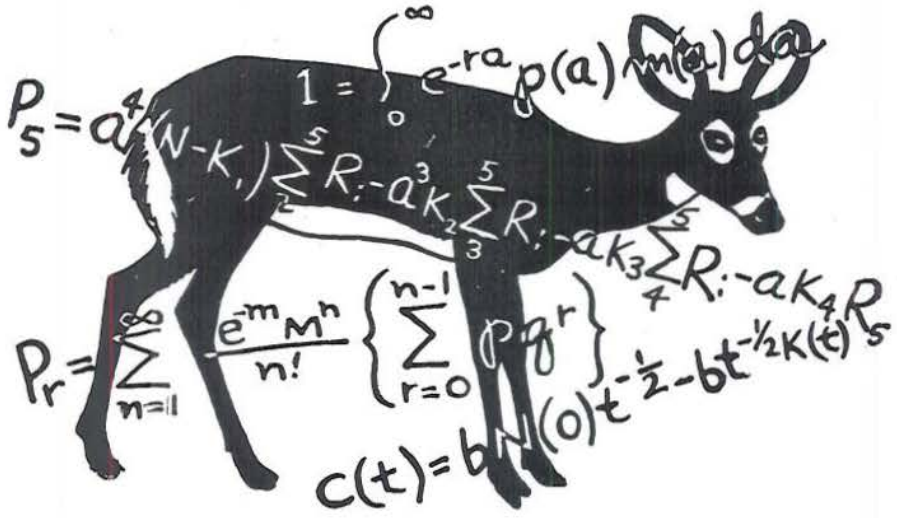
ESTIMATION OF VITAL CHARACTERISTICS OF MICHIGAN DEER HERDS

Lee Eberhardt



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ESTIMATION OF VITAL CHARACTERISTICS OF MICHIGAN DEER HERDS

by

Lee Eberhardt

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PREFACE

This report is a compromise, and like all compromises, will probably be unsatisfactory from several points of view. The biologist may find too much mathematics here, but the biometrician or statistician will quite surely find the analyses to be inadequate and incomplete in several respects. Those responsible for field management of deer herds will very likely find too many of the results given here to be either contradictory or not sufficiently explicit for direct application.

The genesis of this report is my belief that many of the data collected on Michigan deer herds have been inadequately exploited. Furthermore, we often find it necessary or expedient to obtain records in ways which are not wholly in accord with the dictates of a sound sampling program. I feel that justification for the use of such information must depend heavily on the overall consistency of the results, so that I have here attempted to examine as many aspects of the data as is feasible in the available time.

I am indebted to the Game Division, and particularly to Mr. H. D. Ruhl, Chief, for the opportunity to conduct the research reported here. Literally hundreds of the employees of the Michigan Department of Conservation have participated in collecting data used in this study, and I should judge that a majority of the biologists and technical specialists in the Game Division have contributed directly in one way or another. Especial mention should be made of the participation of the following Game Division personnel: I. H. Bartlett, D. W. Douglass, L. D. Fay, R. A. MacMullan, Mrs. Robert Murray, L. A. Ryel, and S. C. Whitlock. I am grateful to Dean Armstrong (draftsman) and Mrs. Rex Caster (typist) for their care and patience in preparing final copy for the report.

I also wish to express my appreciation to Professors G. A. Petrides, J. E. Cantlon, D. W. Hayne, and G. J. Wallace for their advice and counsel in presentation of this analysis as part of the requirements for the Ph.D. degree at Michigan State University. Special credit is due to Dr. Don W. Hayne for his many useful suggestions during the last ten years.

Many of the data used in this report were obtained in the course of investigations under Federal Aid in Wildlife Restoration Project Michigan 96-R.

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I. INTRODUCTION

Scope. This report is chiefly concerned with methods of estimating the relative abundance and certain vital characteristics (in the demographic sense) of the white-tailed deer (Odocoileus virginianus) in Michigan. The basic information used here is derived principally from the following sources:

(1) Records of the age and sex of deer shot by hunters and subsequently examined by biologists employed by the Michigan Department of Conservation.

(2) Estimates of numbers of deer killed in hunting seasons and of hunting effort, as obtained through use of mailed questionnaires.

(3) Field surveys designed to estimate deer population levels and overwinter mortality.

(4) Records of the number of embryos borne by female deer in the spring of the year (obtained mainly through autopsy of deer accidentally killed on highways).

(5) A variety of sources which may serve as indices to deer abundance, such as roadside counts.

Areas and years. Data used here have been obtained throughout Michigan, but the greatest volume and variety of information pertain to the northern Lower Peninsula over the years 1952 to 1958.

Auspices of the study. Virtually all of the data used here have been collected by employees of the Michigan Department of Conservation in the

course of research and management activities conducted by the Game Division. I have participated in the collection and tabulation of field data in the capacity of biometrician for the Game Division, but my chief responsibility has been for statistical design of the sample surveys and particularly for analysis of the data as presented here.

Background. Michigan's deer herd usually numbers in the neighborhood of 700,000 animals in the fall of the year (Jenkins and Bartlett, 1959, Ryel, 1959b). In recent years from 70,000 to 100,000 deer have been legally harvested annually by about 450,000 hunters (Eberhardt and Jenkins, 1959). Precise figures are not available, but deer hunting is certainly a multimillion dollar business in Michigan, and deer are also an important tourist attraction in many areas.

A major part of the deer range is now, and has been for many years, overpopulated with deer. In much of the area, available food supplies are inadequate during the winter, resulting in both starvation and reduced reproductive success (Bartlett, 1938, 1950, Jenkins and Bartlett, 1959).

From 1921 through 1951 Michigan deer hunters were legally restricted to one adult male deer per year, except that beginning in 1941 a limited number of antlerless deer were taken, under permit, to alleviate crop damage by deer in certain areas. Legislation in 1952 gave the Conservation Commission (governing body for the Department of Conservation) much broader authority, and significant numbers of antlerless deer have been taken in most of the succeeding years. The harvesting of antlerless deer is still a controversial issue, with many people sincerely contending that there are not too many deer, and that shooting does and fawns is improper and will result in destruction of the herd.

Biology of the white-tailed deer. A brief description of pertinent biological aspects may be useful to readers who are not familiar with the species. My reference for the following paragraphs has been The Deer of North America, edited by Taylor (1956), which provides much more detail than can be summarized here.

The white-tailed deer (Odocoileus virginianus) is a hoofed mammal having average adult weights of 100 to 200 pounds, depending on age and plane of nutrition. The species is found in a wide range of habitats, but major populations of the northeastern United States and Canada are found in areas of immature or second-growth forests interspersed with openings and coniferous swamps. A great variety of plant foods are eaten by deer, but the basic winter diet is composed of twigs of trees and shrubs. In northern areas of deep snow, deer congregate in sheltered areas (frequently coniferous swamps) during the winter months. Such concentrations may result in rapid depletion of local food supplies, followed by many deaths from starvation. Usually the youngest animals (fawns) are most affected.

Sexual capability is ordinarily reached at 18 months. Under the very best of food conditions, however, some females may breed and give birth to a single fawn during their first year of life. Females might be classed as fully mature at 3 or 4 years of age, but maximum reproductive rates may not be achieved until about the sixth year of life (Part V of this report). In northern areas breeding is restricted largely to the fall of the year, reaching a peak in November. A gestation period of a little over 200 days results in the birth of most fawns in early June. Reproductive rates vary considerably with age and nutritive conditions, but the maximum average rate seems to be about

two fawns per mature doe.

Adult male deer grow antlers each summer and shed them in late winter, so that sexes of adult animals may readily be distinguished during fall hunting seasons. This sex differentiation combined with the fact that males will mate with more than one female permits sex-discriminate hunting regulations.

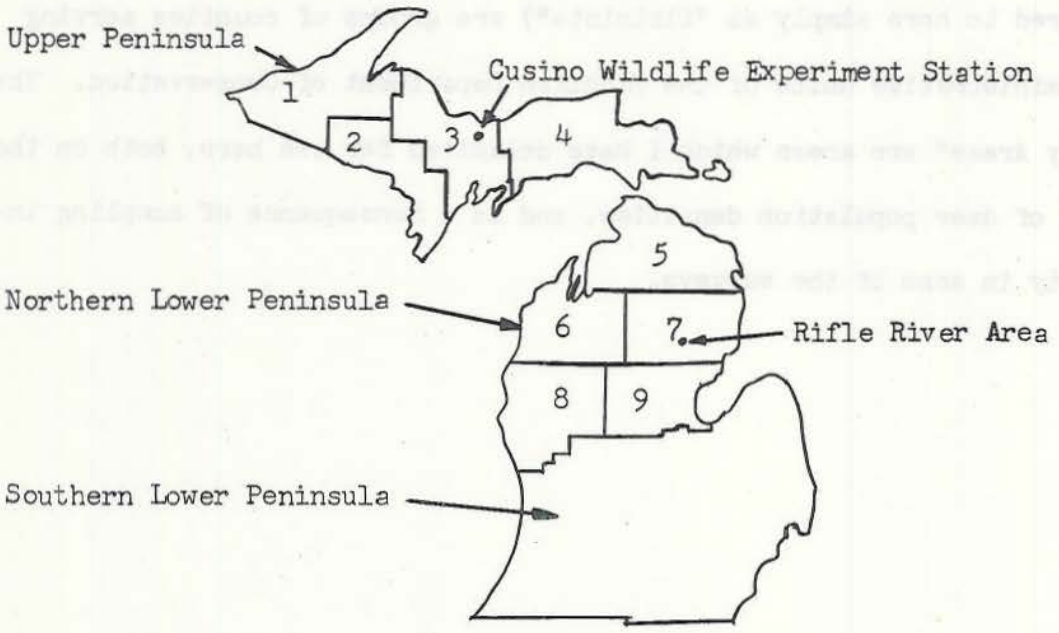
Definition of terms. For clarity and convenience, certain terms and areas are defined here. "Buck" and "doe" refer to male and female deer in at least their second year of life, and "fawn" refers to the age class of animals between birth and one year. The word "population," unless otherwise identified, is used to identify aggregates of the white-tailed deer in Michigan.

