low, and will remain so until the entire population is shot. We don't know the over-all magnitude of the error but we might obtain some notion of its behavior by considering that the Lincoln Index estimate (Lincoln, 1930) is customarily formed as follows:

$$\text{Population estimate} = \frac{x}{p}$$

where  $x$  = number of animals tagged, and  $p$  = proportion bearing tags of those shot.

A variation of  $p$  from 0.3 to 0.2 will then result in an increase of the estimated population from  $3.3x$  to  $5.0x$  or about 50 per cent. There are variations approaching this magnitude in the Rose Lake data, and we have no way of knowing how much lower the proportion tagged will decline as the "trap-line" population is exhausted. Presumably it will reach the true proportion tagged when all rabbits on the area are dead, and this can never occur.

With the above in mind, and since it seems unlikely that we can materially change the behavior of hunters, we probably will need to change the pattern of any future trapping program to include an attempt to place tags essentially at random, rather than assuming that the hunter shoots rabbits at random from the entire population.

Anticipating a later discussion of the relative vulnerability of adults and juvenile rabbits, we note here that Lincoln Index computations possibly should be carried out separately by sex and age by reason of differences in vulnerability to hunting.

#### MORTALITY

This section deals principally with mortality as determined from the return of tagged animals in hunting from 1938 to 1955. During this period we live-trapped, ear-tagged, and released 3,223 rabbits. Some of the data presented here are from a Master's thesis by one of the authors (Schofield, 1957).

A great deal of evidence indicates that

mortality in rabbits is exceedingly high, and this is apparently a necessary corollary to the high reproductive rate. There are, however, few quantitative data available, or at least such data presented to date offer little in the way of independent checks on the estimates presented as mortality rates.

Southern (1940) reported from his study of the wild rabbit of Europe, *Oryctolagus cuniculus*, "The main thing is the high disappearance rate which occurs at the beginning or soon after the beginning of the season . . . This must be attributed mostly to a heavy mortality in the stages soon after weaning . . ." Kline and Hendrickson (1954), in a study of the eastern cottontail in Iowa, reported on the apparent mortality or disappearance of about 85 per cent of 284 live-trapped rabbits between September 1 and January 1. Tyndale-Biscoe and Williams (1955) in their excellent study of the wild rabbit in New Zealand wrote, "The survival rate of young rabbits was found to be about 70 per cent per 26 days, or 20 per cent per annum, which was also the adult survival rate."

Ingles (1941) in a study of the Audubon cottontail, *Sylvilagus audubonii*, in California found, "A period of 19 months is the longest time recorded for any one of the 29 rabbits followed . . . Only 7 rabbits are known to have lived longer than one year on this area." Haugen (1942), for the eastern cottontail in Michigan, observed "a minimum of 25 per cent of the 1938 adult population lived to an age of approximately 21 or more months."

Allen (1939b) studied eastern cottontails in Michigan also and reported, "Of 70 rabbits marked in this study during the first 3 months of 1936, only 12 are known to have lived to the following November. Ten survived to the December shooting, and 5 of these were still alive after January 1 . . . Two rabbits are known to have lived to an age of approximately 2½ years."

Data used in this section cover the experiment station operations from 1938 to 1955. Records given elsewhere in this paper deal chiefly with the period 1951 to 1957.

The latter selection is based on our adoption in 1951 of aging rabbits by examining the humerus. The earlier data are acceptable for use here by using mortality estimates for female rabbits only. Aging by examining the humerus indicates generally acceptable accuracy in external aging of females, but is of questionable accuracy for males.

Records from single years are too few to permit calculation of any estimates other than recovery rates of animals tagged immediately prior to hunting. At the other extreme, we can estimate natural mortality rates efficiently only for all years as one unit. Groups of years (1938–1945, 1946–1950, and 1951–1955) are useful in estimating total annual mortality and hunting removal rates. This subdivision is desirable since the hunting kill has increased considerably over the years, and it would be advantageous if we could produce natural mortality estimates for shorter periods. We have virtually no data which will furnish direct estimates on crippling loss, and, as elsewhere in this paper, we can do little more than speculate about its magnitude.

Here we are estimating total annual survival on the basis of returns of animals tagged in a given year and recovered in successive hunting seasons, using Ricker's (1948) equation for computing survival of fish:

$$S = \frac{K_a T_b}{T_a K_b}$$

where,

$S$  = annual rate of survival,

$K_a$  = kill in year  $b$  of rabbits tagged in year  $a$ ,

$K_b$  = kill in year  $b$  of rabbits tagged in year  $b$ ,

$T_a$  = number of rabbits tagged in year  $a$ , and

$T_b$  = number of rabbits tagged in year  $b$ .

Since relatively few such returns occur in any one year, we group the data for the 3 periods of years for use in the above equation by summing the set of years in the

group and representing these sums as "years"  $a$  and  $b$  in the equation above. As an example the calculation of the survival rate for juvenile female rabbits during the last period (1951–1955) follows:

$K_a = 18$  (18 rabbits tagged in period  $a$  survived one hunting season and were killed by hunting in the following year),

$K_b = 155$  (155 rabbits tagged in period  $b$  were killed during the first hunting season following tagging),

$T_a = 371$  (371 rabbits were tagged in period  $a$ ), and

$T_b = 409$  (409 rabbits were tagged in period  $b$ ).

Thus,

$$S = \frac{18 (409)}{371 (155)} = 0.128 .$$

(Period  $a$  = 1951 to 1954 inclusive, period  $b$  = 1952 to 1955 inclusive.)

Then we convert the survival rates obtained as above to instantaneous rates of mortality (Table 3) following Ricker (1948, 1958). The instantaneous rate is the natural logarithm of the surviving fraction and in the case of mortality is always negative.

To estimate natural mortality (used here in the same way as by Ricker [1958] to represent losses from causes other than hunting), we consider the percentage return in the hunting season of rabbits tagged at increasing lengths of time prior to the

TABLE 3.—CALCULATED ANNUAL INSTANTANEOUS MORTALITY RATES OF FEMALE RABBITS FOR 3 PERIODS OF YEARS AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

	Period	$K_a$	$K_b$	$T_a$	$T_b$	Proportion Surviving
Adult Females						
	1938–45	8	41	205	241	0.229
	1946–50	11	35	172	186	0.340
	1951–55	9	27	134	113	0.281
Juvenile Females						
	1938–45	9	72	247	317	0.160
	1946–50	10	69	267	272	0.148
	1951–55	18	155	371	409	0.128

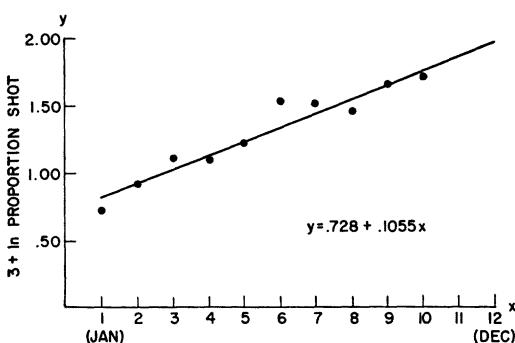


FIG. 8. Estimates of natural mortality among adult female rabbits at the Rose Lake Wildlife Experiment Station.

season (but in the same year). Logically, we should expect to recover in a given hunting season proportionately fewer of the rabbits marked at the greater intervals prior to the season. If we assume survival to be at a uniform rate, and if hunters take tagged animals independently of the time of tagging (we show elsewhere in this report that hunters probably take tagged animals at a greater rate than untagged, and adults and juveniles at different rates, so we can expect these results to reliably represent only the tagged animals), then we can describe the above situation symbolically as follows:

$$N(t) = N(0)S^x$$

where,

$N(t)$  = rabbits surviving to hunting season,

$N(0)$  = initial population of rabbits tagged  $x$  months before hunting season, and

$S$  = monthly survival rate (proportion).

Now if hunters take some over-all fraction,  $k$ , of rabbits in hunting, then we may rearrange the above to:

$$k \frac{N(t)}{N(0)} = kS^x.$$

Taking natural logarithms (base  $e$ ) of the above we get

$$\ln \left\{ k \frac{N(t)}{N(0)} \right\} = \ln k + x \ln S.$$

This is the equation of a straight line which we may fit by linear regression methods from sample data. In doing so, we have taken time in months from December (mid-point of the hunting season). The data and regression lines for adult and juvenile females are shown in Figures 8 and 9, respectively. Since the logarithms of proportions are negative, we have added 3 to each value for ease in calculation. The shorter span for juveniles results from the definition of juveniles as only those animals so classified in the hunting season, and since we seldom catch very small juveniles, records for April and May are lacking. This means that the records and rates given here are really for juveniles large enough to be trapped. The classification "adults" is somewhat ambiguous, too, since sizable numbers of these animals were in fact "juveniles" not long before they were tagged; i.e., those tagged in late winter and early spring would have been classified as juveniles, had they been handled in the hunting season immediately preceding. The point we need to make here is that "juvenile" really pertains only to the first 8 months or so of life as far as these records go. In our study, all young of the year were classified as adults on January 1.

The regression slope, as indicated in the figures, if given a negative sign, is the estimate of instantaneous natural mortality rate, since it is then the negative natural logarithm of the monthly survival rate. Figure 9 does not show any evidence of

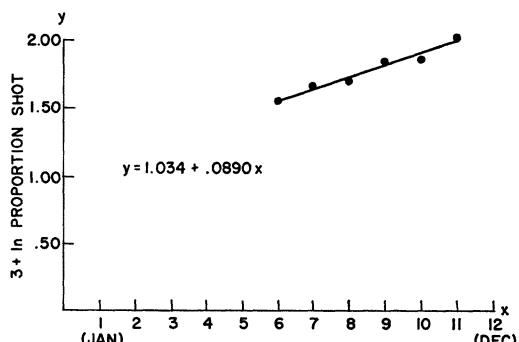


FIG. 9. Estimates of natural mortality among juvenile female rabbits at the Rose Lake Wildlife Experiment Station.

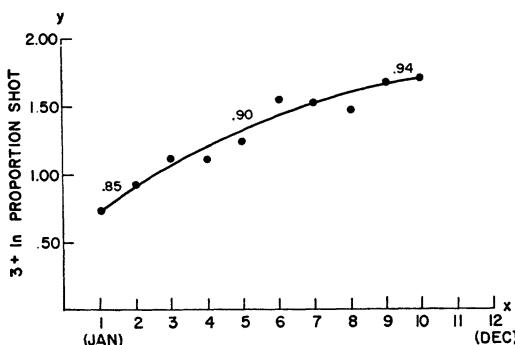


FIG. 10. Estimates of natural mortality among adult female rabbits at the Rose Lake Wildlife Experiment Station. The data are the same as in Figure 8, the curve was fitted by inspection.

curvature, suggesting that the juvenile female natural mortality rate is constant from June through November. We would not, however, expect this to be true if we had data to represent all juveniles. In other words, we suppose that the mortality (or survival) rates may be effectively constant beyond a certain size of rabbit. If we had handled many smaller rabbits, we would not expect this linear relationship.

In Figure 8, there seems to be a suggestion of curvature. If a curve is fitted by inspection (Fig. 10), it seems likely that this relationship will provide both a better fit and a logically more meaningful situation. This is so because: (1) in the earlier months (January to March or April) times are much harder for rabbits since cover and food are at a minimum and, (2) many of the rabbits involved (born the previous summer) may logically become more wary as they get older. These notions are borne out by the decreasing slope of the curve (represented by monthly survival rates plotted at three points on Fig. 10 and estimated from tangents to the curve), indicating decreasing mortality (and increasing survival). We have not attempted to fit any particular curved functions to these points by statistical methods largely because we do not know of any such function that has a biological basis.

To allow a computation of a weighted mean slope, we calculated the slope of a

weighted linear regression as outlined by Snedecor (1956):

$$\text{Slope} = \frac{\sum (SWX)(SWY)}{\sum SWX^2 - \frac{(\sum SWX)^2}{\sum SW}}$$

where,

$S$  = summation,

$W$  = number of female juvenile rabbits handled during a particular month,

$X$  = time (in months) from this particular month to December, and

$Y$  = natural logarithm of proportion killed by hunters from those animals handled in this particular month.

The regression slope for female juveniles is:

$$\text{Slope} = \frac{-4398.63 - \frac{(3642)(-1327.97)}{1126}}{1216.10 - \frac{(3642)^2}{1126}}$$

$$= -0.0850 = \ln \text{monthly survival rate.}$$

The proportion of juvenile female rabbits surviving each month of natural mortality is the antilog of -0.0850 or 0.919. This compares with the 0.914 survival found by the unweighted regression technique. Calculating the weighted mean slope for the female adults produced a monthly survival of 0.916, compared to the 0.900 given above. We have arbitrarily used 0.914 for the juvenile monthly survival rate in the discussion that follows.

The remaining information on mortality used here is the recovery of tagged animals in the hunting season immediately following tagging. We make further detailed use of such data for the years 1951–1957 in later sections of this paper. Here we simply sum up the data for the 3 groups of years (Table 4) to represent the recovery of rabbits marked in “Lincoln Index” tagging immediately before the hunting season. These recovery rates are not direct measures of the mortality resulting from hunting. Hunters

TABLE 4.—PROPORTIONS OF TAGGED FEMALE RABBITS SHOT DURING THE HUNTING SEASON IMMEDIATELY AFTER TAGGING, FOR 3 PERIODS OF YEARS AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Period	Trapped	Shot	Proportion Shot
Adult Females			
1938–45	94	22	0.234
1946–50	44	12	0.273
1951–55	136	43	0.316
Juvenile Females			
1938–45	178	46	0.258
1946–50	129	38	0.294
1951–55	394	161	0.409

are competing with "natural" causes of mortality throughout the long hunting season and would take appreciably more rabbits if other causes of mortality become inoperative. Since we carry on no live-trapping during the hunting season, we must use the rates of natural mortality obtained before the season in calculations applying to the hunting season. The method we use is that of Ricker (1958:25). Neyman (1950) discussed in detail the concept involved ("competing" causes of mortality). Following Ricker's suggestion (1958:26), we use 2 periods for the computations to avoid the bias involved in spreading hunting mortality over the year, (1) the hunting season (taken as 4 months, November through February), and (2) the balance of the year.

We use Ricker's (1958) notation as follows (rearranged to apply to 2 periods);

1. Expectations of death (during hunting season):

$a$  = from all causes (fraction of animals alive at beginning of season that die during season),

$u$  = from hunting,

$v$  = from natural causes, so that

$a = u + v$ .

2. Instantaneous mortality rates (expressed on a monthly basis; different rates may be used for different parts of the year):

$p$  = from hunting,

$q$  = from natural causes, so that

$4p + 4q$  = total for hunting season.

The total expectation of death from hunting then is:

$$u = \frac{4p}{4p + 4q} \left\{ 1 - e^{-4p - 4q} \right\}.$$

Dealing now only with female juveniles, we have available the values of  $u$  and  $q$  (estimated from the data obtained prior to hunting in the linear regression relationship) and may thus estimate values of  $p$ , the instantaneous rate for hunting. Results are:

Period	$u$	$4p$	$4q^*$	$1 - a$
1938–45	0.258	0.361	0.356	0.488
1946–50	0.294	0.423	0.356	0.459
1951–55	0.409	0.649	0.356	0.366

\* Estimated as 0.0890 per month in Figure 9.

The increasing over-all rate of hunting mortality and decreasing over-all survival during the hunting season ( $1 - a$ ) in the above tabulation is logical. Since 1938 there has been a steady increase in hunting effort at the experiment station. The right-hand column ( $1 - a$ ) above is survival through the hunting season of rabbits alive at the beginning of the season. The remaining calculation of importance is the continuation of estimates through the year in order to compare them with the independent estimate of total annual mortality (we use "independent" here in a rather loose sense since these estimates are all based on tagged animals and essentially the same set of data). What we need is an estimate of natural mortality through the rest of the year. Probably the best estimate available at present is that shown in Figure 10 for "adult" animals, since we also include the "juveniles" of above in the basic data for this figure (after the hunting season "juveniles" are adults). Reading instantaneous mortality rates as tangents to the curve at 3 points (shown as monthly survival rates, 0.85, 0.90, and 0.94 on the curve), we combine them as follows:  $3(0.162) + 3(0.105) + 2(0.062) = 0.925$ , on the assumption that the 3 rates represent 3, 3, and 2 months, respectively, in the remaining 8 months of the year. By converting this rate to a survival rate for the rest of the year,  $e^{-0.925} = 0.396$ ,

and multiplying this rate by those for the hunting seasons above, we get a series of annual survival rates comparable to the "independent" estimates of Table 3.