The "regular season" or "buck season" pertains to the statutory deer hunting season wherein male deer having antlers at least three inches long may be taken during the period November 15 to 30, inclusive, in any part of Michigan. "Special" seasons are those in which any deer may be taken, regardless of sex or age, either by any licensed hunter, or only by those specifically authorized to do so under permits issued by the Michigan Department of Conservation. Since dates and regulations for such seasons have varied during the period covered by this study, descriptions are provided at the appropriate places in the text.

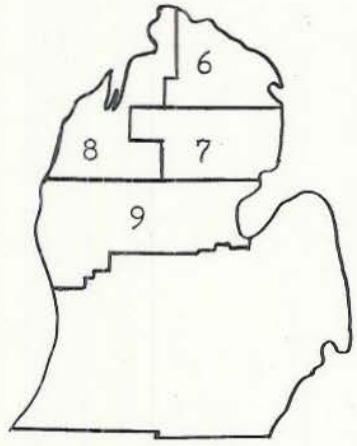
The word "we" is used, in cases where specific references are not available, to identify practices, procedures, and policies employed by the Game Division of the Michigan Department of Conservation.

Study areas. Two sets of geographic subdivisions of Michigan (Figure 1) are used throughout this report. The Game Management Districts (usually

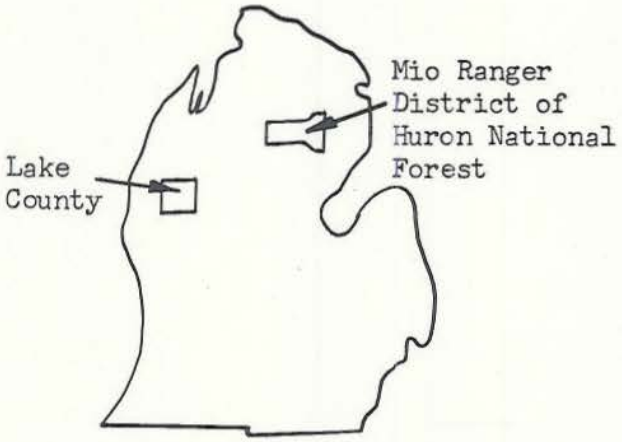
referred to here simply as "Districts") are groups of counties serving as administrative units of the Michigan Department of Conservation. The "Study Areas" are areas which I have delimited for use here, both on the basis of deer population densities, and as a consequence of sampling intensity in some of the surveys.



Game Management Districts, Michigan Department of Conservation



Major Study Areas



Areas of special studies

Figure 1. Geographic subdivisions of Michigan used in this report.

II. METHODS OF MEASURING POPULATION LEVELS

Introduction. Four different types of data for measuring deer population levels are considered in this report: (1) fecal pellet-group counts, (2) sex, age, and kill data, (3) kill and hunting-effort records, and (4) various indices (e.g., roadside counts). The first three sources are used for direct estimates of total population, and the fourth yields a composite index. Data for large areas can be obtained from these sources at a reasonable cost. Many other possibilities exist (Hazzard, 1958), which have not been extensively tested in Michigan, or which are not well suited for use on a continuing basis over large areas.

Two principal problems turn up repeatedly here: (1) Bias. Practically all of the estimates used in this report depend on various assumptions of uncertain validity. Since there is no way of directly testing these assumptions, I have relied on comparisons of different estimates of the same quantity as a measure of bias, and have therefore attempted to make individual estimates as nearly independent of each other as possible. (2) Efficient use of the available information. When estimates can be formed in different ways, the question of the "best" estimate includes not only whether or not it is unbiased, but also whether a particular form of the estimate will have a smaller sampling error than others, or whether several different estimates can be combined to yield a single value more precise than the individual estimates. In attempting to keep different estimates of the same quantity independent, I have necessarily lost in efficiency in order to appraise the possibilities of bias.

The four major methods of estimating population level are described in this part of the report, and Part III deals with comparison of the individual methods.

PELLET-GROUP COUNTS

The method. The method depends basically on measurement, by sampling, of the accumulation of fecal pellet-groups over some protracted period of time. Various features of pellet-group count investigations in Michigan were reported by Eberhardt and Van Etten (1956) and Ryel (1959a). Some general aspects are reviewed here.

Results of sample counts may be reported simply as the average number of pellet-groups found per unit of area, and thus serve only as an index to deer abundance. Use of the method in Michigan has, however, depended on conversion of pellet-group counts to estimates of actual numbers of deer present on the area sampled. The discussion (and use) here is therefore in terms of estimates of deer numbers. While survey results have not always been satisfactory, we have found the method sufficiently useful to warrant using it for annual surveys of all the major Michigan deer range.

Some remarks on the several assumptions basic to the method follow:

(1) A knowledge of the average daily defecation rate is essential for conversion of counts to deer-days of use for a particular area. Average daily defecation rates vary somewhat both with diet and size of deer, but are remarkably constant from day to day. Both our earlier experience (Eberhardt and Van Etten, 1956) and more recent unpublished Michigan studies confirm this, but Rogers et al. (1958) have reported higher defecation rates for mule deer (Odocoileus hemionus hemionus).

(2) Length of the deposition period represented in the samples must be determined, either by advance clearing of pellet-groups from the plots, or by depending on the autumnal fall of leaves as a reference point. Nearly all Michigan work with the method has been based on a

fall-to-spring accumulation of pellets. Summer use of the method does not seem feasible because of the short deposition period, and the rapid deterioration of pellets deposited in late spring and early summer.

Leaf-fall dates are recorded each year by biologists living in the various parts of the state. In northern Michigan, leaves of most deciduous trees and shrubs fall during a fairly short period, but those of some of the oaks may persist on the trees until late in the winter or into early spring. Under these oak stands it seems certain that some pellet-groups are covered by leaves after the date used as the starting point for the winter pellet-group accumulation. We find, however, that even in an area of rather extensive oak cover in southern Michigan (The Edwin S. George Reserve, of the University of Michigan), reasonable care in searching the plots will apparently turn up most of the groups present, although often only a few pellets are visible, and the risk of missing groups is thereby increased.

In open areas, or under coniferous cover, it becomes necessary to estimate the age of pellet-groups. A few criteria have been described that help in this process (Eberhardt and Van Etten, 1956), but actual field experience, including the examination of groups of known age under various conditions, provides the best basis for such determinations.

(3) Additional important assumptions are that sampling is representative and adequate, and that all winter-deposited groups on sample plots are tallied. These points are covered in more detail beyond.

Sampling. Sampling methods for pellet-group surveys necessarily depend on the particular situation and on the kind and quality of results needed.

For very small areas systematic or "grid" samples may be preferable, for ease in locating the plots. On larger areas, however, which usually show considerable variation in deer populations, considerations of time and cost dictate the use of stratified sampling methods to increase sampling efficiency (Eberhardt, 1957b).

A rectangular plot 12 feet by 72.6 feet (1/50 acre) has been used as the basic unit in Michigan, but it is necessary to locate several such plots fairly close together in order to reduce travel time and costs which are a major item in surveys covering several thousand square miles.

The section (square mile) is used as a sampling unit, and eight plots are located on a half-mile line penetrating the section from a random starting point on the periphery. There is some evidence (Ryel, 1958) that fewer plots at a location might be desirable.

The Michigan surveys are based on four or five strata of estimated over-winter deer population levels. The actual classification of each section of a given area into one of the several strata is done by Game Division field men, and has proved to be fairly accurate. An initial difficulty of some importance has been that of getting the several people involved to think in roughly the same terms in defining strata. We find that general terms ("high," "medium," and the like) are not satisfactory for this purpose, and that actual estimates of numbers of deer per square mile are best. In nearly every case it has been initially necessary to hold two meetings, one to outline the basic plan of stratification, and the other to compare maps prepared by individual biologists. The ensuing discussions usually result in revision of maps and fair agreement in strata at the joint boundaries of the various districts.