Period	Hunting season survival	Survival for remainder of year	Annual survival	Annual survival from Table 3	Difference
1935–45	0.488	0.396	0.193	0.160	0.033
1946–50	0.459	0.396	0.182	0.148	0.034
1951–55	0.366	0.396	0.145	0.128	0.017

Considering the variation and numerous sources of error, the differences in the two estimates above are not surprising. They are, however, larger for the first 2 periods than we would expect from the one remaining source of mortality (crippling loss) not considered in the calculations. We can demonstrate this by taking the estimates of total annual mortality from Table 3 as the actual values and working backwards. We assume the same survival for the 8 months outside the hunting season (0.396) and obtain a new set of hunting season survival values (0.404, 0.374, and 0.323) for the 3 periods. We further represent the total expectation of death from hunting during the hunting season period ( $u$ ) by a relationship which now includes a component for crippling loss:

$$u = \frac{4p}{4p + 4q + 4m} \left\{ 1 - e^{-4p - 4q - 4m} \right\},$$

where  $m$  now represents the monthly instantaneous rate of mortality by crippling loss. The over-all survival through the hunting season is now:

$$1 - a = e^{-4p - 4q - 4m}.$$

To solve these equations from the given data, we need one further assumption, that the crippling rate is a constant fraction of the rate of hunting removal, or that  $m = bp$  where  $b$  is a constant. This seems entirely reasonable from what we know of crippling loss, since some constant fraction of the animals hit and killed will not be recovered. Rewriting the above equations using this assumption gives:

$$u = \frac{4p}{4p(1+b) + 4q} \left\{ 1 - e^{-4p(1+b) - 4q} \right\}$$

$$1 - a = e^{-4p(1+b) - 4q},$$

and we can thus form the following table of data:

Period	Hunting season survival	$u$	$4q$	$4p$	$b$	$4m$
1938–45	0.404	0.258	0.356	0.392	0.403	0.158
1946–50	0.374	0.294	0.356	0.462	0.360	0.166
1951–55	0.323	0.409	0.356	0.683	0.133	0.091

Examining the values of  $b$  above we see that the supposed values of the crippling loss ( $m$ ) are suspiciously high for the first two groups of years, amounting to about 40 per cent of the hunting kill. Only in the last period does the value, about 13 per cent of the hunting kill, seem reasonable. Since our estimates of natural mortality depend (as do those of total annual mortality) on the recovery of tags in hunting, and since the last period is the one of greatest such recovery, it seems quite possible that the natural mortality rate may have decreased in recent years, and that the value we have is biased towards the value of recent years by the greater volume of returns. In other words, natural mortality may have been numerically greater in the earlier years, and decreased recently by virtue of the accompanying increase in hunting mortality. On the other hand, our estimates of total annual mortality depend on rabbits remaining on the area and retaining tags for a longer period of time than required for any of the other estimates used here. Both loss of tags and drift of animals out of the area would tend to cause overestimates of the total annual mortality; the best present course is to consider annual mortality to be between the two estimates obtained here, with crippling loss as some unknown part of the difference.

One further item of survival and mortality information is lacking. We do not assume that our estimates of juvenile mortality can apply to very young rabbits. For the sake of completeness, but without much hope of accuracy, we make the following estimate of such rates. If we take the monthly adult female survival rate to be about 0.90, corresponding to the rate for spring and early summer in Figure 10, the corresponding instantaneous mortality rate is 0.105. We can use this rate to carry a

contingent of breeding females up to the hunting season. (According to Fig. 10, we should change over to a somewhat lower rate towards fall, but we have not done so here.) If we further assume that adult females produce 3 litters of 5 young each year, a generally acceptable assumption not supported by much precise quantitative data, we can then show the production of young females by some contingent of adult females to be:

Date	Months from April 15	Size of adult female population	Production of young females at 2.5 per adult
April 15	0	1,000	2,500
May 15	1	900	2,250
June 15	2	810	2,025
October 15	6	532	

We may now consider the survival of juvenile females in terms of some fall age ratios, expressed in the following equation:

$$\text{Fall age ratio} = \frac{2,500e^{-6x} + 2,250e^{-5x} + 2,025e^{-4x}}{532}.$$

A few values of  $x$ , the monthly instantaneous mortality rate for juvenile females with their corresponding fall age ratios are:

Selected instantaneous rate ( $x$ )	0.100	0.150	0.200	0.250
Computed age ratio	7.69	5.99	4.68	3.66

From the above estimates, it seems that we need to use a juvenile mortality rate at least twice that estimated for older juveniles by the regression method in order to get a fall age ratio comparable to those actually observed (see Age Ratios). If our assumptions in the above procedures are at all near reality, it would seem that early (nestling?) juvenile mortality must be very large indeed for the observed rates to hold for the period from trapping to hunting. In general, we suppose it is likely that mortality rates decrease steadily with age up to at least 1 or 1½ years of age.

#### MOVEMENT

Movement of tagged rabbits from the experiment station, and their replacement by untagged rabbits moving in from surrounding areas, or an influx of rabbits from the surrounding area, could account for the

observed decline in the proportion of tagged rabbits in the bag, as the hunting season progresses. However, we are inclined to doubt that movements can satisfactorily account for decreases of the magnitude observed in most years.

One of the arguments against movement as the source of our difficulties has already been discussed under the Lincoln Index, where we described results of grid trapping.

As a direct measure of the magnitude of movement we have records on the number of rabbits tagged in one hunting unit of the station (Fig. 1) and shot in another (Table 5). These data show that only about

TABLE 5.—NUMBERS OF RABBITS TAGGED AND SHOT IN EACH OF 7 SEPARATE HUNTING UNITS, AND ALL UNITS COMBINED, FOR 3 HUNTING SEASONS, USED AS AN INDEX TO MEASURE MOVEMENT AMONG UNITS AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Hunting Unit	Tagged and Shot in Same Unit	Tagged in One Unit But Shot in Another	Shot in One Unit But Tagged in Another
1955–1956			
Red	5	5	2
Orange	51	1	1
White	11	1	2
Blue	12	2	0
Green	18	3	5
Yellow	6	1	4
Brown	7	1	0
Total	110	14	14
1956–1957			
Red	9	2	0
Orange	20	1	3
White	9	0	1
Blue	3	0	1
Green	6	1	0
Yellow	6	0	0
Brown	3	1	0
Total	56	5	5
1957–1958			
Red	9	1	2
Orange	49	2	4
White	15	4	2
Blue	7	1	0
Green	24	1	1
Yellow	11	1	2
Brown	7	1	0
Total	122	11	11

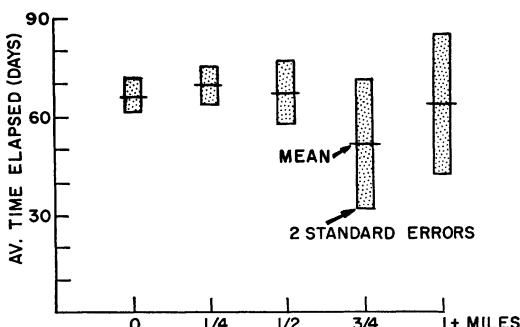


FIG. 11. Time elapsed between tagging and shooting of rabbits compared with the distance moved during the intervening period, Rose Lake Wildlife Experiment Station.

10 per cent of the tagged kill in a unit was actually tagged in some other unit. Most of the recorded movements were from one unit to an immediately adjacent unit. If, however, we assume rabbits leave the station at this rate and are replaced by rabbits entering from outside, and further accept 30 per cent tagged in the kill early in the season as the true proportion of tagged rabbits, then a subsequent loss and replacement of 10 per cent of the tagged rabbits will, at most, reduce the proportion tagged from 0.30 to 0.27, a definitely smaller decline than that observed in most years. This expected decrease is, however, about that noted in "grid" trapping (Fig. 5).

Furthermore, there seems to be no correlation between the length of time elapsed between tagging and shooting, and the distance moved (Fig. 11). If rabbits tend to "drift" off the area, then we would expect long movements to take more time than short movements. The observed behavior, however, is in accord with most experience. Rabbits tend to have a fairly small home range and persistently return to the same area, a delight to the man who hunts with hounds and waits for rabbits to "circle." There also seems to be little difference in distance moved by any sex or age class. Longer average movements by juveniles should accompany the greater drop in proportion tagged shown by that class, if movements are responsible for the decline.

Some tagged animals have moved rather great distances (Fig. 11), but it appears that most animals moved from one trapline to another. This may simply be because traplines are in "cover edges." Apparently, rabbits move from one habitat to a similar one.

Winter rabbit cover immediately adjacent to the experiment station seems generally poorer than on the station. However, much of the surrounding area provides acceptable summer habitat. Thus, it is quite possible that there is an inducement for rabbits to move onto the area in early winter. Whether they do so in face of the much heavier hunting pressure on the station, we cannot say. Hunters on the station may also deplete the rabbits in excellent habitat, making space for off-station rabbits, although we have little evidence to confirm this notion. Probably we can obtain a satisfactory answer only by tagging rabbits outside.

In a final test of the effects of movements, we divided the tagged population in two, the first part composed of rabbits tagged during the first half of the trapping period, the second part composed of those tagged during the second half. Considering only the tagged rabbits in the hunting kill and the 2 halves as "marked" samples (Table 6), we made 2 independent estimates of the tagged population. For example, in 1957,

TABLE 6.—ESTIMATES OF THE SIZE OF RABBIT POPULATIONS BASED ON RABBITS TAGGED DURING THE FIRST AND SECOND HALVES OF THE TRAPPING PERIOD AND SHOT DURING THE FOLLOWING HUNTING SEASON FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Year	Actual Tagged Population	Estimates of Tagged Population	
		From First Half	From Second Half
1951	181	219	154
1952	167	152	186
1953	266	223	329
1954	245	228	265
1955	292	292	292
1956	197	221	178
1957	337	319	357

337 rabbits were tagged, 168 during the first half of the trapping period and 169 during the second half. Of those 337, 133 were shot, 70 having been tagged during the first half of the trapping period and 63 during the second half. Thus, by simple proportion ( $70/133:168/X$ ) an estimate of 319 is obtained based on the sample from only the first half of the trapping period. Similarly, an estimate of 357 rabbits ( $63/133:169/X$ ) is obtained from the data for the second half of the trapping period. The resulting 2 sets of estimates do not differ consistently in size, as would be expected if there were an appreciable movement of tagged rabbits off the area.

#### RECOVERY RATES

The term "recovery rate" here refers to the proportion of rabbits tagged in September and October that hunters shoot in the hunting season immediately following. We use this term in preference to "exploitation rate" or "expectation of death from hunting," since we believe hunters shoot tagged rabbits at a greater rate than the untagged.

Presumably at least 2 factors, hunting effort and the prevailing rate of natural mortality, affect these recovery rates. If hunters concentrate on areas where the tagging is done, we must assume that the ratio of effort on these areas to effort on other areas is relatively constant from year to year before we can do much with kill-effort relationships. This is a largely unsupported assumption beyond the usual rather negative arguments that the area has not changed much in recent years, hunters seem to behave about the same, and so on. The effect of natural mortality on the harvest has been ignored by most workers. For a species like the cottontail, we must account for such losses in some manner if we are to obtain any useful analysis of population statistics. Our attempts to do so in this paper are admittedly not satisfactory, but we believe they at least indicate the importance of a provision for measurement of natural mortality in any such study.

TABLE 7.—CALCULATED PROPORTIONS OF TAGGED RABBITS RECOVERED BY HUNTERS FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION. The rates are computed from recoveries in the hunting season immediately following trapping and do not include recoveries in subsequent years. Also, these rates are based on rabbits trapped in September and October and thus do not include summer trapping. "Natural" (base  $e$ ) logarithms are used in the ratio of logarithms of the complements of recovery rates. Rates for "all" juveniles are based on weighted averages of males and females, as are the estimates for adults. These results differ considerably from a similar table in an earlier paper on this material (Peterle and Eberhardt, 1959) because of the corrections used here.

Year	Juveniles		$r_j$ All Juveniles	$r_a$ Adults	$\ln(1 - r_j)$ $\ln(1 - r_a)$	Total Rabbits Tagged
	Males	Females				
1951	0.32	0.31	0.32	0.29	1.13	181
1952	0.30	0.26	0.28	0.44	0.57	167
1953	0.40	0.35	0.37	0.36	1.04	266
1954	0.40	0.38	0.39	?	?	245
1955	0.49	0.39	0.44	0.38	1.21	292
1956	0.29	0.34	0.32	0.29	1.13	197
1957	0.37	0.43	0.40	0.39	1.03	337

We base our estimates of recovery rate (Table 7) on 2 methods for determining age. Classification at time of trapping necessarily depends on external characters, while the shot sample is aged by examining the humerus. Methods for determining young of the year have been described by Thomsen and Mortensen (1946), Hale (1949), and Petrides (1951). We have used both humerus and X-ray aging at Rose Lake and find close agreement between the methods up to November 15. All age data in this discussion are based on the examination of the humerus. Errors in sexing animals in the field have been minor. A total of 8 errors occurred in 636 determinations where autopsy of shot animals followed.

If we accept the sex and age classification of the shot sample as valid, we must then estimate the true sex and age composition of the trapped animals before computing valid recovery rates. We cannot use simple proportionate corrections if, as suggested in Table 7, the several sex and age groups dif-

fer in vulnerability to the gun and consequently have different probabilities of appearing in the shot sample. We proceed as follows:

(1) In the total trapped sample ( $T$ ) there may be the following categories:

Apparent classification at trapping	True (humerus) classification				
	Adult males	Adult females	Juvenile males	Juvenile females	Total trapped
Adult males	$a_{11}$	$a_{21}$	$a_{31}$	$a_{41}$	$A_{am}$
Adult females	$a_{12}$	$a_{22}$	$a_{32}$	$a_{42}$	$A_{af}$
Juvenile males	$a_{13}$	$a_{23}$	$a_{33}$	$a_{43}$	$A_{jm}$
Juvenile females	$a_{14}$	$a_{24}$	$a_{34}$	$a_{44}$	$A_{jf}$
					$T$

In the above data,  $a_{11}$ ,  $a_{22}$ ,  $a_{33}$ , and  $a_{44}$  represent animals correctly classified when they were trapped. All other symbols represent animals incorrectly classified at trapping. Thus,  $a_{13}$  represents adult males mistakenly called juvenile males at the time they were trapped,  $a_{42}$  represents juvenile females mistakenly classified as adult females, and so on. Not all such combinations will be expected to occur, but presumably all are possible.

Only the tagged kill ( $K$ ), which will be less than the total number tagged, will be available as a check on mistakes in sexing and aging. If vulnerability to hunting differs in the several classes, then the more vulnerable classes will be present in the shot sample in proportionately greater numbers than the less vulnerable classes. To show this, we suppose that there are 4 different "recovery" rates,  $r_{am}$ ,  $r_{af}$ ,  $r_{jm}$ , and  $r_{jf}$ , defined as:

$$r_{am} = \frac{\text{tagged adult males recovered in hunting}}{(\text{true}) \text{ total of adult males tagged}}.$$

A new tabulation will then show composition of the shot sample:

Apparent classification at trapping	True (humerus) classification			
	Adult males	Adult females	Juvenile males	Juvenile females
Adult males	$r_{am}(a_{11})$	$r_{af}(a_{21})$	$r_{jm}(a_{31})$	$r_{jf}(a_{41})$
Adult females	$r_{am}(a_{12})$	$r_{af}(a_{22})$	$r_{jm}(a_{32})$	$r_{jf}(a_{42})$
Juvenile males	$r_{am}(a_{13})$	$r_{af}(a_{23})$	$r_{jm}(a_{33})$	$r_{jf}(a_{43})$
Juvenile females	$r_{am}(a_{14})$	$r_{af}(a_{24})$	$r_{jm}(a_{34})$	$r_{jf}(a_{44})$

The magnitude of each element here depends on the size of the group so classi-

fied at trapping ( $a_{ij}$ ) and the true recovery rate for the class ( $r_{pq}$ ). Thus  $r_{am}$  ( $a_{13}$ ) represents the number of adult males mistakenly classified as juvenile males when trapped, but properly identified in the shot sample, and whose recovery rate is correctly that of all adult males.

Neither of the components of the elements of the above table is known. Our immediate purpose is to estimate the values of  $r_{am}$ ,  $r_{af}$ ,  $r_{jm}$ , and  $r_{jf}$ . If we relabel the elements of the above table as  $A_{11}$ ,  $A_{12}$ , etc., so that  $r_{am}$  ( $a_{11}$ ) =  $A_{11}$ ,  $r_{af}$  ( $a_{23}$ ) =  $A_{23}$ ,  $r_{jf}$  ( $a_{42}$ ) =  $A_{42}$ , and so on, and also define a set

of coefficients  $b_1 = \frac{1}{r_{am}}$ ,  $b_2 = \frac{1}{r_{af}}$ ,  $b_3 = \frac{1}{r_{jm}}$ ,  $b_4 = \frac{1}{r_{jf}}$ , then we can write a system of equations as follows:

$$\begin{aligned} b_1 A_{11} + b_2 A_{21} + b_3 A_{31} + b_4 A_{41} &= A_{am} \\ b_1 A_{12} + b_2 A_{22} + b_3 A_{32} + b_4 A_{42} &= A_{af} \\ b_1 A_{13} + b_2 A_{23} + b_3 A_{33} + b_4 A_{43} &= A_{jm} \\ b_1 A_{14} + b_2 A_{24} + b_3 A_{34} + b_4 A_{44} &= A_{jf}. \end{aligned}$$

Sums of these equations are known, since

the elements are  $b_1 A_{11} = \frac{r_{am} A_{11}}{r_{am}} = a_{11}$ ,  $b_4 A_{43} = \frac{r_{jf} A_{43}}{r_{jf}} = a_{43}$ , etc., and the sums of

these elements are known, being (from the first table above) the total numbers actually trapped. As an example, the first equation is:

$$a_{11} + a_{21} + a_{31} + a_{41} = A_{am} = \text{total classified as adult males in trapping.}$$

We now have a system of 4 linear equations in 4 unknowns and can solve for the unknowns by algebraic methods. One further difficulty exists, a small fraction (usually 10 per cent or less) of the tagged animals in the hunting bag were not aged by the humerus. We assume this to be random and have assigned these individuals to the various classes in proportion to those that were aged by the humerus. The basic data corresponding to known qualities in the set of linear equations are given in Table 8.

There seem to be fairly consistent dif-

TABLE 8.—COMPARISON OF AGES OF RABBITS DETERMINED IN THE FIELD WITH THOSE DETERMINED BY EXAMINATION OF THE HUMERUS FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Determined in Field	Determined from Humerus				
	Adult Males	Adult Females	Juvenile Males	Juvenile Females	Total Trapped
1951					
Adult males	8	0	2	0	25
Adult females	0	5	0	1	29
Juvenile males	0	0	20	0	62
Juvenile females	0	0	0	20	65
1952					
Adult males	8	0	2	0	22
Adult females	0	7	0	1	24
Juvenile males	3	0	17	0	63
Juvenile females	0	0	0	15	58
1953					
Adult males	7	0	2	0	24
Adult females	0	7	0	2	26
Juvenile males	3	0	40	2	114
Juvenile females	0	0	1	35	102
1954					
Adult males	10	0	15	0	34
Adult females	0	10	0	1	21
Juvenile males	1	0	35	0	88
Juvenile females	0	0	0	38	101
1955					
Adult males	8	0	7	0	44
Adult females	1	13	0	6	39
Juvenile males	3	0	44	0	101
Juvenile females	0	0	0	42	108
1956					
Adult males	4	0	2	0	24
Adult females	0	7	0	2	27
Juvenile males	1	0	18	0	66
Juvenile females	0	0	0	27	79
1957					
Adult males	12	0	7	0	35
Adult females	0	10	0	1	41
Juvenile males	2	0	49	2	139
Juvenile females	0	3	2	45	122

ferences in recovery rates (Table 7), presumably representing differences in vulnerability to hunting. Evidently juvenile males are most vulnerable, with juvenile females intermediate, and adults of both

sexes least vulnerable. If juveniles have a higher rate of natural mortality (as already shown in the section on mortality), then the true differences in vulnerability are greater than exhibited here, since relatively more juveniles than adults die from natural causes and are not available to hunters.

The relationship between juvenile and adult recovery rates warrants further consideration. To do this, we introduce some mathematical models. These models are no doubt less sophisticated than the situation merits, but a more elaborate treatment seems to require better data than we have on the spatial distribution of hunting pressure and on natural mortality. We believe the relationships given here will at least show the nature of the problems involved.

For immediate purposes, and for the present neglecting natural mortality, we assume a relationship between hunting effort and proportion of the population harvested as follows:

$$r_j = 1 - e^{-m_1 n}$$

$$r_a = 1 - e^{-m_2 n}$$

where:

$r_j$  and  $r_a$  = hunting recovery rates for tagged juvenile and adult rabbits,

$m_1$  and  $m_2$  = juvenile and adult "catchability" rates as defined by DeLury (1947); referring to proportion of the population taken by one unit of hunting effort, and

$n$  = units of hunting effort applied to the population and producing the observed recovery rate.

Rearranging and taking natural logarithms:

$$\ln(1 - r_j) = -m_1 n$$

$$\ln(1 - r_a) = -m_2 n .$$

Now, under our assumption of a differential hunting effort between tagged and untagged portions of the population,  $n$  becomes unknown. We assume here that adult and juvenile tagged rabbits are not segregated and are subject to the same unknown hunting effort, so that we may com-

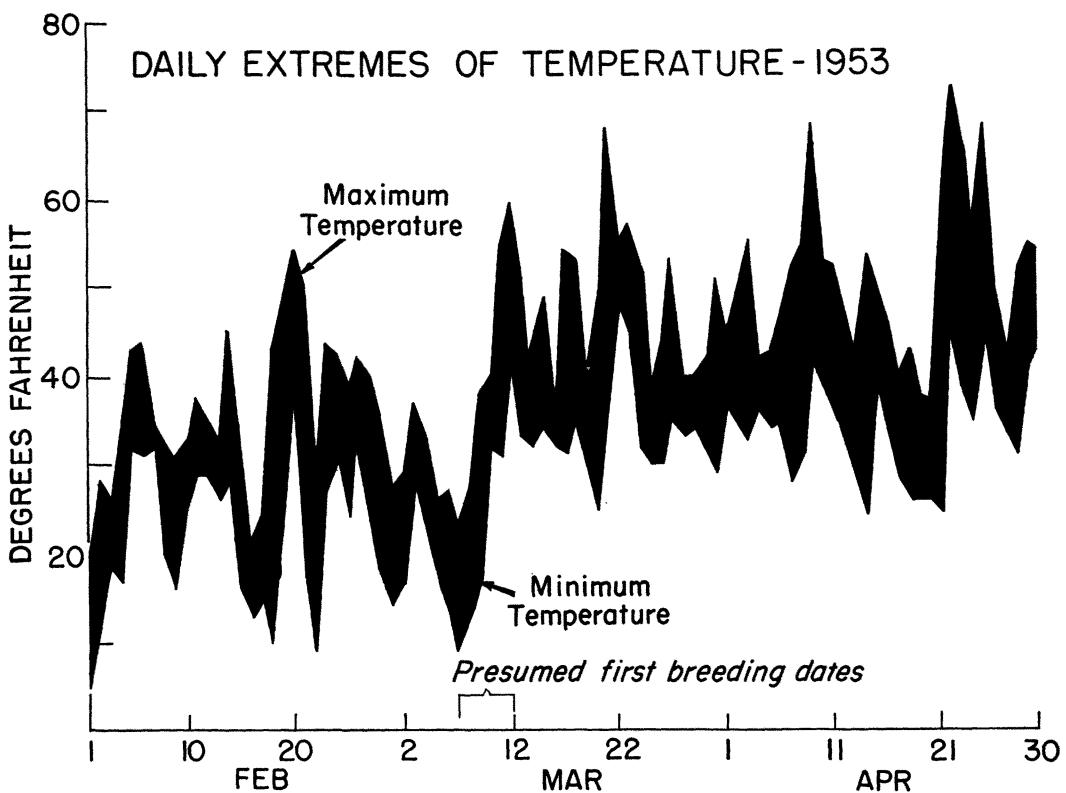


FIG. 12. A typical temperature graph used to estimate the initiation of the breeding season for rabbits at the Rose Lake Wildlife Experiment Station.

bine the 2 equations, both being functions of  $n$ ,

$$\frac{m_1}{m_2} = \frac{\ln(1 - r_j)}{\ln(1 - r_a)}.$$

This shows that the ratio of the "vulnerability" or "catchability" rates is the ratio of the natural logarithms of the complements of the recovery rates.

These ratios (Table 7) vary somewhat over the years. It seems reasonable to argue that the adult rate should vary the least from year to year, so that fluctuation of the ratio (apart from chance or "sampling" variations) might principally be caused by changes in juvenile vulnerability. We might further suppose that such changes would be associated with the average age of juveniles in the hunting season. At the time, we did not have any useful direct measures of juvenile ages, but an indirect measure is

available in terms of initial breeding dates. These are the dates when spring temperatures show a pronounced increase which is maintained from then on (Fig. 12), as described by Friley (1955). Olsen (1959) has observed a similar phenomenon in his study of the biology of muskrat (*Ondatra zibethica*) breeding at Delta, Manitoba. A new technique for aging rabbits, using the lens of the eye, described by Lord (1959) may eventually be helpful in this case.

When the ratio of juvenile and adult vulnerability is plotted against initial breeding date there is some degree of correlation (Fig. 13). Without some less circumstantial means of corroboration, we hesitate to claim that this relationship is anything more than suggestive and logical. There is, too, an alternate explanation or at least a complicating factor, in the possibility that the early born juveniles may be mistakenly

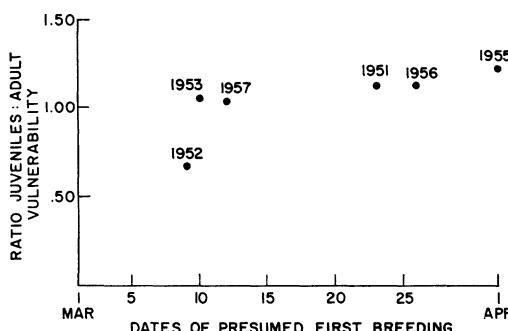


FIG. 13. A comparison of the dates of presumed first breeding by rabbits, with the ratio of vulnerability between juvenile and adult rabbits, at the Rose Lake Wildlife Experiment Station.

identified as adults. We do not have any evidence that such errors occur in age determinations based on examination of the humerus, but if they do, the above relationship might simply reflect the degree of error, rather than any real fluctuation in vulnerability of juveniles.

We have neglected natural mortality in the above discussion. Losses from causes other than hunting are undoubtedly large and will, in our long hunting seasons, have an effect on relationships of the sort discussed here. We have no basis for assuming such losses to be the same for adults and juveniles or constant from year to year. On the contrary, we are inclined to the view that much "natural" mortality will be from predation, and higher vulnerability to human predation (hunting) probably implies an increased vulnerability to other predators. However, the recovery rates by hunters are based on animals tagged 3 to 5 weeks before hunting begins, any effects of natural mortality on those rates operate just before and during the hunting season. In this connection the year 1952 seems aberrant in that juveniles apparently are less vulnerable to hunting than adults. We suppose that this could actually be the result of some unusually high losses in juveniles, possibly disease, or differences in hunting conditions, e.g., low temperatures might have decreased juvenile vulnerability to the gun.

Without independent satisfactory esti-

mates of natural mortality for each year of the study, we can do little to include this effect in the above relationship.

#### AGE RATIOS

The differences in recovery rates of tagged juvenile and adult rabbits, if they truly represent differences in vulnerability rates, necessarily result in kill-age ratios (juveniles per adult) somewhat higher than the true ratios in the populations. The degree of bias varies with fluctuations in the ratio of juvenile to adult vulnerability. In 7 years analyzed, kill-age ratios (Fig. 14) exceed trap ratios in varying degrees, but rather more so in some years than can be explained by the relatively small differences in recovery rates (see section on Recovery Rates). A logical alternate or supplemental explanation is that juveniles are not caught as readily as adults in some or all years. This may be examined in 2 ways from the available data: (1) by considering the proportions tagged in the adult and juvenile kill, and (2) by the relative frequency of capture of the two classes.

How representative trap-age ratios are, depends on the relative "trapability" of juveniles and adults, and, in our case, on

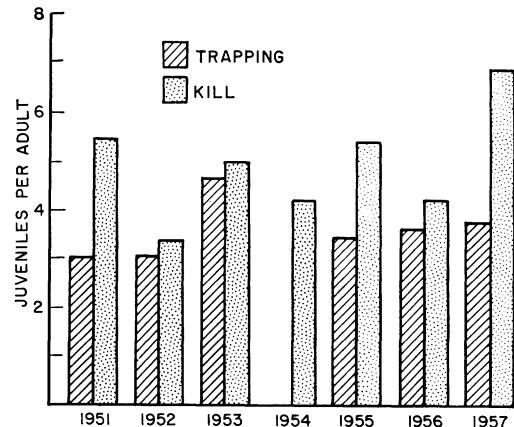


FIG. 14. Age ratios of rabbits, as indicated by the number of juveniles per adult, in samples of trapped and killed animals for 7 years, 1951–1957, inclusive, at the Rose Lake Wildlife Experiment Station. No data for trapping for 1954 are available because of the large number of errors in age determination.

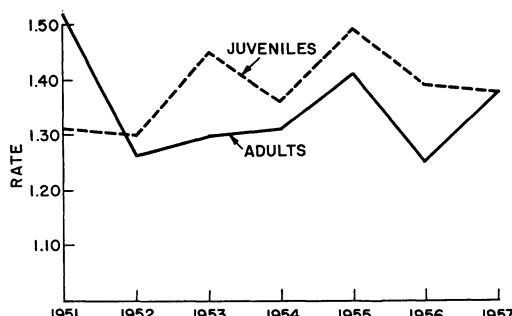


FIG. 15. Mean frequencies of capture by live traps of adult and juvenile rabbits during the 7-year study period, 1951–1957, inclusive, at the Rose Lake Wildlife Experiment Station.

whether or not age composition of rabbits in the trapped areas is the same as in areas not trapped. On this subject we have no data and simply leave it as one of the many uncertainties in this study.

In regard to "trapability" we have only the relative frequency of capture for the age and sex classes as possible measures. At Rose Lake, very small juveniles rarely enter traps, and there is considerable evidence that all rabbits do not have the same probability of capture in trapping (Geis, 1955, for example). We do not, however, know of any evidence to show conclusively that this latter point is not largely a matter of geography or "home range," i.e., accessibility to traps.

In any case, the data we have pertains only to rabbits we have tagged that enter traps one or more times. We further restrict our attention to animals trapped in September and October, on the premise that earlier, many rabbits would be too small to be caught. These fall trapping periods are short (usually 11 days), a fact of some importance here since the differences in "natural" mortality rates do affect frequency of recapture. The juvenile recapture rate is lower over any protracted time span simply because relatively more juveniles than adults die during the course of the trapping.

Over-all differences in trapability between adults and juveniles seem apparent (Fig. 15). Juveniles return to the traps

more frequently than adults in most years. This observation pertains, of course, only to animals caught one or more times and really indicates only whether or not an animal of one class once caught, will return more or less frequently on the average than will one of another class. Presumably, a higher proportion of the more wary adults may actually be tagged, but do not return to traps as readily after one capture. We will return to this subject in the section on frequency of capture.

Turning to the proportions of tagged rabbits in the kill, adults generally seem to be tagged at a higher rate (Table 9). We must not, however, overlook the effect here of an apparent differential in the relative rates at which tagged and untagged rabbits are shot. The decline in ratio of tagged to untagged rabbits in the bag suggests that tagged individuals are taken at a higher rate. Since juveniles usually are taken at a somewhat higher rate than adults, one would expect this reduction of proportion tagged in the kill to proceed more rapidly in juveniles than in adults. Even if both classes were initially tagged at the same rate, a lower proportion tagged would be expected in the bag of juveniles.