Allocation of sample plots among strata has been based on past survey results, and is described in detail in several reports (Eberhardt,

1957a, Ryel, 1958, 1959b). Assumption of the negative binomial as the theoretical frequency distribution most closely fitting pellet-group tallies seems to provide a satisfactory basis for sample allocation (Eberhardt, 1957b).

Some improvement of the stratification seems possible on the basis of our accumulated results, and possibly aerial photographs may aid the process. It may, however, be difficult to improve on intimate field familiarity with the areas as a basis for stratification.

Permanently located plots may have several advantages. In most past years, we have changed the areas to be sampled from year to year, ranging from rather small (about county size) areas of particular interest in some years, to half or all of the 30,000 square miles of major deer range in others. While the sampling flexibility of the pellet-group count method does make it particularly suitable for such changes in scope, a continuity of records from year to year on the same area is also desirable. For one thing, counts on permanently located plots should give better estimates of change in population level from year to year, and thus of trends in population, than do new samples taken each year. (Cochran, 1953). A further important point is that it is often difficult to get the necessary arrangements, plot locations, and so on, set up in the spring sufficiently far ahead of the time when counts can be started. When the plots are permanently located, field biologists can begin visiting them as soon as the snow melts.

A disadvantage to permanently located plots, since the stratification is fixed for a number of years, is losing the chance to take into account over-winter conditions each year. Stratification in a year of deep snows may be considerably different from that in a year of relatively

mild conditions when deer can range far out from heavy cover. It is likely, though, that an intermediate system may prove practicable, where part of the plots are changed annually; various possibilities are discussed in the standard references for sampling (e.g., Cochran, 1953).

Combined surveys. If pellet-group surveys can be conducted simultaneously with those for other purposes, an appreciable reduction of overall effort may be possible. No very explicit studies have been made in Michigan of the advantages of combining other investigations with the pellet-group counts, but I believe that much time and effort may be saved providing the stratification is approximately the same, as it may well be in the case of deer mortality and range surveys, or where it is possible to add an additional feature with little change in the total effort involved.

Errors in pellet-group counting. An obvious and probably the most common source of error in the pellet-group survey is that of missing groups on the sample plots. I suspect that this type of error increases in importance in direct ratio to the amount of area any individual worker tries to cover in a given period of time. A good deal of experience has shown that it does not pay to try to hurry on such a survey. This particular source of error is often insidious, in that the worker can easily decide that things are really going pretty well and that no groups are being missed. There is also evidence that individuals differ appreciably in their ability to detect pellet-groups (Ryel, 1959a).

In 1955, a few biologists attempted to survey the northern Lower Peninsula in a very short period of time. As a result, the estimated population was approximately half of that believed present in the area.

The same degree of error also occurred that year in an area of known population (the George Reserve), but here a recheck of a number of plots (Ryel, 1959a) showed that the original counters had missed a sizable proportion of the groups present.

After 1955, we planned to recheck 20 per cent of the sample plots. Such a system requires that all of the original plots be marked accurately, inasmuch as the counter cannot be permitted to know that only certain plots will be rechecked. Some difficulty was encountered in finding the plots and in being sure that the exact plot outline was used in the recheck. The use of aluminum (or steel) disks to mark all groups found on the first check helped on this score, as did the use of two colors of disks, whereby the "old" (pre-leaf fall) and "new" group classification by the first man was available to the rechecker. In most cases, the recheck results increased the survey estimates by 15 to 20 per cent, but in a few instances apparent mistakes in classification of the age of pellet-groups resulted in decreasing the estimates. In any case, the addition of the recheck not only increased the survey effort by 20 per cent or more, but the added estimation procedure increased the computed sampling error appreciably, inasmuch as the final estimates must include not only the number of pellet-groups present, but also the proportion missed on the first count (Eberhardt, 1957a).

Since the 1959 survey also included searches for dead deer, we used a two-man team, and had the individuals of the team check up on each other, and so did not use a subsequent subsample recheck. So far as we can tell, this procedure worked satisfactorily; at least on the George Reserve it has proved adequate (Ryel, 1959a).

The difficulty in sorting out groups which have been deposited

before the time of leaf-fall might possibly be avoided by clearing the plots of groups just after leaf-fall. This was attempted in two Districts in the fall of 1958, but we found altogether too many groups in the spring of 1959 that were clearly deposited before leaf-fall, and consequently discarded the system. The only sure way of clearing plots is to remove each individual pellet, and we find that this is a great deal more work than the actual survey itself, and must be done with even more care than the final counting, inasmuch as a few missed pellets may well show up in the spring. I do not believe that this doubling of the effort for the survey is justified except perhaps as a special check on overall results.

Effect of over-winter mortality. If any deer die on the survey area between fall and spring, the pellets they dropped will make the estimates represent some sort of an "average over-winter population" rather than a true measure of the spring or fall population. Fortunately, the two major sources of mortality seem to be concentrated in such a manner as to make for useful estimates of fall populations. The effects may be listed as follows:

(1) Legal harvest occurs not long after leaf-fall, and is measured rather accurately; so suitable corrections may be made.

(2) Illegal kills in the hunting season appear to represent a sizable portion of the annual herd mortality, and are not well accounted for. These deer will be present for only about 1/6 of the period covered and will thus not contribute very many pellet-groups to the spring total.

(3) Deer removed by poaching are quite likely taken in greatest numbers before the hunting season and will thus have little effect on the survey.

(4) Losses through starvation occur mainly early in the spring, and when mortality survey data are available, corrections may be used for these losses. We frequently do not have such data, however, and will thus tend to overestimate the size of the spring population on this score, but will come reasonably close to estimating the numbers present in the fall. Quite likely many losses from other causes, including dog-kills, are greatest in the late winter and early spring and thus have an effect similar to that of starvation losses.

In general, it seems that estimates of the fall populations are to be preferred, and the effect of most losses will be in the direction of under-estimation of the fall population level. While this is undesirable, if we must err we would rather err on the conservative side. When results of winter-loss surveys are available, approximate adjustments for winter losses can be made.

Tests of the method. Data on accuracy of the pellet-group count method on Michigan areas of known populations (the Cusino enclosure in the Upper Peninsula, and the George Reserve in southern Michigan) are given in papers by Eberhardt and Van Etten (1956) and Ryel (1959a). A summary of the results is depicted in Figure 2. Confidence limits on the estimates indicate that several of the survey errors have been too large to be due to chance causes alone. Some possible reasons for this are given in the above-mentioned papers. I believe that mistakes in aging pellet-groups and failure to count all groups on the plots are the chief errors.

Comparisons between pellet-group counts on large areas and other population estimates for the same areas are given in Part III of this report, and provide a basis for further appraisal of the method.