A further complicating factor in the analysis of sex and age ratios based on trapping or hunter-kill records is the weather. Peterle (1957) analyzed 6 of the years (1951–1956) involved here and found that in colder weather hunters kill a higher proportion of adult rabbits. Since the 1952

TABLE 9.—PROPORTIONS OF DIFFERENT AGE CLASSES OF TAGGED RABBITS IN HUNTERS' KILL FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Year	Proportion Tagged Adults in Adult Kill	Proportion Tagged Juveniles in Juvenile Kill
1951	0.220	0.134
1952	0.266	0.156
1953	0.225	0.221
1954	0.284	0.250
1955	0.316	0.243
1956	0.174	0.131
1957	0.333	0.206

hunting season was the coldest of the 6 years, this may in part be responsible for the high adult recovery rate that year. Low temperatures during the hunting season of 1952 may also have decreased the recovery of juvenile females. Temperatures at the time of trapping may also influence sex and age in the trapped sample. For instance, we caught fewer females when nightly minimum temperatures decreased during trapping. We recognized the difficulty in interpreting animal behavior using a single factor in a highly complex environment; hence the reader must consider these suggestions concerning the influence of temperature on sex and age classes as hypothetical. They do, however, offer some possible explanations for discrepancies in our data.

We will examine the above situation in some further detail by use of simple mathematical models. Before doing so, we note that in 1953, juveniles and adults were tagged at essentially the same rate (Table 9) and that age ratios in trapping and the kill are nearly the same (Fig. 14). Figure 15 also suggests a greater than usual disparity in frequency of recapture for 1953.

Perhaps the simple explanation that juveniles do not enter traps as readily as adults is sufficient here so that one might best use the age ratio in the bag as approximately representing that of the population ("approximately," since juveniles are somewhat more vulnerable than adults to hunting).

Further study of age ratios in the kill leads inevitably back to our major problem, the decline in proportion of tagged rabbits in the bag as the hunting season progresses. Any attempt to deal with this matter requires some sort of mathematical model, again probably oversimplifying the true situation, but perhaps roughly representing the state of affairs as we see it. We proceed as if 2 discrete populations of rabbits exist on the area, one tagged and hunted more intensively than the other. In essence, we employ a "deterministic" model with 2 sets

of fixed constants, where the real situation no doubt requires a "probabilistic" or statistical model with probabilities of capture (trapping, hunting, and perhaps predation) varying continuously throughout the area and rabbit population (and quite probably also in time). Further, we largely neglect the influence of natural mortality except to suggest possible effects.

The reader may be tempted, perhaps justifiably, at this point to suppose that the above restrictions leave us little hope of making any progress. At various stages of this analysis we have been of somewhat the same opinion, but cannot avoid the conclusion that there are too many pieces to this particular puzzle to be handled without some sort of symbolic or mathematical representation.

We have previously defined recovery rates as:

$$r_a = \frac{K_{ta}}{A_t} \quad r_j = \frac{K_{tj}}{J_t}.$$

Here:

$K_{ta}$  = hunting kill of tagged adults,

$K_{tj}$  = hunting kill of tagged juveniles,

$A_t$  = population of tagged adults, and

$J_t$  = population of tagged juveniles.

These representations may be combined as:

$$\frac{K_{tj}}{K_{ta}} = \frac{r_j J_t}{r_a A_t} = \text{age ratio in tagged kill},$$

and a natural temptation is to apply these rates ( $r_a$  and  $r_j$ ) to the total kill to get a "correct" age ratio estimate:

$$\text{"corrected" age ratio} = R' = \frac{r_a}{r_j} \frac{K_j}{K_a}.$$

Here  $K_j$  and  $K_a$  represent the total hunting kill of juveniles and adults, respectively. The "corrected" ratio then presumably takes into account the difference in hunting vulnerability rates of adults and juveniles and might thus be compared with trapping-age ratios for confirmation.

The pitfall in such a comparison is best illustrated by replacing the symbols  $r_a$  and  $r_j$  with their definitions:

$$R' = \frac{\frac{K_{ta}}{A_t} K_j}{\frac{K_{tj}}{J_t} K_a} = \frac{J_t}{A_t} \frac{K_{ta}}{K_a} \frac{K_j}{K_{tj}}.$$

One can then see that 2 right-hand quantities are the *proportions* tagged in the adult and juvenile kill, and if these quantities are equal, they cancel out (farthest right item is actually the reciprocal of the proportion of tagged juveniles in the juvenile kill), leaving the age ratio in tagging as our "corrected" age ratio.

Presumably, then, if the proportions tagged in the adult and juvenile kill are identical, we may argue that the 2 classes were tagged in proportion to their true numbers and simply adopt the tagging ratio as the true age ratio. In our case, however, there is the difficulty previously described that the proportions tagged in the kill decrease as the hunting season progresses, with a greater rate of decrease usually apparent for juveniles.

We are thus forced to consider this behavior and its implications in terms of a model for juveniles, assuming a similar situation for adults (but with a lower hunting vulnerability rate):

$$K_{jt} = J_t (1 - e^{-m_1 n_1}), \text{ and}$$

$$K_{ju} = J_u (1 - e^{-m_1 n_2}),$$

where the symbols are as before with the addition of the subscript *u* to represent untagged animals and:

- $m_1$  = vulnerability of juveniles (see section on recovery rates),
- $n_1$  = total hunting pressure on tagged population, and
- $n_2$  = total hunting pressure on untagged population.

Now the ratio of tagged to untagged juveniles in the kill is:

$$\frac{K_{jt}}{K_{ju}} = \frac{J_t}{J_u} \frac{(1 - e^{-m_1 n_1})}{(1 - e^{-m_1 n_2})}$$

and so long as  $n_1$  exceeds  $n_2$  the right-hand term exceeds unity and the ratio in the kill exceeds the true value, as will the propor-

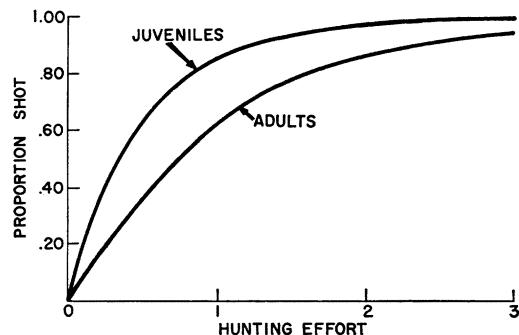


FIG. 16. Theoretical increase in the proportion of juvenile and adult rabbits killed with increased hunting effort at the Rose Lake Wildlife Experiment Station. The juveniles are considered twice as vulnerable to hunting as the adults.

tion tagged, making the Lincoln Index calculation an underestimate.

When  $n_1$  and  $n_2$  are fairly small (early in the hunting season), the first two terms of the series expansion of the exponential quantity may be used as an approximation,

i.e.,  $e^{-x} = 1 - x + \frac{x^2}{2!} - \frac{x^3}{3!} + \dots$  giving as an approximation:

$$\frac{K_{jt}}{K_{ju}} = \frac{J_t}{J_u} \frac{n_1}{n_2}$$

so that the upper limit, so to speak, of the kill ratio will be the true ratio multiplied by the ratio of the two hunting efforts. The lower limit, as  $n_1$  and  $n_2$  become very large,

will be the true value  $\frac{J_t}{J_u}$ , but this is reached

only when the populations are all or virtually all shot.

If we treat adults similarly (but with a lower vulnerability rate,  $m_2$ ) the proportions shot may be shown graphically (Fig. 16).

If we assume that  $n_1$  and  $n_2$  hold some constant ratio throughout the hunting season so that  $n_2 = bn_1$ , then the ratio of tagged to untagged animals in the kill becomes:

$$\frac{K_{jt}}{K_{uj}} = \frac{J_t}{J_u} \frac{1 - e^{-m_1 n_1}}{1 - e^{-bm_1 n_1}}.$$

This may be examined for maximum or minimum values by differentiating with respect to  $n_1$  and setting the resulting equation equal to zero. Using this process, and simplifying the resulting expression we get:

$$e^{bm_1n_1} - 1 = b(e^{m_1n_1} - 1),$$

and expanding both side as a series and factoring out  $b$ :

$$\begin{aligned} m_1n_1 + \frac{b(m_1n_1)^2}{2!} + \frac{b^2(m_1n_1)^3}{3!} + \dots &= \\ m_1n_1 + \frac{(m_1n_1)^2}{2!} + \frac{(m_1n_1)^3}{3!} + \dots, \end{aligned}$$

and since  $b$  is less than unity the left side is less than the right side and no maxima or minima exist (other than  $n_1 = 0$ ), and the kill ratio diminishes throughout the season between the limits previously enumerated.

We then have, from the model, essentially the same situation as observed. One further useful step is to consider behavior of the above equation if  $m_1$  is varied. To do this we use the last-given expression, differentiate with respect to  $m_1$ , and simplify to get

$$\begin{aligned} \frac{d}{dm_1} \left\{ \frac{J_t}{J_u} \frac{1 - e^{-m_1n_1}}{1 - e^{-bm_1n_1}} \right\} &= \\ \frac{J_t}{J_u} \left\{ \frac{n_1be^{-m_1n_1(b+1)}}{[1 - e^{-bm_1n_1}]^2} \right\} m_1n_1 + \frac{b(m_1n_1)^2}{2!} + \\ \frac{b^2(m_1n_1)^3}{3!} + \dots - m_1n_1 - \frac{(m_1n_1)^2}{2!} - \\ \frac{(m_1n_1)^3}{3!} - \dots, \end{aligned}$$

so that for some fixed value of  $n_1$ , increasing  $m_1$  will reduce the value of the ratio tagged to untagged in the kill, (as indicated by the negative sign of the above expression), and this then shows that the ratio should diminish more rapidly for juveniles than for adults, and for juveniles in years of greater juvenile vulnerability over years of lower juvenile vulnerability. Thus we see that, if juveniles and adults start out with the same proportion tagged, by the end of the hunting season the juvenile proportion tagged should ordinarily be less than that of adults.

Table 9 gives proportions tagged for juveniles and adults, and we see that this is true in all years. There are, however, considerable differences in degree of difference, making it appear that in some years juveniles may start out with an appreciably lower fraction tagged than adults.

A further application of the model shows the expected behavior of age ratios in the kill as the hunting season progresses. Using the same symbols as before, we may write the kill-age ratio as:

$$\frac{K_{tj}}{K_{ta}} = \frac{J_t}{A_t} \frac{(1 - e^{-m_1n_1})}{(1 - e^{-m_2n_1})}$$

Since this is essentially the same situation as discussed for tagged-to-untagged ratios, we may make the same kind of statements for expected behavior of age ratios:

(1) Early in the season ( $n_1$  small) the age ratio in the bag is approximately

$$\frac{m_1}{m_2} \frac{J_t}{A_t}.$$

(2) The lower limit ( $n_1$  very large) approaches  $\frac{J}{A}$  as the population is exhausted.

(3) The ratio declines with increasing effort (as the season progresses).

In view of the small sample sizes (Table 10) and small differences in recovery rates, we probably should not expect the theoretical expected decrease in age ratios to be very evident in actual data. Age ratios for tagged rabbits only (Fig. 17) and for all rabbits shot (Fig. 18) fluctuate considerably but show some evidence of a decline in several years. We plot the ratio in Figure 18 by week, while grouping data for several weeks in Figure 17, because of smaller samples of tagged rabbits.

All of the above fails to consider mortality from causes other than hunting ("natural" mortality). We proceed in this fashion simply to avoid the additional complication of terms representing such losses in the theoretical models. Actually, we believe natural mortality in the hunting season cannot be

TABLE 10.—NUMBERS OF HOURS HUNTED (GUN HOURS), AND NUMBERS OF TAGGED (T) AND UNTAGGED (U) JUVENILE AND ADULT RABBITS KILLED DURING EACH WEEK OF THE HUNTING SEASON, AND FOR THE HUNTING SEASON AS A WHOLE, FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Week of Hunt- ing Season	1951				1952–1953				1953–1954				1954–1955				1955–1956				1956–1957				1957–1958										
	Juvenile Kill		Adult Kill		Juvenile Kill		Adult Kill		Juvenile Kill		Adult Kill		Juvenile Kill		Adult Kill		Juvenile Kill		Adult Kill		Juvenile Kill		Adult Kill		Juvenile Kill		Adult Kill								
	Gun Hours	T U	Gun Hours	T U																															
1	2,502	10	29	2	8	2,576	4	19	4	7	2,351	11	29	1	4	3,070	10	21	4	7	3,159	15	27	2	5	3,382	7	18	3	8	3,158	22	62	2	7
2	1,186	7	32	5	3	930	1	18	1	3	1,213	5	19	1	4	1,279	5	24	0	4	1,123	6	23	0	6	1,864	3	19	0	3	1,707	16	33	5	6
3	667	3	27	0	2	875	2	15	0	3	730	8	18	2	2	1,182	17	29	5	5	920	11	45	3	5	1,194	2	13	0	1	883	14	28	2	3
4	357	7	46	1	4	119	3	6	0	1	163	7	10	0	1	238	5	19	0	2	256	5	16	3	2	106	1	7	1	1	202	4	31	1	0
5	246	5	28	0	4	124	2	8	2	3	116	1	7	1	1	190	5	7	0	1	325	3	10	2	1	258	2	13	2	0	337	6	30	3	4
6	439	2	27	2	4	372	6	26	3	5	409	8	23	0	2	326	2	19	2	3	403	15	30	2	5	551	4	40	0	7	425	4	35	1	0
7	317	3	27	1	9	368	6	30	1	4	229	7	11	1	3	431	9	27	4	2	405	7	32	3	4	483	11	80	0	12	537	4	23	2	4
8	294	4	24	0	6	373	4	13	1	5	282	2	20	1	4	579	10	56	3	10	368	7	17	1	2	413	5	22	3	6	401	12	36	3	4
9	316	0	15	1	5	152	1	15	1	1	498	22	57	4	13	393	4	7	1	7	394	8	23	3	5	243	5	12	0	3	231	9	10	0	4
10	110	1	8	1	0	187	2	5	0	0	672	2	46	2	4	284	5	10	0	4	458	6	20	0	4	323	0	7	0	1	313	3	17	1	4
11	163	1	16	0	1	498	3	20	4	6	402	5	20	1	6	280	1	10	0	2	584	7	28	1	6	445	1	34	2	2	516	4	19	0	2
12	205	1	10	0	4	340	2	14	1	2	151	1	5	0	0	223	2	8	0	4	243	1	21	1	4	387	2	27	0	4	66	1	7	0	0
13	66	0	2	0	0	242	2	12	1	7	208	8	8	2	1	256	2	4	0	0	216	2	6	0	3	172	0	7	0	2	82	1	6	3	2
14	183	0	2	0	0	94	1	3	0	0	212	3	11	1	3	376	3	19	3	1	273	3	20	0	4	322	3	25	1	4	161	1	4	0	3
15	150	1	6	0	5	159	0	3	0	2	136	2	8	1	7	204	2	6	2	4	245	2	12	0	2	87	0	5	1	0	84	0	4	2	1
16																																			
17																																			
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	6,597	43	279	13	46	7,178	36	195	17	47	7,900	83	292	16	55	8,959	87	261	23	58	9,454	99	308	25	54	10,239	49	324	12	57	10,071	106	409	27	54

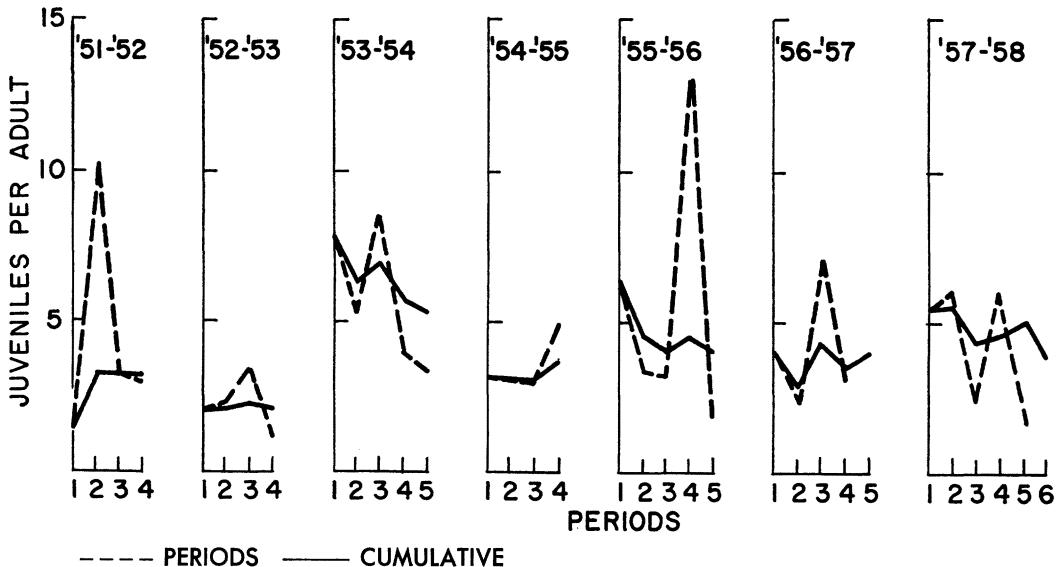


FIG. 17. Age ratios of tagged rabbits, as indicated by the number of juveniles per adult, during each of 7 seasons at the Rose Lake Wildlife Experiment Station.

neglected in any analysis attempting to estimate population parameters (i.e., the constants in our theoretical models), and we suggest its possible effect later in a section on catch-effort relationships. Here we suggest that the general behavior of the relationships used above remains essentially similar, but that natural mortality may change the various limits.

To exhibit these effects we must realize that natural and hunting mortality "compete" with each other, so that following Neyman (1950) or Ricker (1958) we have, for example

$$K_{jt} = J_t \frac{m_1 n_1}{m_1 n_1 + rt} \left[ 1 - e^{-m_1 n_1 - rt} \right],$$

where  $r$  = rate of natural mortality per unit of time and  $t$  = time during which  $n_1$  (hunting effort) is exerted; but  $t$  begins at trapping rather than at the beginning of the hunting season.

The right side (exponential part) of this equation now represents the total proportion of the initial population, killed while the

factor  $\frac{m_1 n_1}{m_1 n_1 + rt}$  represents the fraction of

this total which falls to the hunter. We should also consider, no doubt, crippling loss as a third factor. For the present we will consider such losses as part of the natural mortality, although properly they probably are more nearly proportional to hunting mortality.

If we now examine the tagged-to-untagged ratio:

$$\frac{K_{jt}}{K_{ju}} = \frac{J_t}{J_j} \left\{ \frac{m_1 n_1}{m_1 n_1 + rt} \right\} \left\{ \frac{m_1 n_2 + rt}{m_1 n_2} \right\} \left\{ \frac{1 - e^{-m_1 n_1 - rt}}{1 - e^{-m_1 n_2 - rt}} \right\}$$

the approximation to the upper limit (early in the season) remains unchanged at

$J_t \left( \frac{n_1}{n_2} \right)$ . We cannot evaluate the lower

limit (as the population is exhausted) as before, when, so to speak, we treated the situation as though the two populations stood around waiting to be shot. In this case we must consider that natural mortality takes an increasingly larger share as the hunting season continues; or, mathematically, that as  $n_1$  and  $n_2$  increase indefi-

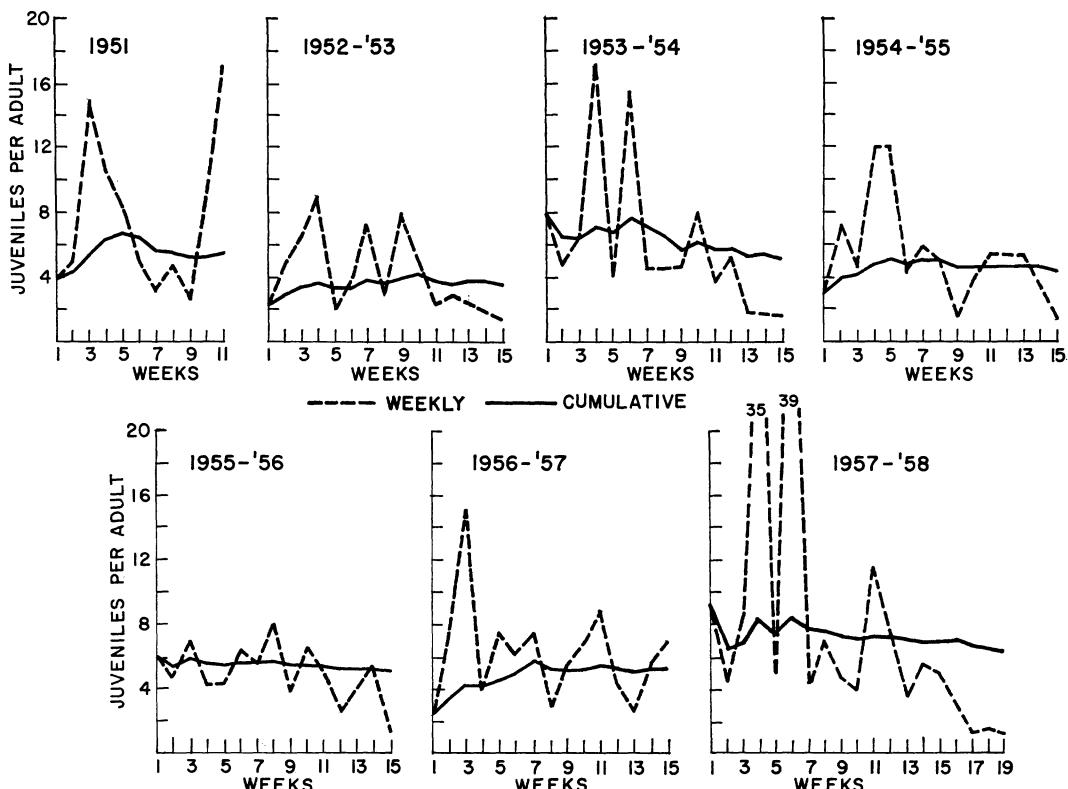


FIG. 18. Age ratios of all rabbits killed, as indicated by the number of juveniles per adult, on a weekly basis, for each of 7 hunting seasons at the Rose Lake Wildlife Experiment Station.

nately,  $t$  also increases. If we suppose  $n$  (and thus necessarily  $n_1$ ) and  $t$  become large enough so that the right side of the equation (exponential part) becomes approximately unity, then the ratio in the kill will be approximately:

$$\frac{J_t}{J_u} \left\{ \frac{m_1 n_1}{m_1 n_1 + rt} \right\} \left\{ \frac{m_1 n_2 + rt}{m_1 n_2} \right\} = \\ \frac{J_t}{J_u} \frac{n_1}{n_2} \left[ 1 - \frac{m_1 (n_1 - n_2)}{m_1 n_1 + rt} \right],$$

reflecting the fact that higher rate of hunting effort applied to the tagged population puts a proportionately larger share of the tagged animals in the bag, so that the tagged-to-untagged ratio does not approach the true value in the limit.

As an alternative (perhaps more satisfactory from a mathematical standpoint), we may consider  $n_1$  and  $n_2$  as functions of

time (i.e., constant rates of hunting) and suppose  $n_1 = b n_2$  and  $n_2 = ct$ , with  $b$  greater than unity; then:

$$\frac{K_{jt}}{K_{ju}} = \frac{J_t}{J_u} \left\{ \frac{m_1 bct}{m_1 bct + rt} \right\} \left\{ \frac{m_1 ct + rt}{m_1 ct} \right\} \\ \left\{ \frac{1 - e^{-m_1 bct - rt}}{1 - e^{-m_1 ct - rt}} \right\},$$

so that the limit as  $t$  becomes very large is

$$\frac{J_t}{J_u} \left\{ \frac{m_1 bc}{m_1 bc + r} \right\} \left\{ \frac{m_1 c + r}{m_1 c} \right\} = \\ \frac{J_t}{J_u} \left\{ \frac{1 + \frac{r}{m_1 c}}{1 + \frac{r}{m_1 bc}} \right\},$$

again showing that the ultimate ratio will exceed the true value for the population.

This is perhaps an unnecessarily complicated way of saying that a short, intensive hunting season puts more rabbits in the bag than a longer season with the same amount of hunting effort, because of fewer losses from natural mortality.

Turning to age ratios, the same general conditions apply:

$$\frac{K_{tj}}{K_{ta}} = \frac{J_t}{J_a} \left\{ \frac{m_1 n_1}{m_1 n_1 + r_1 t} \right\} \left\{ \frac{m_2 n_1 + r_2 t}{m_2 n_1} \right\} \\ \left\{ \frac{1 - e^{-m_1 n_1 - r_1 t}}{1 - e^{-m_2 n_1 - r_2 t}} \right\},$$

and the upper (early-season) approximate limit is again  $\frac{m_1}{m_2} \frac{J_t}{A_t}$ , but the lower limit

(late-season) will depend on the relative magnitudes of  $m_1$  and  $m_2$ , and  $r_1$  and  $r_2$ . If we assume relatively constant relationships so that  $m_1 = am_2$  (with  $a$  greater than unity),  $n_1 = bt$ , and  $r_1 = cr_2$ , then:

$$\frac{K_{jt}}{K_{at}} = \frac{J_t}{J_a} \left\{ \frac{am_2 bt}{am_2 bt + cr_2 t} \right\} \left\{ \frac{m_2 bt + r_2 t}{m_2 bt} \right\} \\ \left\{ \frac{1 - e^{-am_2 bt - cr_2 t}}{1 - e^{m_2 bt - r_2 t}} \right\},$$

and as  $t$  becomes very large this reduces to:

$$\frac{K_{jt}}{K_{at}} = \frac{J_t}{A_t} \left\{ \frac{1 + \frac{r_2}{m_2 b}}{1 + \frac{cr_2}{am_2 b}} \right\},$$

and the deviation of the ultimate age ratio from the population value will depend on

the ratio  $\frac{c}{a}$  and thus on the relative magni-

tudes of natural and hunting mortality rates in juveniles and adults. If, as we are inclined to suppose, the two sets of values

have about the same ratios, i.e.,  $\frac{r_1}{r_2} = \frac{m_1}{m_2}$ ,

then the lower limit will tend toward the true value for the population.

We have thus far largely dealt with

models representing tagged-to-untagged or juvenile-to-adult ratios on a cumulative basis, i.e., the ratio in the entire kill up to some particular time. Models based on weekly ratios in the kill, while much more variable (Fig. 18), seem easier to handle mathematically.

On the basis of the above notation, the population of tagged juveniles at any point in the hunting season is:

$$J_t e^{-m_1 n_1 - rt},$$

and the kill in some short interval will be:

$$K_{ts} = \left\{ \frac{m_1 n_{1s}}{m_1 n_{1s} + rt_s} \right\} \left\{ 1 - e^{-m_1 n_{1s} - rt_s} \right\} \\ J_t e^{-m_1 n_1 - rt},$$

where the subscript  $s$  denotes measurement over the short interval rather than cumulatively as before. If the time interval  $t_s$  is short, we may reduce this expression to:

$$K_{ts} = m_1 n_{1s} J_t e^{-m_1 n_1 - rt},$$

equivalent to DeLury's equation 2.9 (1951: 296). The ratio of tagged to untagged animals will be:

$$\frac{K_{ts}}{K_{us}} = \frac{m_1 n_{1s}}{m_1 n_{2s}} \frac{J_t}{J_u} e^{-m_1 n_1 + m_1 n_2}.$$

If we now suppose that division of hunting effort between the tagged and untagged populations remains relatively constant so that:

$$\frac{n_2}{n_1} = \frac{n_{2s}}{n_{1s}} = b \text{ and thus}$$

$$n_1 - n_2 = \frac{1 - b}{1 + b} \{ n_1 + n_2 \},$$

then

$$\frac{K_{ts}}{K_{us}} = \frac{1}{b} \frac{J_t}{J_u} e^{-m_1} \left[ \frac{1 - b}{1 + b} \right] [n_1 + n_2].$$

Taking natural logarithms of this expression, we have a relation of the form:

$$Y = A - BX.$$

We may treat this by standard (least squares) linear regression methods in terms of the available population data, ratio of tagged to untagged animals, and cumula-

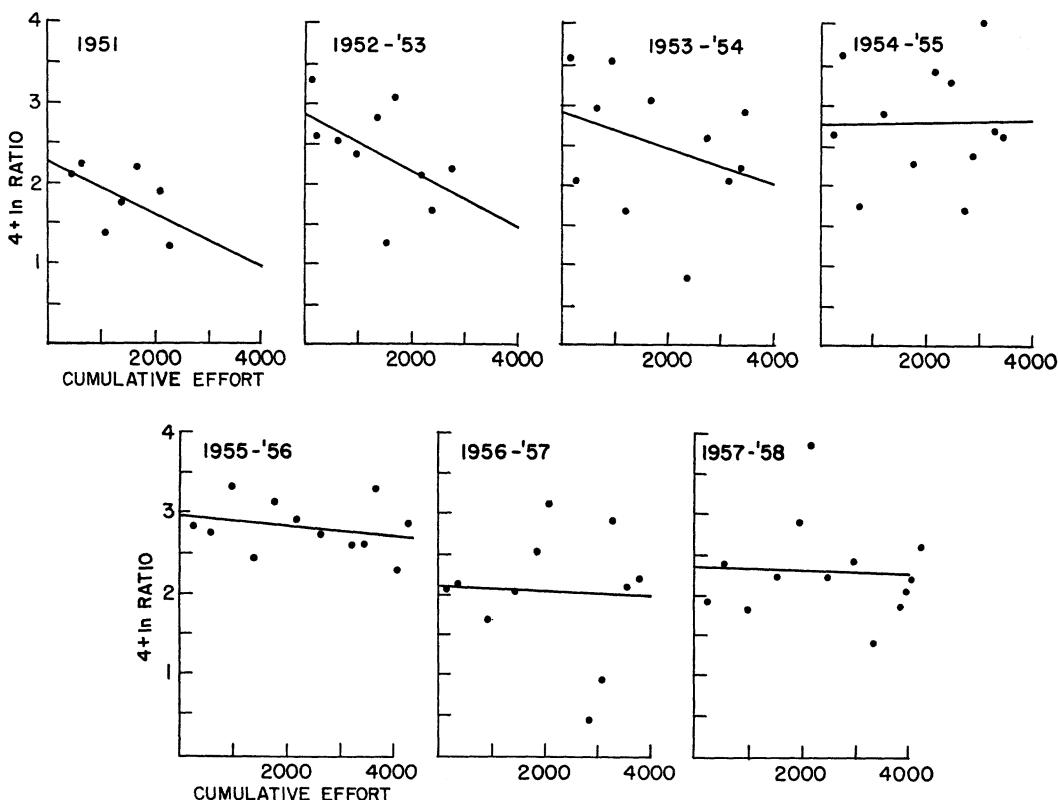


FIG. 19. Ratios of tagged to untagged juvenile rabbits on the basis of hunting effort for each of 7 hunting seasons at the Rose Lake Wildlife Experiment Station.

tive total hunting effort. Apart from the previously mentioned difficulty that our model treats the tagged and untagged populations as 2 discrete groups (they are actually intergraded or intermingled) the above relationship enables us to exhibit the tagged-to-untagged ratio without having to estimate natural mortality (beyond the assumption that the rate is the same for both populations). We do not, however, know how year-to-year variations in constants in regression lines fitted to the data are related to changes in vulnerability ( $m_1$ ) or division of hunting effort ( $b$ ). We have already shown some evidence that vulnerability of juveniles varies from year to year.

Figure 19 shows the regression lines along with weekly values of  $4 + \ln \frac{K_{ts}}{K_{us}}$  plotted

at cumulative hunting effort (cumulated up to the period in question). We use the

logarithms of  $4 + \ln \frac{K_{ts}}{K_{us}}$  simply to avoid

handling negative terms and note that they will not affect the slope. However, we must

take this into account in estimating  $\frac{1}{b} \frac{J_t}{J_u}$  from the regression constant.

Comparing the individual regression lines in an analysis of covariance (Table 11) gives some notion as to the existence of differences between years. We doubt that the assumptions basic to covariance analysis hold strictly true here, but the method provides at least a gesture in the direction of taking into account the variability about the regression lines. The average regression

TABLE 11.—ANALYSIS OF COVARIANCE OF RATIOS OF TAGGED TO UNTAGGED JUVENILE RABBITS FOR THE 7-YEAR PERIOD, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Source	Sum of Squares	Degrees of Freedom	Mean Square
Regression slopes			
within cells	1.1955	6	0.199
Linearity of cell means	6.8976	5	1.380 <sup>1</sup>
Remainder	1.7883	2	0.894
Deviations	26.5054	62	0.428
Total	36.386	75	

<sup>1</sup> Significant at 1% level.

slope is significantly different from zero and the  $y$ -intercepts differ, but do not show significant differences between years, indicating differences in proportion tagged and/or  $b$ , the ratio of hunting efforts. The form of analysis is that of Mood (1950) where cell frequencies differ.