The results on areas of known populations indicate that the method

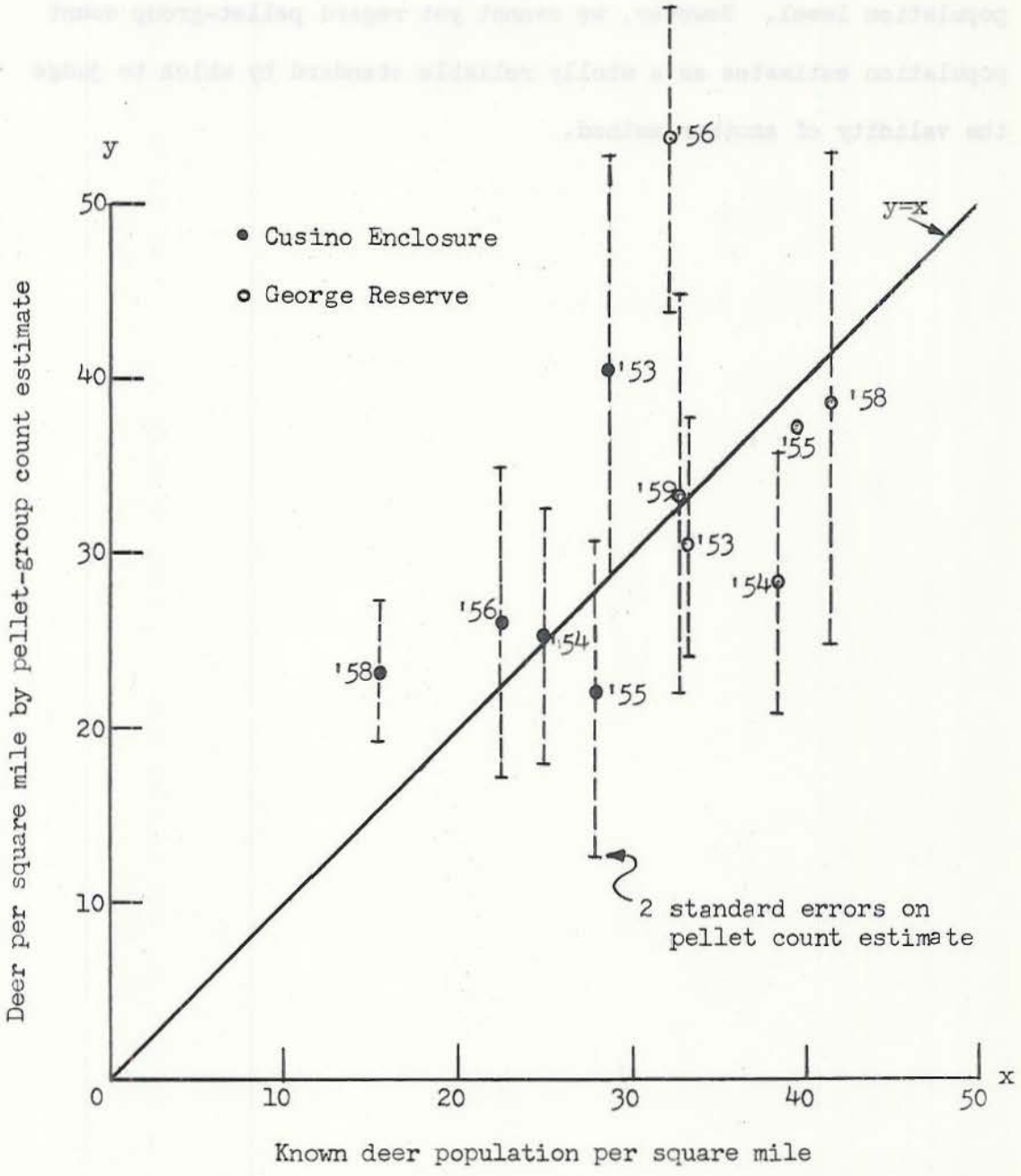
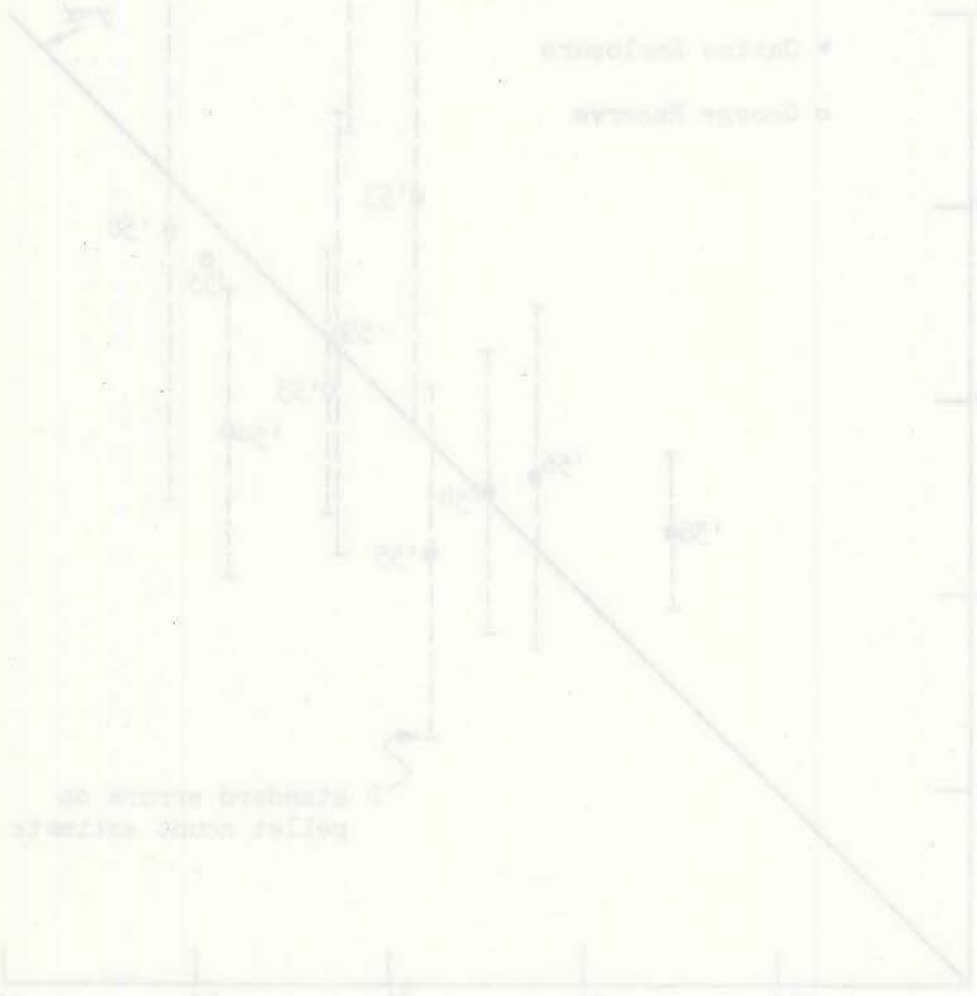


Figure 2. Comparison of pellet-group count estimates with actual populations.

does work, and may provide satisfactory estimates of the actual deer population level. However, we cannot yet regard pellet-group count population estimates as a wholly reliable standard by which to judge the validity of another method.



POPULATION ESTIMATES FROM SEX, AGE, AND KILL DATA

When all sex and age classes are harvested, the ready availability of samples of age and sex structure may provide a means of estimating population size. The hunting regulations prevailing in Michigan during the period covered by this report and a marked difference in the causes of mortality in adult males and antlerless deer make it logical to divide the treatment of such population data into two classes, one dealing with adult bucks only and the other with all deer.

Since in many of the areas and in some of the years covered in this report there have been no seasons on antlerless deer, the data on antlerless deer are less complete than the continuous set available for adult bucks.

This section will thus be split into two parts: (1) Buck population estimates. (2) Total population estimates.

BUCK POPULATION ESTIMATES

Basis of the method. A number of attempts have been made (Ricker, 1958, Beverton, 1954) to estimate animal populations on the basis of a knowledge of the harvest and age structure.

One of the principal problems in forming such estimates is the usually unknown, but often large, loss from causes other than legal harvest. In the case of adult bucks, it seems that such losses are not particularly large and may, in fact, be only a very small proportion of the fall population.

In our extensive mortality surveys (Part IV of this report), we found very few adult male deer. One of the commonest deer hunting stories is that of wounding a buck and tracking it to the point where some other hunter has killed it. However, adult bucks are probably taken out of season by poachers, and we have no adequate means of measuring such losses.

The methods used here to estimate the population of adult males are essentially similar to those known in fisheries work as estimates of "virtual" populations (Ricker, 1958), in which the annual catches of a given year-class are summed until the class disappears from the catch. An important difference in my use of the method is that the natural mortality is unquestionably much smaller than in fish populations. Furthermore, I have used a rough estimate of the natural mortality rate to obtain estimates of the actual total population, and not the minimal values given by adding up the known harvest.

Natural mortality. Mortality from causes other than legal harvest is used here as a constant rate over all years and areas. This is done simply for lack of any better information beyond the mortality-survey evidence that

such losses are small. The rate is applied from the close of one hunting season to the beginning of the next, and is based roughly on the losses recorded in the mortality surveys (Part IV), which cover a period from November to April. Crippling losses from hunting are probably a major factor in such so-called natural mortality.

The estimates of natural mortality of bucks may well be a weak point in the whole procedure. If the natural mortality rate is assumed to be constant, any error in its estimation will result in a proportionate constant change in the calculated population level. Here, as in most of the rest of this report, I do not expect to obtain a precise direct measure of the degree of biases, but can only depend on the comparison of independent estimates to determine overall validity of the population figures. These buck population estimates are used in the next section of this report as a basis for computing total deer populations. In a later section (Part III) comparing the end results with pellet-group count estimates provides a measure of the reliability of the results obtained here.

Chronology. Since hunting is the major mortality factor for adult bucks, it is convenient to start population calculations as of the opening of the deer hunting season. The present mail survey system of determining legal harvest was initiated in 1952. Inasmuch as that year was also the first in which we obtained extensive age samples, the chain of figures used here to obtain buck population estimates begins in 1952.

Essential data and assumptions. The necessary data include age ratios, number of deer legally killed, and hunting effort records, as well as the assumption of a specific rate of natural mortality. Aging must be accurate in at least the separation of $1\frac{1}{2}$-year-olds from older deer, since the

$1\frac{1}{2}$-year-olds are here regarded as "recruits."

A further essential assumption is that the $1\frac{1}{2}$-year-olds are neither more nor less vulnerable than older deer. The possibility of greater vulnerability of the $1\frac{1}{2}$-year-old class does not seem to be a matter for major concern in Michigan (Table 1), although Maguire and Severinghaus (1954) have reported a higher vulnerability of $1\frac{1}{2}$-year-olds in New York. The converse situation, however, is important here inasmuch as a sizable proportion of the Upper Peninsula $1\frac{1}{2}$-year-old class evidently is not as vulnerable as are older deer. Evidently these $1\frac{1}{2}$-year-olds either have antlers less than the 3 inches required by law, or else their antlers are short enough to prevent many hunters from taking a chance on shooting such deer. The existence of this situation is evident in graphs of age distributions of Upper Peninsula bucks (Districts 1 to 4 in Figure 3).