The failure of the analysis to show differences between years cannot, of course, be taken as evidence that differences do not exist, but does suggest at least that the variation is great enough to mask such differences (if they really do exist) in the test. If we plot the regression coefficients (Table 12) against total hunting effort (excluding the first three weeks of hunting; the "pheasant season") we find (Fig. 20) that the lower values are associated with higher hunting effort. This may indicate a shift in hunting effort, so that as the hunting season progresses, hunters who normally concentrate on the trapline areas move out into the untrapped areas, equalizing the distribution of hunting effort over the area. It might further mean that the Lincoln Index estimates are more nearly correct (less biased) in years of higher hunting effort. We give further consideration to this matter in taking up catch-effort relationships in the next section of this report.

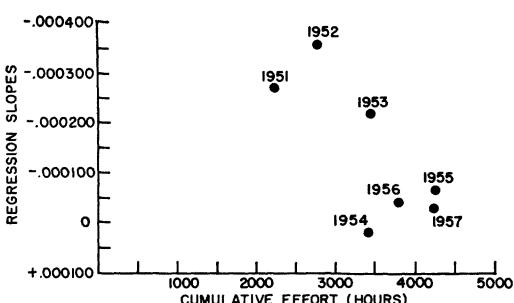


FIG. 20. Comparison of regression slopes of ratios of tagged to untagged rabbits on the basis of cumulative hunting effort. These data are listed in Table 12.

RELATIONSHIPS BETWEEN HUNTING EFFORT AND KILL

The use of relationships between hunting effort and kill, as described by DeLury (1947, 1951, 1954), offers some further insight into the behavior of Rose Lake rabbit populations. We see little immediate prospect of getting accurate estimates of the rabbit population from such data, but we submit that the study of hunting success is very important in its own right since it represents the culmination of our management efforts. Furthermore, relationships between hunting effort and kill may yield further useful information on variation in vulnerability of juveniles.

Inherent difficulties are such that this study can perhaps do no more than serve as a basis for further investigations. One of the major problems in our situation is that tagged and untagged rabbits are hunted at different levels of intensity, or, more explicitly, that hunting pressure is not distributed randomly, but concentrated on cover edges. This is not serious if hunting pressure is applied in proportion to the population, but this is evidently not so in

TABLE 12.—COMPARISON OF CONSTANTS FROM REGRESSION OF RATIOS OF TAGGED TO UNTAGGED RABBITS (SLOPE) WITH CUMULATIVE HUNTING EFFORT ( $y$ -INTERCEPT)

Year	Slope	$y$ -intercept
1951	-0.000272	2.215
1952	-0.000356	2.901
1953	-0.000219	2.904
1954	+0.000022	2.738
1955	-0.000061	2.965
1956	-0.000044	2.108
1957	-0.000032	2.395

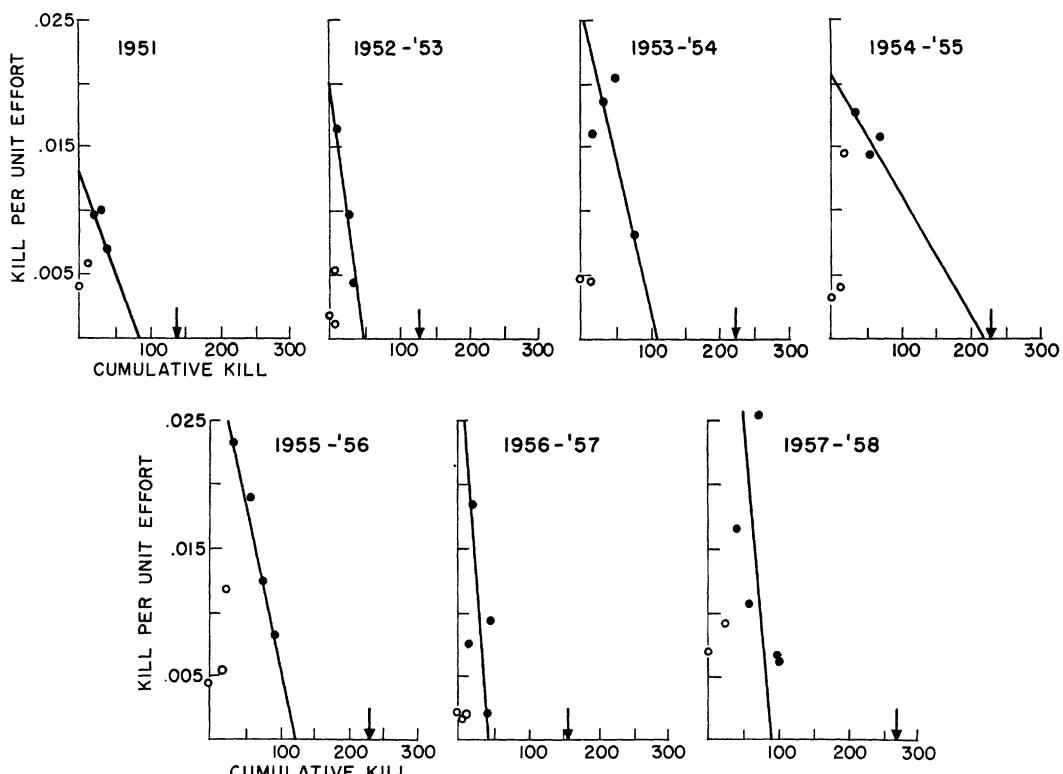


FIG. 21. Kill per unit effort compared with cumulative kill for tagged juvenile rabbits for each of 7 hunting seasons at the Rose Lake Wildlife Experiment Station. The arrows indicate the estimated sizes of the tagged populations mentioned earlier. The open circles are for data gathered during the pheasant-hunting season; the solid dots are for data gathered during the rabbit-hunting season.

our study as evidenced by the decline in proportion of tagged rabbits in the kill. We suspect that this is likely to be the general rule, rather than an exception, and note that it will not affect tagging data if the tags are put out essentially at random. At Rose Lake, one segment of the population has been tagged intensively and that segment has also evidently borne the brunt of hunting effort.

Further difficulties include natural mortality, crippling loss, and differences in vulnerability to hunting, which we discuss in some detail, but, by way of introduction, note that their principal effect is likely to result in an underestimation of the size of the population. For anyone dismissing these methods as of little value, we note, as does DeLury (1954), that no one method is

likely to provide adequate information about an animal population. Only painstaking consideration of all possibilities is likely to succeed since, as DeLury maintains, no method is known which will take a truly random sample of an animal population.

Our principal efforts with catch-effort analyses have been concerned with only the tagged juvenile population. This is because (a) quite probably adult and juvenile rabbits differ in vulnerability to hunting, (b) our adult rabbit sample is too small, and (c) we need to begin with a known population if we are to learn much about these difficulties.

Beginning with DeLury's equation (1947: 146):

TABLE 13.—NUMBERS OF HOURS HUNTED (GUN HOURS) FOR EACH OF SEVERAL PERIODS AGGREGATING ABOUT 1,000 HOURS, TOGETHER WITH THE NUMBERS OF TAGGED JUVENILE RABBITS KILLED DURING EACH PERIOD FOR EACH OF 7 HUNTING SEASONS AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Weeks	Gun Hours	Tagged Kill	Kill per Gun Hour	Cumulative Kill	Weeks	Gun Hours	Tagged Kill	Kill per Gun Hour	Cumulative Kill
1951									
1	2,502	10	0.0040		1	3,159	15	0.0047	
2	1,186	7	0.0059	10	2	1,123	6	0.0053	15
3-4	1,024	10	0.0098	17	3	920	11	0.0120	21
5-7	1,002	10	0.0100	27	4-6	984	23	0.0234	32
8-11	883	6	0.0068	37	7-9	1,167	22	0.0189	55
				43	10-11	1,042	13	0.0125	77
1952-1953									
1	2,576	4	0.0016		12-15	1,059	9	0.0085	
2	930	1	0.0011	4					99
3-4	994	5	0.0053	5	1956-1957				
5-7	864	14	0.0162	10	1	3,382	7	0.0021	
8-10	712	7	0.0098	24	2	1,864	3	0.0016	7
11-15	1,102	5	0.0045	31	3	1,194	2	0.0017	10
				36	4-6	915	7	0.0077	12
1953-1954									
1	2,351	11	0.0047		7-9	1,139	21	0.0184	
2	1,213	5	0.0041	11	10-12	1,011	2	0.0020	
3-5	1,009	16	0.0159	16	13-15	734	7	0.0095	40
6-8	920	17	0.0185	32					49
9-10	1,170	24	0.0205	49	1957-1958				
11-15	1,237	10	0.0081	73	1	3,158	22	0.0070	
				83	2	1,707	16	0.0094	
1954-1955									
1	3,070	10	0.0033		3-4	1,085	18	0.0166	
2	1,279	5	0.0039	10	5-7	1,299	14	0.0108	
3	1,182	17	0.0144	15	8-10	945	24	0.0254	
4-7	1,185	21	0.0177	32	11-12	903	6	0.0066	
8-9	972	14	0.0144	53	13-19	974	6	0.0062	94
10-15	1,271	20	0.0157	67					100
				87					106

$$C(t) = kN(0) - kK(t),$$

where:

$C(t)$  = kill per unit of effort,

$N(0)$  = initial population ( $J$  or  $A$  used elsewhere in this report),

$K(t)$  = cumulative kill, and

$k$  = proportion of population taken per unit of effort ( $m_1$ ,  $m_2$  of this report),

we find (Fig. 21) that regression estimates generally fall far short of the tagged population (lines are fitted by inspection in these graphs). The points shown here, because of the small samples in any week, represent grouping of weeks of the season aggregating about 1,000 hours of hunting (Table 13). We omit the first 2 or 3 periods (in

pheasant-hunting season with low rabbit-hunting success) from the regression computations.

Geis (1956) indicated that crippling losses may be important, amounting to as much as 20 per cent of the total recovered kill. To us it seems reasonable that such losses are fairly constant. We thus examine DeLury's equation in this light, adding crippling loss as a constant fraction ( $d$ ) of the retrieved kill,  $K(t)$ :

$$C(t) = k[N(0) - K(t) - dK(t)],$$

where  $dK(t)$  is the total crippling loss up to the time  $t$ , and is consequently also subtracted from the initial population,  $N(0)$ .

This may be rewritten as:

$$C(t) = kN(0) - k(1 + d)K(t),$$

and, if we then use standard (least-squares) regression methods, the “slope” will be an overestimate,  $k(1 + d)$ , of the proportion of the population taken (here, retrieved) by hunters, and thus we underestimate the initial population size. This result is given by DeLury (1951:296–297) to show that the relation between  $C(t)$  and  $K(t)$  may be linear in the presence of sizable unmeasured losses from the population.

The relative magnitude of underestimates due to crippling loss we may consider by examining the population estimate (regression intercept divided by the apparent slope):

$$\frac{kN(0)}{k(1 + d)} = \frac{N(0)}{1 + d}.$$

If  $d$  ranges from 0.1 to 0.2, as suggested above, we might expect the estimates to lie within 0.83 to 0.91 of the true population; errors meriting concern, but much smaller than those in Figure 21.

Turning our attention to natural mortality, we use the rate estimated in the section on mortality for juveniles in the months just prior to hunting. The rate obtained there amounts to a monthly rate of 0.0890 (“instantaneous” rate), or 0.0222 weekly.

To combine hunting and natural mortality, we again use the equations given by Neyman (1950) or Ricker (1958) and used earlier in this report:

$$K_{jt} = J_t \frac{m_1 n_1}{m_1 n_1 + rt} \left[ 1 - e^{-m_1 n_1 - rt} \right].$$

Here we apply this equation successively to the periods (weeks grouped to include about 1,000 hours of effort) used in Figure 21 and Table 13, and compute the population as of the beginning of each period; i.e.,  $J_t$  is now the number of rabbits alive at the beginning of a period,  $n_1$  is hunting effort during the period, and  $t$  is the number of weeks in the period. Neglecting crippling losses, and beginning with the trapped population, we can supply all values in the above equation except  $m_1$ , which we estimate (by iterative or “trial and error” methods) for each period. These computations are set forth in Table 14. Here we are using total

hunting effort for  $n_1$  since we do not at present have any way of dividing the total between tagged and untagged populations.

We may review these computations in several ways. One is to graph kill per unit effort against cumulative kill (Fig. 22), this time using the total kill (hunting and natural losses). The similarity between this relationship and the function used before [ $C(t) = kN(0) - kK(t)$ ], may be seen by approximating the exponential part of the equation next above by using the first two terms of the expansion, that is,  $1 - e^{-x} \doteq 1 - (1 - x) = x$ . The equation then reduces to  $K_{jt} \doteq J_t m_1 n_1$  and, since the variable terms here represent kill, population, and effort for the period only (not cumulated up to the period as in our first use of DeLury’s equation), is equivalent to:

$$C(t) = \frac{K_{jt}}{n_1} \doteq m_1 \left\{ N(0) - L(t) \right\},$$

where  $L(t)$  represents cumulative losses up to the  $t^{\text{th}}$  period from both hunting and natural mortality. Error from the approximation is greater when the exponent is large; in our study, the exponent ( $-m_1 n_1 - rt$ ) averages about 0.20 so the approximation  $C(t) \doteq m_1 J_t$  is comparable to  $C(t) = m_1 J_t$  (0.91). One might reduce this bias by using shorter periods, but then the smaller number of rabbits involved makes “sampling” error even more of a nuisance.

As it stands, this representation (Fig. 22) still does not accurately estimate the initial population since the true initial population value is the basis of the horizontal scale,  $L(t)$ . As we see it now, these graphs suggest, from behavior of the plotted points, that one may well use the “DeLury” methods in studying rabbit populations if he can satisfactorily dispose of several problems, chiefly natural mortality and sample size.

Increasing the estimated natural mortality rate closes the gap between actual initial population and the ordinal intercept of the regression line (Fig. 22) but we need also to consider the bias mentioned above in any attempt to estimate natural mortality.

TABLE 14.—ESTIMATES OF VULNERABILITY OF TAGGED JUVENILE RABBITS, TOGETHER WITH DATA ON SIZES OF POPULATIONS, NUMBERS AND PROPORTIONS KILLED, AND MORTALITY AND SURVIVAL RATES, FOR EACH OF 7 HUNTING SEASONS AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Year	Period	Length in Weeks	Initial Population	Killed Animals Recovered	Proportion Killed	$r_t$ Natural Mortality Rate	$m_{1n_1}$ Hunting Mortality Rate	Survival Rate	Gun Hours	Estimate of Vulnerability ( $m_1$ )	Average Value of $m_1$
1951	Pre-season	4	136	0	0	0.089	0	0.915	—		
	1-2	2	124	17	0.137	0.044	0.151	0.823	—		
	3-4	2	102	10	0.098	0.044	0.106	0.861	1,024	0.000104	0.000110
	5-7	3	88	10	0.114	0.067	0.125	0.823	1,002	0.000122	
	8-11	4	72	6	0.083	0.089	0.091	0.835	883	0.000103	
1952-53	Pre-season	5	126	0	0	0.111	0	0.895	—		
	1-4	4	113	10	0.088	0.089	0.096	0.831	—		
	5-7	3	94	14	0.149	0.067	0.167	0.791	864	0.000193	0.000139
	8-10	3	74	7	0.094	0.067	0.102	0.844	712	0.000143	
	11-15	5	62	5	0.081	0.111	0.090	0.818	1,102	0.000082	
1953-54	Pre-season	5	219	0	0	0.111	0	0.895	—		
	1-2	2	196	16	0.082	0.044	0.087	0.877	—		
	3-5	3	172	16	0.093	0.067	0.101	0.845	1,009	0.000100	0.000134
	6-8	3	145	17	0.117	0.067	0.128	0.822	920	0.000139	
	9-10	2	119	24	0.202	0.044	0.231	0.760	1,170	0.000197	
	11-15	5	90	10	0.111	0.111	0.124	0.790	1,237	0.000100	
1954-55	Pre-season	4	230	0	0	0.089	0	0.915	—		
	1-3	3	210	32	0.152	0.067	0.171	0.856	—		
	4-7	4	180	21	0.117	0.089	0.131	0.803	1,185	0.000110	0.000122
	8-9	2	144	14	0.097	0.044	0.105	0.862	972	0.000108	
	10-15	6	124	20	0.161	0.133	0.189	0.725	1,271	0.000149	
1955-56	Pre-season	4	227	0	0	0.089	0	0.915	—		
	1-3	3	208	32	0.154	0.067	0.174	0.786	—		
	4-6	3	163	23	0.141	0.067	0.157	0.799	984	0.000160	0.000143
	7-9	3	130	22	0.169	0.067	0.192	0.772	1,167	0.000164	
	10-11	2	100	13	0.130	0.044	0.142	0.828	1,042	0.000136	
	12-15	4	83	9	0.108	0.089	0.120	0.812	1,059	0.000113	
1956-57	Pre-season	4	154	0	0	0.089	0	0.915	—		
	1-3	3	141	12	0.085	0.067	0.092	0.853	—		
	4-6	3	120	7	0.058	0.067	0.062	0.879	915	0.000068	0.000112
	7-9	3	105	21	0.200	0.067	0.231	0.742	1,129	0.000205	
	10-12	3	78	2	0.026	0.067	0.027	0.910	1,011	0.000027	
	13-15	3	71	7	0.098	0.067	0.107	0.840	734	0.000146	
1957-58	Pre-season	5	267	0	0	0.111	0	0.895	—		
	1-2	2	239	38	0.159	0.044	0.177	0.801	—		
	3-4	2	191	18	0.094	0.044	0.101	0.865	1,085	0.000093	0.000100
	5-7	3	165	14	0.085	0.067	0.092	0.853	1,299	0.000071	
	8-10	3	141	24	0.170	0.067	0.193	0.771	945	0.000204	
	11-12	2	109	6	0.055	0.044	0.058	0.903	903	0.000064	
	13-19	7	98	6	0.061	0.155	0.068	0.800	974	0.000070	

DeLury (1951) suggested that an equation of the form

$$\ln C(t) = \ln [m_1 N(0)] - m_1 n_1 - rt,$$

where the symbols are those previously identified (but are here cumulative) might be fitted by multiple regression methods, thus estimating the several parameters (population size, proportion taken per unit

of effort, and rate of natural mortality) simultaneously.