In Figure 3, each line represents the age sample obtained in one hunting season, with the ages arranged in sequence from left to right ($1\frac{1}{2}$ to $4\frac{1}{2}$-year-old classes are shown). The dates given are those of the "year-class," i.e., the points plotted above, say, 1955, represent the bucks born in that year, but examined as $1\frac{1}{2}$-, $2\frac{1}{2}$-, and $3\frac{1}{2}$-year-olds in the hunting seasons of 1956, 1957, and 1958. This arrangement makes it possible to trace the history of one particular year-class through the years of its major contribution to the harvest. The vertical scale is the logarithm of the proportion of each class in each year's sample. Further details of the use of the "catch-curves" are described for fisheries studies by Ricker (1958), and for deer investigations by Hayne and Eberhardt (1952).

The age distributions of Lower Peninsula bucks do not suggest pronounced shortages of $1\frac{1}{2}$-year-olds, and the effects are not apparent in population estimates, while in the Upper Peninsula such estimates simply

TABLE 1

RESULTS OF CHI-SQUARE TESTS OF HETEROGENEITY--FRACTION $1\frac{1}{2}$-YEAR OLDS BY DAY OF SEASON

Area	Year	Number of deer examined	Overall proportion of $1\frac{1}{2}$-year-olds	Proportion of $1\frac{1}{2}$-year-olds on Nov. 15	Chi-square value	Degrees of freedom*	Probability of chi-square value
Upper Peninsula	1955	1,909	.456	.480	6.96	5	$.20<p<.30$
	1957	1,530	.348	.356	4.95	9	$.80<p<.90$
	1958	2,618	.476	.501	16.86	7	$.01<p<.02$
Northern Lower Peninsula	1955	3,027	.620	.616	6.04	5	$.30<p<.50$
	1957	4,132	.659	.669	17.75	9	$.02<p<.05$
	1958	4,370	.694	.699	5.32	8	$.70<p<.80$

*Days combined late in season due to small samples.

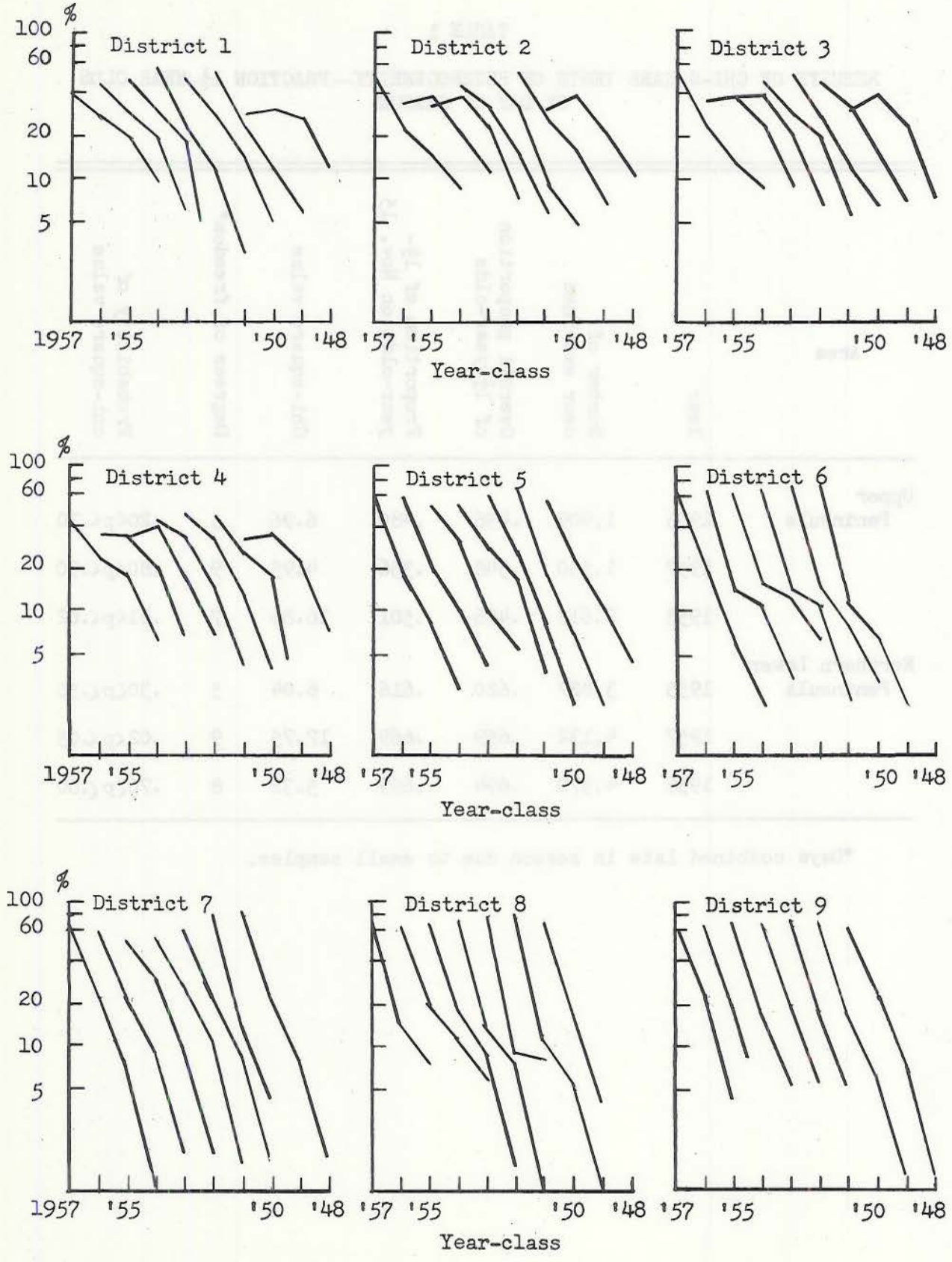


Figure 3. Age composition of legal buck kill. (See text, p. 22.)

do not "work" in most areas and years if one attempts to regard the $1\frac{1}{2}$-year-old class as recruits. However, special season harvests in some overpopulated Lower Peninsula areas yielded appreciable numbers of "short-horn" $1\frac{1}{2}$-year-olds. This may be partly due to a tendency for members of a hunting party to take a chance on bucks with short antlers and to turn any sub-legal kills over to those partners who have special season permits. In the case of special seasons following the regular buck season, the population of legal bucks has been reduced to a point where even a small number of sub-legal bucks will constitute a fairly high proportion of the bucks taken.

The problem of bucks with sub-legal antlers may be partly avoided by dealing initially only with the population of bucks $2\frac{1}{2}$-years-old and older, and later adding legal $1\frac{1}{2}$-year-olds according to their proportion in the harvest. This results in a loss in efficiency by virtue of the additional partitioning of the data, and increased possibility of errors in aging, and yields estimates only of the population of legal bucks.

Valid use of the method described here also requires reliable estimates of buck harvests and hunting pressure. Evaluation of sampling error and of the possible biases in such data is beyond the scope of this paper, but it seems pertinent to note that the hunting data are obtained from an annual mail survey of about 10,000 deer hunters, and the samples for age determination (obtained at highway checking stations) include some 6,000 to 8,000 legal bucks each year (Eberhardt and Fay 1957, 1958, 1959).

The method. The method can best be demonstrated algebraically: Let R_i be the ratio of all adult bucks to those $2\frac{1}{2}$-years-old and older; multiplication by R_i thus increases the population surviving to the beginning of the hunting season ($2\frac{1}{2}$-years-old and older) to include the $1\frac{1}{2}$-year-olds being recruited. Here the subscript, i, indicates the year, beginning

with 1952 and numbering years in series. N represents the population of legal bucks just before the hunting season of 1952, K_i represents the total legal harvest of bucks (including both regular and special seasons), and the survival rate from the end of one hunting season to the beginning of the next is represented by a. This rate (a) is arbitrarily assumed constant throughout at a value of .90.

Population sizes may be shown in a table as follows:

Year	Subscript	Pre-season population (P_i)
1952	1	$P_1 = N$
1953	2	$P_2 = R_2(N-K_1)a$
1954	3	$P_3 = R_3\left[R_2(N-K_1)a-K_2\right]a$
1955	4	$P_4 = R_4\left\{R_3\left[R_2(N-K_1)a-K_2\right]a-K_3\right\}a$

The equations may be expressed in reduced form, giving for 1956:

$$P_5 = R_5R_4R_3R_2Na^4 - R_5R_4R_3R_2K_1a^4 - R_5R_4R_3K_2a^3 - R_5R_4K_3a^2 - R_5K_4a$$

Since R_i and K_i are assumed known from kill data, the equation thus inclues two unknowns, N (the 1952 population) and P_5 (the 1956 population). The equation is indeterminate as it stands. Solutions might be obtained by assuming that a constant proportion is harvested in all years so that more equations than unknowns could be built up from a sequence of years. This scheme is unsatisfactory due to the fact that Michigan hunting pressure does change from year to year, both in regular seasons and as a result of varying special season regulations. There is also evidence (Eberhardt, 1958) that, in at least one year (1954), hunters were less efficient than in other years, harvesting a markedly lower proportion of the available deer, but without detectable changes in hunting effort or weather conditions during the hunting season.