We have not obtained satisfactory results in applying this equation to our data on tagged juveniles, and we suspect that a major reason may be in the small numbers we have to deal with. One further possibility, not as yet investigated, is to "fit" the multiple regression equation subject to the

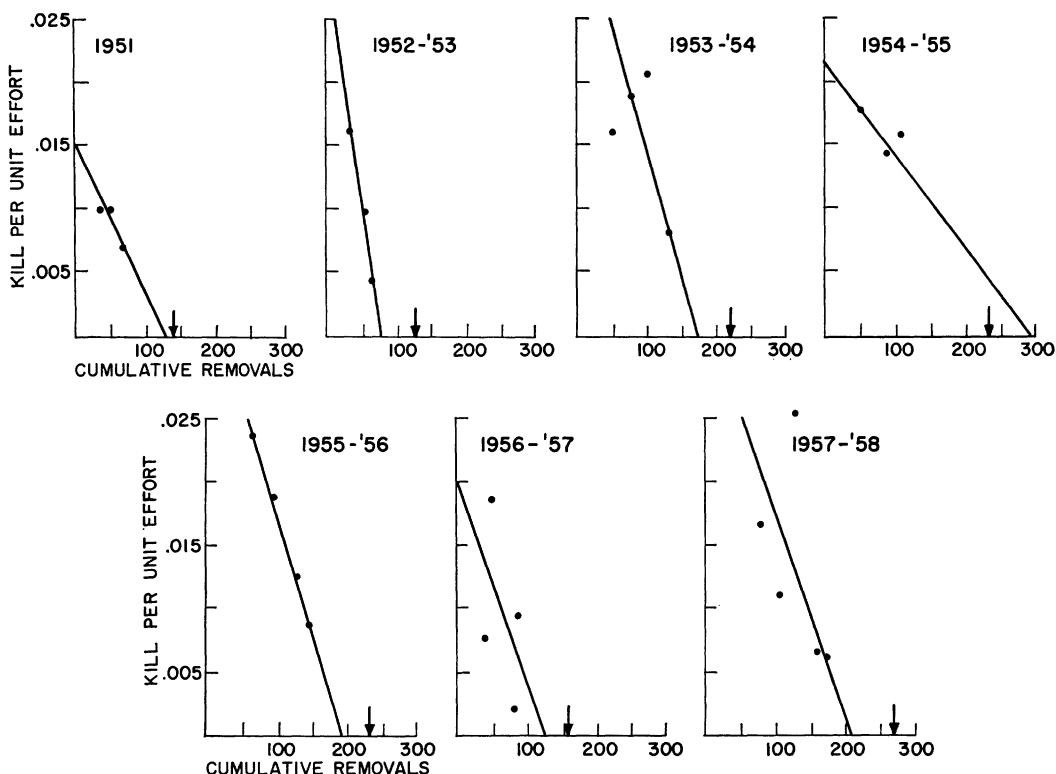


FIG. 22. Kill per unit effort and cumulative total kill of tagged juvenile rabbits for each of 7 hunting seasons at the Rose Lake Wildlife Experiment Station. The curves were fitted by inspection.

restriction that the regression constant ("y-intercept") equal  $\ln m_1 N(0)$ ; i.e., that the number of animals tagged be introduced as the population value so that only  $m_1$  and  $r$  are estimated (see, for example, Deming, 1943).

For further appraisal of the above calculations (Table 14), we turn to a study of the estimated values of  $m_1$  (Fig. 23). Here we see that the estimates are rather erratic, but do not show the consistent trends one would expect if the value for natural mortality is much too high or too low, or if extensive movement of tagged rabbits off the Rose Lake Area should occur. So far as we can see, however, these two factors are indistinguishable since both simply remove rabbits from observation.

The declining vulnerability in 1952 suggests that natural mortality may have been

higher in that year than the rate used here, a situation which would explain the low recovery of juveniles in that year.

In view of the extreme variation in estimated values of  $m_1$  within years, especially 1956 and 1957, we can scarcely maintain that these estimates are very precise. Probably some measure of the expected magnitude of chance fluctuation would help a great deal. We have not attempted this since the mathematics of such a measure are complicated and would be greatly compounded if we attempted to include the several biologically reasonable sources of variation previously described.

We have not yet mentioned weather as a factor possibly bearing on estimates of vulnerability, but we suppose most rabbit hunters would certainly propose that hunting success varies at least with extremes in

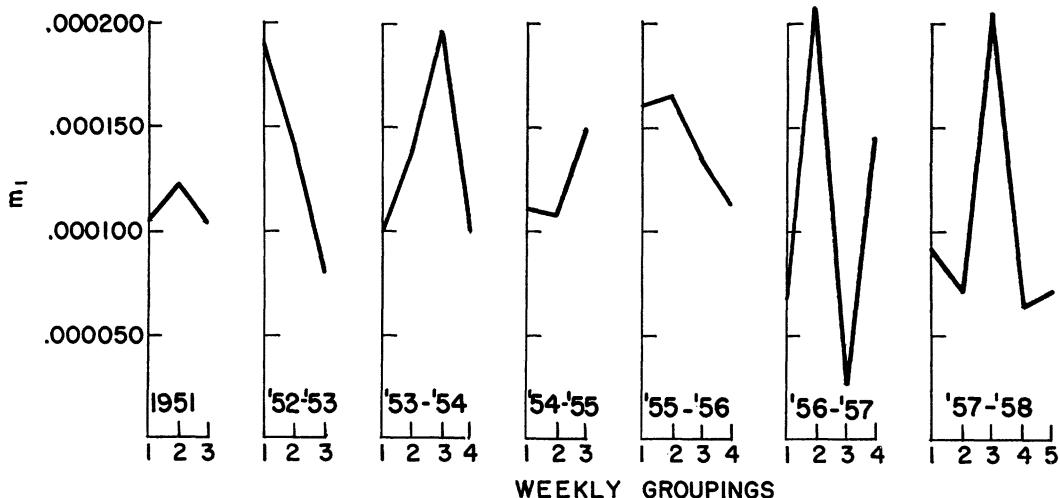


FIG. 23. Estimates of the proportion ( $m_1$ ) of the population of rabbits taken per unit effort during each of 7 hunting seasons at the Rose Lake Wildlife Experiment Station.

weather. A rather careful examination of records of temperature and snow depth yielded nothing to support this notion although there is little doubt weather conditions affect hunting effort. Kill per unit effort and our estimates of juvenile vulnerability do not seem to fluctuate with any grossly evident climatological factor. We do not, however, presume to assert that such an effect is not present. In fact we have indicated in a previous section (Age Ratios) that such a relationship may be evident. The collective feeling of many rabbit hunters and the rather consistent increase in over-all kill per unit effort (all rabbits) in the weeks immediately following the pheasant season indicate that some factor or factors, probably associated with weather, influence hunting success.

In rabbit seasons longer than 3 months, juvenile vulnerability to hunting may well decrease late in the season; especially if, as the data suggest, vulnerability is correlated with age. No evidence of such a trend is apparent in Figure 23.

We have used total hunting effort in the above calculations as though all effort were applied to the tagged population, whereas, one of our basic premises is that hunting effort is not uniformly applied to the popu-

lation; i.e., tagged rabbits are hunted more intensively than are untagged rabbits. At best, we can assume that the division of effort is constant; but, of course, one of the weaknesses in our model is that the simplification into two discrete populations is no doubt unrealistic.

Some further treatment of the data is possible if we now use the notion that only part of the effort ( $n_1$ ) is applied to the tagged population, and further select the

first values of  $\frac{m_1 n_1}{n_1 + n_2}$  (Table 14) as being

least affected by the error in using a constant value of the natural mortality rate;

then we may exhibit the value  $\frac{m_1 n_1}{n_1 + n_2}$  as:

$$\frac{m_1 n_1}{n_1 + n_2} = \frac{m_1}{1 + \frac{n_2}{n_1}} = \frac{m_1}{1 + b}$$

Dividing this value by the slope of the regression lines described in the section on age ratios (see Table 12), we have:

$$\frac{\frac{m_1}{1 + b}}{m_1 \left\{ \frac{1 - b}{1 + b} \right\}} = \frac{1}{1 - b}$$

which provides an estimate of sorts of the magnitude of  $b$ . These values of  $b$  might then be used with the “ $y$ -intercept” values

of Table 12 ( $\ln \frac{1}{b} \frac{J_t}{J_u}$ ) to estimate roughly

the true value of the tagged-to-untagged ratio.

If we actually attempt to calculate values

of the ratio of  $\frac{1}{1-b}$  from data in Tables 12

and 14, we find:

Year	Regression “Slope” (Table 12)	$\frac{m_1 m_2}{n_1 + n_2}$ (Table 14)	$\frac{1}{1-b}$
1951	0.000272	0.000104	—
1952	0.000356	0.000193	—
1953	0.000219	0.000100	—
1954	0.000022	0.000110	5.00
1955	0.000061	0.000160	2.62
1956	0.000044	0.000068	1.54
1957	0.000032	0.000093	2.91

Thus the first 3 of the 7 years’ data give results not compatible with the definition of  $b$ . The fault may lie in the crude methods of estimation employed, or in our use of an oversimplified model; i.e., tagged and untagged populations are not separate entities in a spatial sense and are subject to 2 distinct categories of hunting. If we accept the models as being a reasonable approximation of what actually has occurred, then some form of joint estimation is undoubtedly necessary; i.e., using the available data for simultaneous estimation of the true proportion tagged instead of attempting to combine several separate estimates.

#### FREQUENCY OF CAPTURE

Calhoun and Casby (1958) described the concept of home range for small mammals in terms of a mathematical model. They adopted the circular normal distribution as a model to describe the spatial distribution or “probability density” of an individual animal’s activity. They considered only animals for which trapping records indicate a more or less fixed “center of activity” (Hayne, 1949) and excluded animals that apparently shift home ranges during the course of study.

We do not have sufficient data to determine the distribution of activity of individual rabbits in the manner described by Calhoun and Casby (1958), since only a small fraction of the traps at Rose Lake are in a regular or grid pattern, and most trapping periods are too short to obtain enough captures to yield much information about behavior of individuals. Certainly it is sufficiently evident that most rabbits spend their time in a restricted area; whether they tend to spend more time in one portion of their home range or not is uncertain. At least during periods of abundant food and cover, one might speculate that a rabbit’s activity might be fairly uniformly spread over its home range. We might also argue that a preference for cover “edges” would make for oblong home ranges.

Here we suggest that the frequency of capture may be a function of home range and may potentially provide additional information on behavior of individual animals to supplement data obtained on their spatial behavior. If different individuals and/or the several sex and age classes have different sizes of home ranges, and if trap densities are not high, then animals with large home ranges have a higher probability of exposure to traps and presumably of capture.

For some class (or group) of animals with the same size of home range, one might logically assume a frequency of capture of the Poisson distribution:

$$f(x) = \frac{e^{-m} m^x}{x!}$$

where  $f(x)$  is the proportion of animals in the group caught  $x$  times ( $x = 0, 1, 2, 3, \dots$ ) and  $m$  is the mean value of all capture frequencies, or the average capture rate. In circular home ranges for a group having the same radius  $r$ , the area will be  $\pi r^2$ , and the average capture rate  $m = d\pi r^2$ . The factor  $d$  should include (1) the density of traps in the area (so an individual’s contact with traps will depend on both size of home range and trap density), and (2) an element to reflect the fact that “contacts” with

traps do not all result in capture. For present purposes, we consider  $d$  a constant.

So far, we have said only that some group of like individuals has a distribution of capture frequencies which follow the dictates of chance, e.g., a Poisson distribution. A distinction needs to be made at this point as to what  $r$ , the radius of home range, actually is. One can adopt the view that all of an individual's time is distributed rather evenly within some fixed radius, or, as suggested by Calhoun and Casby (1958) that the frequency of distances  $r$  for an individual is represented by:

$$f(r) = \frac{r}{\sigma^2} e^{-r^2/2\sigma^2}$$

where  $\sigma^2$  is a constant pertaining to the individual animal. In this instance, the individual can theoretically be found at any distance from his center of activity but with probability dependent on distance.

Theoretically there are an infinite number of equations that might be used as above; we will examine the above-mentioned possibilities only to suggest prospects for further study.

Considering the circular normal distribution first, we find the expected (or mean) value of  $m$ , the mean rate of capture for animals having the same value of  $\sigma^2$ , to be:

$$\begin{aligned} E(m) &= E(d\pi r^2) = \int_0^\infty \frac{d\pi r^3}{\sigma^2} e^{-r^2/2\sigma^2} dr \\ &= 2d\pi\sigma^2. \end{aligned}$$

If  $\sigma$  is a measure of an animal's range, then a larger range results in a higher average rate of capture.

We further assume that the population is made up of animals having different values of  $\sigma^2$ , and that the relative frequencies of individuals possessing a particular value of  $\sigma^2$  is:

$$f(\sigma^2) = \frac{1}{B} e^{-\sigma^2/B},$$

where  $B$  is a constant of the population. We have no biological evidence to support this assumption; its choice is simply a matter of the end product of these manipulations. We

do note, however, that this (Gamma) distribution has various applications in biology, and that Skellam (1951), for example, has used it for a somewhat similar purpose.

Given the distribution of  $\sigma^2$  in the population, one can obtain the distribution of  $m = 2d\pi\sigma^2$  as:

$$f(m) = \frac{1}{c} e^{-m/c} \text{ where } c = 2d\pi B.$$

Returning now to the assumption that the relative frequency of capture is represented by a Poisson distribution, we find the joint distribution of  $x$  and  $m$  to be:

$$f(x, m) = \frac{m^x e^{-m - (m/c)}}{cx!},$$

and

$$\begin{aligned} f(x) &= \int_0^\infty \frac{m^x e^{-m - (m/c)}}{cx!} dm \\ &= \frac{1}{1+c} \left\{ \frac{c}{1+c} \right\}^x. \end{aligned}$$

This final expression is the geometric distribution or the negative binomial with index  $k$  equal to unity (Feller, 1950).

We can also arrive at the same distribution by starting with the notion that an individual animal's time is distributed uniformly within some fixed radius  $r$ . Here we assume that the distribution of  $r$  in the population of rabbits is given by:

$$f(r) = \frac{r}{\sigma^2} e^{-r^2/2\sigma^2}$$

where  $\sigma^2$  now represents a population constant rather than that of an individual as before. If  $m = d\pi r^2$  as before, then:

$$f(m) = \frac{1}{c} e^{-m/c} \text{ with } c = 2d\pi\sigma^2,$$

and the ensuing results are the same as before, leading to the same distribution of  $f(x)$ , the frequency of capture.