Population estimates may be obtained, however, assuming that the

proportion harvested varies with hunting pressure. Since it seems probable that there is not always a constant relationship between effort and proportion of the legal buck population harvested, I have not attempted to use a fixed or "deterministic" equation, but have rather used subjective adjustments of the population level to obtain a general agreement between hunting effort and computed proportion of the population harvested. Such a procedure requires a starting point, but since a given buck population is virtually all removed in 4 or 5 years the calculated size of the 1952 population is determined within narrow limits by the total legal harvest and the assumed natural mortality rate. This conclusion can be demonstrated numerically by setting up an equation for some given area and trying a few values for the 1952 population. Changes of a few deer, or at most a hundred or so, in 1952 will result in a range of 1957 populations from none surviving to impossibly large numbers. These results cannot, of course, be taken to indicate very precise estimation of the 1952 population; they are precise only in terms of the values used in the equation.

The method provides a direct estimate of the 1952 population size and decreasingly reliable notions as to population levels in subsequent years (i.e., all or nearly all of the bucks alive in 1953 were dead by 1957, so the 1953 population is also closely determined by the equation). In order to provide estimates for all subsequent years, I have assumed the relationship usually postulated between the proportion harvested and hunting effort:

$$p = 1-e^{-kE}$$

where:

p = proportion harvested.

e = base of natural logarithms.

k = a constant representing the proportion of the population taken by one unit of hunting effort (hunter-day).

E = total effort in hunter-days.

Estimates of the hunting effort in the 1952 season were unsatisfactory because of the form of the mail questionnaire; so it is necessary to use 1953 population data to estimate the constant (k) for each area, using the relationship:

$$k = \frac{-\log_e(1-p)}{E}$$

Population estimates have been computed for each of the nine Game Management Districts (Table 2). The graphs (Figure 4) show the assumed relation between effort and proportion of the buck population harvested.

It should be noted that once a 1958 figure has been chosen, the whole sequence of other figures is fixed by the equation containing R_i, K_i, etc., as illustrated above for 1956. This means that the 1952 figures serve as a sort of "pivot," and the subjective element here is in choosing one of a number of possible sequences depending on the 1958 figure finally selected. Some less-subjective method of fitting the data might be preferable (least-squares, for example) but I believe that choice of such a criterion poses a number of questions which cannot be answered at present. What, for example, should be done about the rather consistent deviation of the proportion harvested in 1954? This seems to be due to something other than chance (sampling errors), but I do not know of a criterion other than subjective judgment which could be used in a curve-fitting procedure here.

The kill-effort relationship. The relation of hunting effort to proportion of the population harvested is discussed in more detail later in

TABLE 2

ADULT BUCK POPULATION ESTIMATES BY GAME MANAGEMENT DISTRICTS

A. ESTIMATES BASED ON $1\frac{1}{2}$-YEAR-OLD AND OLDER DEER

District	Year	Nov. 14 Population	Total Kill	Prop. Killed Regular Season	Survivors to Next Year	Surv. Rate	Hunting Effort	R_i
1	1952	12,300	4,660	.379	6,848	.557	-	1.365
	1953	14,230	6,540	.460	6,892	.484	41.1	2.078
	1954	13,410	6,130	.457	6,527	.487	45.6	1.946
	1955	15,150	6,710	.443	7,564	.499	40.8	2.321
	1956	14,460	5,700	.394	7,853	.543	31.9	1.912
	1957	13,840	5,665	.409	7,332	.530	34.8	1.763
	1958	12,030	4,980	.414	6,320	.525	35.4	1.641
6	1952	8,350	6,550	.695	1,613	.193	-	2.962
	1953	7,330	5,297	.685	1,820	.248	96.1	4.543
	1954	6,830	3,981	.559	2,557	.374	86.7	3.755
	1955	8,760	5,680	.648	2,765	.315	85.0	3.428
	1956	7,720	5,064	.637	2,385	.309	100.2	2.794
	1957	7,850	5,105	.650	2,457	.313	94.5	3.290
	1958	8,930	6,600	.739	2,087	.234	104.2	3.634
7	1952	23,590	17,526	.642	5,438	.230	-	3.014
	1953	28,120	19,442	.650	7,782	.277	180.0	5.172
	1954	22,410	12,364	.529	9,006	.402	177.9	2.880
	1955	21,120	12,590	.596	7,644	.362	150.1	2.345
	1956	17,820	9,684	.525	7,290	.409	163.7	2.331
	1957	20,220	12,115	.599	7,265	.359	157.8	2.774
	1958	23,100	14,640	.634	7,584	.328	173.1	3.180
8	1952	9,060	7,740	.731	1,188	.131	-	4.315
	1953	6,580	5,310	.807	1,136	.173	89.7	5.536
	1954	6,160	3,700	.600	2,207	.358	78.5	5.424
	1955	9,810	6,980	.711	2,540	.259	88.3	4.447
	1956	9,210	6,257	.642	2,647	.287	102.6	3.626
	1957	8,050	5,360	.666	2,412	.300	101.4	3.042
	1958	9,990	6,710	.672	2,043	.204	101.0	4.142
9	1952	7,960	6,449	.679	1,351	.170	-	3.012
	1953	5,500	3,790	.689	1,533	.279	88.7	4.072
	1954	6,840	4,590	.671	2,017	.295	103.1	4.463
	1955	7,870	5,830	.741	1,830	.232	109.4	3.902
	1956	7,730	4,988	.631	2,458	.318	126.6	4.224
	1957	8,980	5,635	.628	2,998	.334	125.6	3.654
	1958	10,650	7,990	.750	2,386	.224	139.0	3.553

TABLE 2--Continued

B. ESTIMATES BASED ON $2\frac{1}{2}$-YEAR-OLD AND OLDER DEER

		$2\frac{1}{2}$-year-olds and older					All legal bucks		
District	Year	Nov. 14 Population	Total Kill	Surv. Rate	Hunting Effort	R_1	Prop. $1\frac{1}{2}$-Year-Olds	Total Legal Bucks	Prop. Shot
2	1952	5,650	2,604	.483	-	2.000	.298	8,050	.461
	1953	5,550	2,686	.462	43.6	2.033	.522	11,610	.484
	1954	6,528	2,580	.542	41.9	2.543	.502	13,110	.395
	1955	7,490	3,660	.458	45.8	2.117	.420	12,910	.489
	1956	6,705	3,362	.447	40.2	1.953	.311	9,730	.501
	1957	6,046	2,973	.456	46.0	2.018	.319	8,880	.492
	1958	4,693	2,500	.419	47.6	1.704	.504	9,460	.533
3	1952	7,283	3,320	.488	-	2.024	.301	10,430	.455
	1953	7,772	3,620	.479	51.3	2.188	.454	14,230	.466
	1954	7,814	3,105	.540	44.0	2.100	.508	15,880	.397
	1955	8,273	4,043	.458	47.2	1.960	.458	15,260	.489
	1956	8,333	4,258	.438	48.0	2.198	.346	12,740	.511
	1957	7,330	3,976	.410	54.5	2.007	.321	10,800	.542
	1958	5,558	2,820	.441	55.0	1.849	.514	11,440	.507
4	1952	8,290	4,274	.434	-	1.988	.320	12,190	.504
	1953	7,083	3,798	.416	48.4	1.968	.481	13,650	.553
	1954	7,507	3,471	.482	50.6	2.550	.479	14,410	.468
	1955	8,684	4,896	.391	51.5	2.401	.428	15,180	.572
	1956	8,206	4,356	.420	51.7	2.417	.327	12,190	.585
	1957	7,090	3,537	.449	56.0	2.055	.341	10,760	.544
	1958	5,792	3,598	.339	52.1	1.819	.462	10,770	.621
5	1952	6,022	3,650	.353	-	2.385	.606	15,280	.606
	1953	5,727	2,993	.428	87.7	2.694	.721	20,530	.522
	1954	7,463	3,408	.487	93.4	3.045	.624	19,850	.457
	1955	7,988	5,338	.297	94.4	2.198	.508	16,240	.668
	1956	7,481	4,101	.405	101.5	3.150	.566	17,240	.548
	1957	6,782	3,633	.416	98.1	2.239	.636	18,630	.536
	1958	7,475	3,401	.488	101.8	2.649	.690	24,110	.455

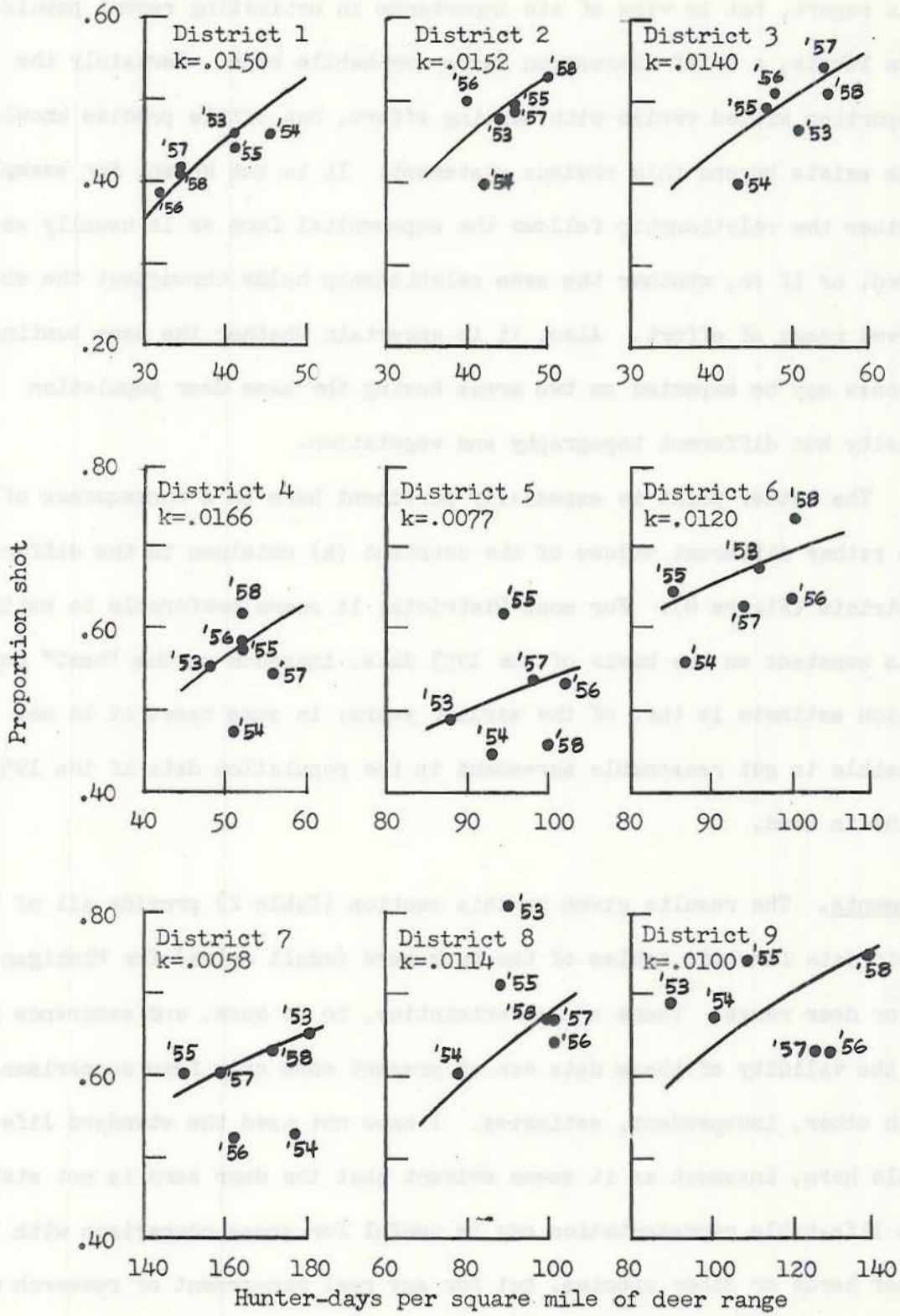


Figure 4. Assumed relations between hunting effort and proportion of buck population harvested. (See text, pp. 28 and 29.)

this report, but in view of its importance in estimating recent population levels, a brief discussion seems worthwhile here. Certainly the proportion killed varies with hunting effort, but little precise knowledge exists beyond this obvious statement. It is not known, for example, whether the relationship follows the exponential form as is usually assumed, or if so, whether the same relationship holds throughout the observed range of effort. Also, it is uncertain whether the same hunting success may be expected on two areas having the same deer population density but different topography and vegetation.

The latter point is especially pertinent here as a consequence of the rather different values of the constant (k) obtained in the different Districts (Figure 4). For most Districts, it seems preferable to estimate this constant on the basis of the 1953 data, inasmuch as the "best" population estimate is that of the earlier years; in some cases it is not possible to get reasonable agreement in the population data if the 1953 value is used.

Comments. The results given in this section (Table 2) provide all of the basic data for life tables of the buck herd (adult males) for Michigan's major deer range. There are uncertainties, to be sure, and assurance as to the validity of these data can at present come only from comparison with other, independent, estimates. I have not used the standard life table here, inasmuch as it seems evident that the deer herd is not static. The life-table representation may be useful for gross comparison with other herds or other species, but for any real management or research use the changing nature of the herd should be measured; dynamics, not statics, ought to be the order of the day.

Several uses of the data in this section are possible. The next

section of this report is principally concerned with further modifications to estimate total deer populations.

As far as practical management is concerned, two points stand out. The first is the marked difference in rates of exploitation between the Upper and Lower Peninsulas. We have long realized that the "U.P." herd is not sufficiently utilized, and the data presented here provide some quantitative measure of this point. The other item is the large numbers of Upper Peninsula 1½-year-old bucks which must have sub-legal antlers (Figure 3). This phenomenon, rather than large changes in size of the herd, may well be the chief reason for marked fluctuations in size of the Upper Peninsula buck harvest in recent years.

ESTIMATES OF TOTAL POPULATIONS FROM SEX, AGE, AND KILL DATA

The method. Deer seasons in which antlerless deer are harvested provide a potential source of data on the overall age and sex structure of the herd. Under Michigan regulations, where such seasons have been either subsequent to the regular season, or limited to relatively small numbers of permittees hunting concurrently in the regular buck season, kill-samples cannot be assumed to represent correctly the proportion of bucks in the pre-season herd. It seems reasonable, however, to assume that there are roughly equal numbers of $1\frac{1}{2}$-year-old bucks and does just before the season, and to use this age-class to connect the two major groups (antlerless deer and adult bucks).

Herd composition data obtained from antlerless deer examined at Michigan roadside checking stations are summarized in Table 3. Records shown there are arranged by study areas (Figure 1) for later comparison with the pellet-group counts on these same areas.

The ratios of all antlerless deer to $1\frac{1}{2}$-year-old does (Table 3), may be multiplied by the estimated numbers of $1\frac{1}{2}$-year-old bucks (computed as in the section on buck populations) to obtain an estimate (Table 4) of total antlerless deer, and, by addition, a total population figure.

Under-representation of fawns. An apparent shortage of fawns in the estimates can be demonstrated by considering the ratio of doe fawns to all adult does in some particular year, and then inspecting the ratio of the same groups one year later (ratio of $1\frac{1}{2}$-year-old does to $2\frac{1}{2}$-year-old and older does). A marked increase in the ratio is apparent in many of the years and on all of the areas. This is most simply interpreted as a

TABLE 3

RECORDS OF AGE AND SEX DATA ON ANTLERLESS DEER EXAMINED AT ROADSIDE CHECKING STATIONS ARRANGED BY STUDY AREA

Study Area	Year	1½-Year Olds	2½-Year-Olds and Older	Fawns		Ratio of Doe Fawns to All Does	Ratio of 1½-Year-old Does to Older Does	Ratio of All Adult Does to 1½-Year-Olds	Ratio of all Antlerless Deer to 1½-Year Olds
				Male	Female				
6	1952	84	253	156	125	.371	.332	4.012	7.357
	1953	54	143	92	81	.411	.378	3.648	6.852
	1954	34	76	32	34	.309	.447	3.235	5.176
	1955								
	1956	32	111	31	50	.350	.288	4.469	7.000
	1957	52	141	42	77	.399	.369	3.712	6.000
	1958	78	188	85	76	.286	.415	3.410	5.474
7	1952	275	762	495	396	.382	.361	3.771	7.011
	1953	254	528	278	283	.362	.481	3.079	5.287
	1954	93	224	91	81	.256	.415	3.409	5.258
	1955								
	1956	71	300	117	125	.337	.237	5.225	8.634
	1957	99	261	129	93	.258	.379	3.636	5.879
	1958	144	356	201	149	.298	.404	3.472	5.903
8	1952	96	221	138	136	.429	.434	3.302	6.156
	1953	71	155	114	104	.460	.458	3.183	6.254
	1954	11	37	18	12	.250	.297	4.364	7.091
	1955								
	1956	70	192	99	85	.324	.364	3.743	6.371
	1957	42	118	69	60	.375	.356	3.810	6.881
	1958	61	116	77	60	.339	.526	2.902	5.148
9	1952	335	767	527	454	.412	.437	3.290	6.218
	1953								
	1954								
	1955								
	1956	127	286	117	93	.225	.444	3.252	4.906
	1957	73	193	80	54	.203	.378	3.644	5.479
	1958	64	158	94	72	.324	.405	3.469	6.062