In the absence of sufficient biological justification for our models, we cannot claim that either situation holds in nature, and we suppose that the same result may be obtained in other ways. Our purpose in

TABLE 15.—OBSERVED AND EXPECTED FREQUENCIES OF CAPTURE OF TRAPPED RABBITS OF DIFFERENT CLASSES, AND FOR ALL CLASSES COMBINED, FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

	Adults		Juvenile Males		Juvenile Females		Total			Adults		Juvenile Males		Juvenile Females		Total	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected		Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
1951																	
0	104.0		274.0		169.0		489.0		0	203.0		200.0		224.0		622.0	
1	37	35.5	54	50.5	45	46.9	136	132.1	1	60	58.9	68	67.1	74	72.8	202	198.7
2	11	12.1	5	9.3	16	13.0	32	35.7	2	16	17.1	23	22.5	20	23.7	59	63.5
3	2	4.1	2	1.7	3	3.6	7	9.6	3	5	5.0	4	7.6	11	7.7	20	20.3
4	3	1.4		0.3	1	1.0	4	2.6	4	1	1.4	4	2.5	2	2.5	7	6.5
5	1	0.5				0.3	1	0.7	5		0.4	2	0.8	1	0.8	3	2.1
6			1				1		6	1	0.1		0.3		0.3	1	0.6
1952																	
0	176.0		305.0		140.0		569.0		0	200.0		136.0		260.0		556.0	
1	38	36.4	51	52.2	42	41.0	131	129.1	1	42	40.6	48	44.4	61	60.6	151	144.9
2	5	7.6	11	8.9	11	12.0	27	29.3	2	6	8.2	8	14.5	13	14.1	27	37.8
3	2	1.6	1	1.5	3	3.5	6	6.6	3	2	1.7	7	4.7	4	3.3	13	9.8
4	1	0.3		0.3	1	1.0	2	1.5	4	1	0.3	2	1.5	1	0.8	4	2.6
5					1	0.3	1	0.3	5		0.1	1	0.5		0.2	1	0.7
									6								0.2
1953																	
0	200.0		232.0		248.0		657.0		0	199.0		386.0		303.0		887.0	
1	44	46.2	78	76.4	73	72.3	195	194.4	1	55	55.0	103	102.2	89	87.0	247	244.2
2	14	10.6	29	25.2	19	21.1	62	57.5	2	17	15.2	25	27.0	21	24.9	63	67.2
3	2	2.4		8.3	8	6.1	10	17.0	3	1	4.2	9	7.2	10	7.2	20	18.5
4		0.6	5	2.7	1	1.8	6	5.0	4	2	1.2	1	1.9	1	2.0	4	5.1
5				0.9	1	0.5	1	1.5	5	1	0.3	1	0.5		0.6	2	1.4
6			1	0.3		0.2	1	0.4	6		0.1		0.1	1	0.2	1	0.4
7									7								0.1
8		1					1										
1954																	
0	178.0		267.0		262.0		700.0										
1	43	42.0	69	66.2	78	72.9	190	180.9									
2	9	9.9	12	16.4	14	20.3	35	46.8									
3	1	2.3	5	4.1	4	5.6	10	12.1									
4	2	0.6	1	1.0	4	1.6	7	3.1									
5	0.1	1	0.2			0.4	1	0.8									
6					1	0.1	1	0.2									

introducing them is to demonstrate that we may consider individuals in a population as having varying probabilities of capture on the premise of at least 2 different modes of behavior, and that the resultant distribution of capture frequencies seems to fit our observed data fairly well.

We do not, of course, know the numbers of rabbits not caught at all, with frequency

of capture  $f(0)$ , but, if the model is valid we can estimate zero frequencies. We have done this with the Rose Lake data using Hartley's (1958) method of fitting a truncated distribution (here with zero frequencies missing) by an iterative process employing the maximum likelihood estimator(s) of the parameter(s) of the distribution (the maximum likelihood estimate of

TABLE 16.—CHI-SQUARE VALUES FOR FREQUENCY OF CAPTURE OF TRAPPED RABBITS OF DIFFERENT CLASSES, AND FOR ALL CLASSES COMBINED, FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION. \*Significance at 5% and \*\*at 1% level for 2 degrees of freedom; however, test is not exact due to small frequencies in some cells not pooled. (We pooled frequencies in fourth and all subsequent cells in contrast to the usual practice of pooling to get 5 or more observations per cell.)

	Adults	Juvenile Males	Juvenile Females	All Rabbits
1951	3.56	3.92	0.94	3.41
1952	2.69	0.99	0.56	1.06
1953	1.86	10.04**	0.91	3.41
1954	3.25	2.03	6.77*	9.42**
1955	0.10	3.94	2.11	0.73
1956	1.59	4.62	0.24	5.03
1957	3.88	0.26	1.97	0.42

the constant  $c$ , above, is simply the mean of the frequencies of capture,  $x$ .

The fitted frequencies in most cases closely parallel the observed data (Table 15). Use of the usual Chi-square criterion for agreement is uncertain here by virtue of low frequencies in the "tails." Chi-square values (Table 16) (grouping observations in the 4th and subsequent cells in all cases and using 2 degrees of freedom in the test) indicate that the proposed distribution does fit the observed data rather closely. We have not investigated the possible application of other distributions here, but assume that the negative binomial might also fit rather closely.

We again emphasize that the agreement of actual trap-frequency data with a particular theoretical distribution provides no conclusive evidence that the behavior postulated by the theory actually occurs in nature. We believe these results suggest possibilities worth further investigation, but we hold no brief for their application without more data on the biological inner workings of the proposed relationships. We do have data suggesting that the trapability of sex and age classes may vary with weather conditions. Colder temperatures seem to increase the number of males in the trap catch.

Totaling the expected frequencies (Table 15) could yield theoretical "populations"—populations of rabbits "exposed to traps." However, the continuous nature of parts of our model as opposed to the finite behavior of rabbit populations leads to various uncertainties as to what population these totals might represent, arguments into which we do not propose to enter here. Then, too, most of our traps are neither randomly nor systematically located; roughly half of the 10-acre units of the experiment station contain traps (Fig. 7).

Table 17 shows "population" totals for the several classes. In most years, these amount to 80 per cent or more of the Lincoln Index population estimates. One might argue, on the basis of the evidence in this paper, that the Lincoln Index estimates are somewhere intermediate between size of the "population exposed to traps" and the

TABLE 17.—THEORETICAL ESTIMATES OF POPULATION SIZE OF 3 CLASSES OF RABBITS, AND FOR ALL CLASSES COMBINED, BASED ON FREQUENCY OF CAPTURE OF TRAPPED RABBITS FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

Year	Populations Estimated From Frequency of Capture						Age Ratios (Juv. per Adult)	
	Adults	Juvenile Males	Juvenile Females	Sum of the Three Classes	All Rabbits	Lincoln Index Estimate	Computed From This Table	In Kill
1951	158	336	234	728	670	1,231	3.6	5.5
1952	222	368	198	788	736	930	2.6	3.6
1953	260	346	350	956	933	1,198	2.7	5.3
1954	233	355	363	951	944	956	3.1	4.3
1955	286	301	332	919	914	1,144	2.2	5.2
1956	251	202	339	792	752	1,427	2.2	5.4
1957	275	525	425	1,225	1,224	1,510	3.4	6.4

TABLE 18.—ESTIMATES OF VALUES OF THE CONSTANT  $c$  FOR EACH OF 3 CLASSES OF RABBITS, AND FOR ALL CLASSES COMBINED, FROM THE FREQUENCY-OF-CAPTURE DISTRIBUTION FOR TRAPPED RABBITS FOR EACH OF 7 YEARS, 1951–1957, INCLUSIVE, AT THE ROSE LAKE WILDLIFE EXPERIMENT STATION

	Adults	Juvenile Males	Juvenile Females	All Rabbits
1951	0.52	0.23	0.38	0.37
1952	0.26	0.21	0.41	0.29
1953	0.30	0.49	0.41	0.42
1954	0.31	0.33	0.39	0.35
1955	0.41	0.50	0.48	0.47
1956	0.26	0.48	0.30	0.35
1957	0.38	0.36	0.40	0.38

total population on the experiment station. The years of greatest discrepancy (1951 and 1956) are also the years of lowest proportion of tagged rabbits in the kill.

Table 18 presents estimates of the constant,  $c$ , from the proposed distribution. Higher values of the constant from the equation indicate a higher proportion of the "population" taken by trapping (lower frequency of zero captures), so that one might argue that either average size of home range or probability of capture after contact with the trap (or at least the product of the two) is greater for juveniles than adults according to data in the table and the postulates of our model.

The age ratios in Table 17 contradict this notion. If we accept kill ratios as approximating those of the population, the ratios in Table 17 argue for a lower proportion of juveniles being taken in trapping, as do the lower proportions of tagged juveniles in the kill (Table 9). This can mean, of course, that our models are not valid, but there are also other possibilities. These include the notion that juveniles spend the early months of their lives in areas remote from traplines (hayfields, pastures, etc.), and the observation that we do not trap small juveniles. So there may be a population of late-born juveniles not trapped, but available to hunters.

A little additional information on the home range of the several age classes is

available from "grid" traplines (see section on Lincoln Index) providing records on animals caught by traps arranged in a systematic pattern on grid lines 330 feet apart. As mentioned previously we usually operate traplines for only 11 days, and do not get large numbers of recaptures on individual animals. Thus, we do not have the volume of data we would like for estimating home ranges. Further difficulties are that our grid lines have relatively few traps, and a considerable proportion of the traps are "peripheral," quite possibly catching animals with home ranges partly outside the scope of the traps.

Considering these difficulties, we have not attempted to calculate home ranges, but have rather compared only successive distances moved for the several age and sex classes, assuming that the mean distances moved between successive captures should give us some notion as to whether some particular class has a larger home range than others during our trapping effort. When successive captures are in the same trap we have arbitrarily assigned one-half the distance between traps (this should, according to Calhoun and Casby [1958] be a little less than half the distance).

For present purposes average movements between captures evidently do not provide any support for the notion that during our trapping period juveniles have larger home ranges than adults:

	Average Movement (feet)	Number of Rabbits
Adult males	480	24
Adult females	396	17
Juvenile males	423	51
Juvenile females	411	65

We have not attempted any test of significance of these differences.

## DISCUSSION

We remind the reader again that we do not consider this paper a final report on live-trapping of rabbits at Rose Lake. We intend it only as a progress report because too much has arisen in the course of the

investigation that needs further study, both from the available records and from field experimentation. As with many similar situations, live-trapping has become a more or less routine operation after the first few years, and workers have taken its principal result, the Lincoln Index population estimate, as a reliable measure of the rabbit population. We have based a great deal of other work on this estimate, assuming that it was reliable. Only within the past few years have we realized that it is not reliable, and many items covered in this report have turned up in the course of searching for some way of determining what was responsible for the difficulty with the Lincoln Index and for a means of correcting the bias.

Further field work on several items covered here is now under way at Rose Lake. One of the principal reasons for delving into the matter was to decide whether further work ought to be carried out, and to guide planning and execution of such work. We also felt that there was a considerable amount of similar data elsewhere, not reported in the literature in sufficient detail to make it possible to determine whether there are uncertainties similar to those discussed here. We hope this report will stimulate such investigations.

We have not attempted to do anything conclusive in terms of mathematical or statistical representations or tests of significance. Our major purpose has been sketching out some of the possibilities, and we leave the more precise work for future consideration when we have further evidence on some of the more puzzling details.

We feel satisfied that the principal difficulty with the Lincoln Index at Rose Lake is that, unconsciously, hunters concentrate on the trapline areas and thus take a higher proportion of tagged than untagged rabbits, or that we deliberately concentrate our trapping effort where rabbits are shot. The major alternate possibility is that some tagged animals are moving to surrounding areas and being replaced with untagged animals from outside. There are several ob-

jections to this supposition, chiefly the tagged-to-untagged ratio on the "grid" trap-lines (Fig. 5). This suggests that use of a grid trap pattern throughout the station may be the answer to measuring populations by the Lincoln Index. It may also give us the best source of data for further work on home range. One objection to "grid" trapping is that it is inefficient, catching too few rabbits for a given number of traps. (At least we believe that this is so but we do not have any good idea just how much of a reduction in catch would occur.) During most of our trapping, the uplands have rather heavy stands of herbaceous cover; there may well be more rabbits there than we suppose. An alternative proposal by Chapman and Junge (1956), using stratification in estimating populations, was considered, but was overruled when it became evident that we could not depend on hunters' reports to be sufficiently accurate to locate kills in the various strata, and particularly in the cover edges along which traplines are located.

One strong objection to the fixed grid pattern of traps (or any fixed pattern) is that animals may form a "trap habit," repeatedly returning to the trap for food. We do not believe this is important here, but we have no way of being sure without repeatedly moving traps. Some form of restricted randomization might be the best approach for at least some parts of future studies. By restricted randomization, we mean the practice of putting say 4 traps out at random in each 10-acre block of the area to be trapped. We feel sure that the workers should select trap sites from a table of random numbers and should faithfully adhere to this plan.

We suppose that the systematic grid pattern is best for the study of home ranges. Restricted randomization might be preferable for investigation of the notion of frequency of capture as a means of estimating size and other characteristics of populations. Quite possibly the best procedure at Rose Lake will be to start out with a systematic pattern for a year or two to see whether this

appears to take care of the difficulty with regard to the Lincoln Index estimates, and then switch over to a randomized scheme for further study of other aspects. We probably also need a longer period of trapping than 11 days to study home ranges.

An attempt to catch small juveniles in live traps seems worth considerably more effort. We do not know of any good possibilities. One time-consuming and difficult possibility would be driving small juveniles into rabbit nets. Closer spacing of traps might also catch a larger number of smaller rabbits if the difficulty is largely that of a small home range. Any great increase in trap density might, however, hinder the development of true home-range estimates (Hayne, 1949). Otherwise, some alternate means of capture seems necessary.

Information on mortality is very expensive to obtain in terms of time and effort. However, since it is essential to any future studies, more intensive trapping for longer periods should be considered. There is, too, a good possibility that better estimates of mortality rates may be obtained from available data by more efficient methods of estimation, for example, the joint estimation of several parameters as mentioned above. The present data are suspect for this purpose, of course, because of the possibility that tagged and untagged populations are subject to different degrees of hunting.

Movement is also of considerable interest for further study. We have not done nearly as much as we would like with available records. If future trap patterns permit the study of home ranges in the manner discussed by Calhoun and Casby (1958), it should be well worthwhile to compare such home-range data with the frequency of recatches and length of movements between trapping and shooting. There are enough movements over relatively great distances to suggest that a number of rabbits wander in the fall and such movement is not restricted to juveniles only.

The mistakes in aging described in this paper seem especially important to rabbit researchers with similar studies in mind or

in hand. The changes instituted by adjusting for these mistakes have made a considerable difference in the results between this paper and our earlier one with the same data (Peterle and Eberhardt, 1959). These errors also make it inadvisable to depend on trapping data alone; apparently the kill information is essential.

We also need additional studies of age ratios. Ratios in the shot sample are likely to be most nearly those existing in the population at the time of shooting, but the differential vulnerability of adults and juveniles to the gun means that the ratio from shooting will overestimate the actual value. It is also important to remember that age ratios truly representative of the fall population still do not reveal the true production of young per female, by virtue of the differences in mortality rates. There is a common tendency to forget that some adult females die between the time litters are born and the hunting season. Both rates must be taken into account.

Frequency of capture provides an interesting potential means of studying rabbit populations that other workers, so far as we know, have not considered. At present, at least, we do not propose to use frequency-of-capture data to estimate population size, but it does pose some interesting possibilities. We note, for example, that juveniles seem to "repeat" more frequently than adults, but not to get caught in the same proportions. We suspect that juveniles beyond a certain size are less wary than adults, but have home ranges of about the same areas. Quite possibly smaller juveniles have much smaller home ranges, and perhaps they are located in areas remote from most of our present traplines. It would be interesting to try some unbaited wooden traps (see Hickie, 1940) in areas of dense herbaceous cover to see if they would take more small juveniles.

Beyond the possibilities of further field studies similar to those described here, and more efficient methods of statistical estimation, we feel that workers should consider large wire enclosures, now in use in Ohio

with known populations of specified sex and age composition (Edwards, 1958). Under penned conditions there is also the possibility of using radioactive materials for marking, not feasible under the present condi-

tions of intensive public use of the area. Recent developments in the use of miniature radio transmitters (LeMunyan *et al.* 1959, and Trefethen *et al.* 1957) may also assist in solving certain phases of the problem.

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