TABLE 4

POPULATION ESTIMATES FOR STUDY AREAS BASED ON AGE, SEX, AND KILL DATA

Area	Year	1½-Year-Old Bucks	Total Bucks	Total Does	Total Antlerless Deer	Direct Estimate of Population		Adjusted Estimate of Fawns	Adjusted Total Population
						Total	Per Sq. Mile		
6	1952	8,070	13,130	32,380	59,370	72,500	23.8	26,070	71,580
	1953	12,450	17,200	45,420	85,310	102,510	33.6	43,240	105,860
	1954	10,110	16,440	32,700	52,330	68,770	22.5		
	1955	9,150	15,870						
	1956	8,110	14,560	36,240	56,770	71,330	23.4	28,480	79,280
	1957	9,620	14,930	35,710	57,720	72,650	23.8	31,570	82,210
	1958	11,910	17,510	40,610	65,200	82,710	27.1		
7	1952	14,080	21,350	53,100	98,710	120,060	34.7	54,400	128,850
	1953	20,240	25,070	62,320	107,010	132,080	38.2	55,090	142,480
	1954	13,680	20,670	46,640	71,930	92,600	26.8		
	1955	10,880	19,150						
	1956	9,560	16,310	49,950	82,540	98,850	28.6	40,320	106,580
	1957	11,740	18,100	42,690	69,020	87,120	25.2	36,740	97,530
	1958	13,340	19,480	46,320	78,750	98,230	28.4		
8	1952	5,380	8,150	17,760	33,120	41,270	9.9	17,320	43,230
	1953	6,090	7,780	19,380	38,090	45,870	11.0		
	1954	5,800	7,950	25,310	41,130	49,080	11.8		
	1955	6,920	9,970						
	1956	5,560	8,580	20,810	35,420	44,000	10.5	15,780	45,170
	1957	5,610	8,510	21,370	38,600	47,110	11.3	23,940	53,820
	1958	7,510	10,100	21,790	38,660	48,760	11.7		
9	1952	9,430	13,210	31,020	58,640	71,850	11.8		
	1953	7,720	9,950						
	1954	8,730	11,050						
	1955	10,580	13,970						
	1956	12,570	16,940	40,880	61,670	78,610	12.9	32,910	90,730
	1957	11,930	14,460	43,470	65,360	79,820	13.1	37,500	95,430
	1958	13,020	17,540	45,170	78,930	96,470	15.9		

lower vulnerability of fawns to hunting, or as a failure of hunters to take fawns as readily as they do older deer. There are, of course, alternate ways in which such a discrepancy might appear. One is that fawns may be taken in larger numbers than we suspect, but are not brought into roadside checking stations as freely as are larger deer. We have no really conclusive evidence on this point, but experience in a few areas where all hunters have been required to submit their deer for inspection does not show a higher proportion of fawns than elsewhere, and most of our experience on checking stations suggests that many hunters do not realize that such checks are, in fact, voluntary.

Some further discussion of the above point is provided in the section of this report dealing with mortality rates (Part IV). The shortage of fawns seems most pronounced in the areas and years in which sex and age samples have been obtained under concurrent antlerless hunting regulations. Evidence presented in the section on population estimates from kill and effort data shows that hunters in these seasons apparently do not take antlerless deer as readily as they do under subsequent special season regulations; the lower fraction of fawns taken under concurrent regulations may thus be due to hunters "waiting for a bigger deer."

The effect of incomplete representation of fawns in the samples may be further examined by computing fawn population levels from ratios of $1\frac{1}{2}$-year-old does to all older does in the next year. Since male fawns are born in somewhat greater numbers than female fawns, a factor of 2.13 has been used to raise the female contingent to total fawns (i.e., estimated fawn population = 2.13 times ratio times total does). The end-product is shown in the last columns of Table 4, and indicates little

change in total population estimates for the earlier years, but a noticeable difference in later years and areas where concurrent regulations have been in force. A difficulty in the use of such corrections is the implicit assumption that 6-month-old deer survive to $1\frac{1}{2}$ years of age at the same rate that applies to $1\frac{1}{2}$-year-old and older does. Whenever starvation is common, this assumption seems invalid, since the bulk of starved deer invariably are fawns. On the other hand, fawns are not so vulnerable to shooting as adults are. I believe a high mortality in adult does occurs from illegal shooting in the hunting season (Part IV of this report). It seems likely that fawns are less vulnerable to this source of mortality much as they are to legal shooting; hence the greater mortality from starvation may thus be partially canceled out.

The higher numbers of buck fawns at birth may invalidate the assumption of equal numbers of does and bucks at $1\frac{1}{2}$ years of age. No substantial evidence is available for deer, but in many species, the higher ratio of males at birth is compensated by a higher male mortality rate. We have no way of knowing at present whether such a differential exists for deer between 6 months and $1\frac{1}{2}$ years of age. For simplicity, I have taken the ratio of males to females at $1\frac{1}{2}$ years of age to be unity. Correction for an excess of males would decrease the estimated total population size somewhat.

Up to the present time, only small samples of antlerless deer have been obtained in the Upper Peninsula. A further obstacle is the evident shortage of $1\frac{1}{2}$-year-old bucks in the legal harvest. Crude estimates of the proportion of sub-legal $1\frac{1}{2}$-year-olds might be made, but the combination of this problem and the small samples make Upper Peninsula population estimates by this method of questionable accuracy.

Estimates of populations by Game Districts (Table 5) have also been prepared from the sex, age, and kill data in the same manner as described above.

Herd composition from roadside counts. Another possible source of data on herd composition exists in the "Summer Deer Counts" made by Conservation Department personnel from July to October of each year. There seems, however, to be no correlation between the ratio of antlerless deer to bucks as observed in these counts and the ratios obtained here. A comparison by study areas is given in Table 6 and Figure 5. Failure to find a correlation may well be due to the fact that many of the records are obtained under uncertain conditions by observers who, though conscientious, are perhaps unable to carry out the very careful observation needed for accurate classification. It is often very difficult to detect a buck's antlers against a wooded background even with good binoculars and a steady rest, so that it seems highly doubtful that records made from a moving automobile can be considered valid.

TABLE 5

ESTIMATES OF DISTRICT DEER POPULATIONS BASED ON SEX, AGE, AND KILL DATA

District	Year	Adult Does	Fawns	1½-Year-Old Does	Proportion 1½-Year Old Bucks	Buck Population Estimates	Total Population	Deer Per Square Mile
5	1952	347	287	87	.606	15,280	82,620	18.7
	1953	203	178	57	.721	20,530	119,340	27.0
	1954	110	66	34	.624	19,850	84,820	19.2
	1955				.508	16,240		
	1956	146	82	33	.566	17,240	84,910	19.2
	1957	222	149	58	.636	18,630	94,580	21.4
	1958	280	169	85	.690	24,110	112,140	25.4
6	1952	399	370	111	.662	8,350	46,650	13.8
	1953	320	282	96	.780	7,330	43,110	12.8
	1954	71	45	18	.734	6,830	39,960	11.8
	1955				.708	8,760		
	1956	303	221	74	.642	7,720	42,920	12.7
	1957	162	109	43	.696	7,850	42,190	12.5
	1958	199	159	65	.725	8,930	44,450	13.2
7	1952	1,183	1,005	306	.668	23,590	136,380	39.3
	1953	841	585	288	.807	28,120	140,620	40.5
	1954	380	192	108	.653	22,410	100,050	28.8
	1955				.574	21,120		
	1956	357	216	73	.571	17,820	97,900	28.2
	1957	399	252	114	.639	20,220	94,060	27.1
	1958	580	380	160	.685	23,100	117,880	34.0
8	1952	1,164	1,065	360	.768	9,060	52,100	12.7
	1953				.819	6,580		
	1954				.816	6,160		
	1955				.775	9,810		
	1956	1,008	508	285	.724	9,210	44,710	10.9
	1957	709	423	211	.671	8,050	37,110	9.0
	1958	574	420	195	.758	9,990	48,630	11.9
9	1952	595	474	153	.668	7,960	45,100	17.6
	1953				.754	5,500		
	1954				.776	6,840		
	1955				.744	7,870		
	1956	105	61	30	.763	7,730	40,630	15.9
	1957	73	44	15	.726	8,980	59,010	23.1
	1958	82	59	24	.718	10,650	56,170	22.0

TABLE 6

RATIOS OF ANTLERLESS DEER TO BUCKS AS COMPUTED FROM TWO SOURCES

Study Area	6		7		8		9	
Year	Kill Data	Summer Counts	Kill Data	Summer Counts	Kill Data	Summer Counts	Kill Data	Summer Counts
1952	4.53	8.72	4.62	6.14	4.07	6.00	4.44	5.84
1953	4.96	5.90	4.27	4.28	4.89	5.18		5.44
1954	3.18	6.89	3.48	5.77	5.18	4.50		4.73
1955		5.64		5.90		4.47		4.75
1956	3.90	5.50	5.06	6.19	4.13	3.34	3.64	5.68
1957	3.86	6.95	3.81	5.88	4.54	4.58	4.53	6.44
1958	3.72	6.48	4.04	4.98	3.83	5.30	4.50	4.88

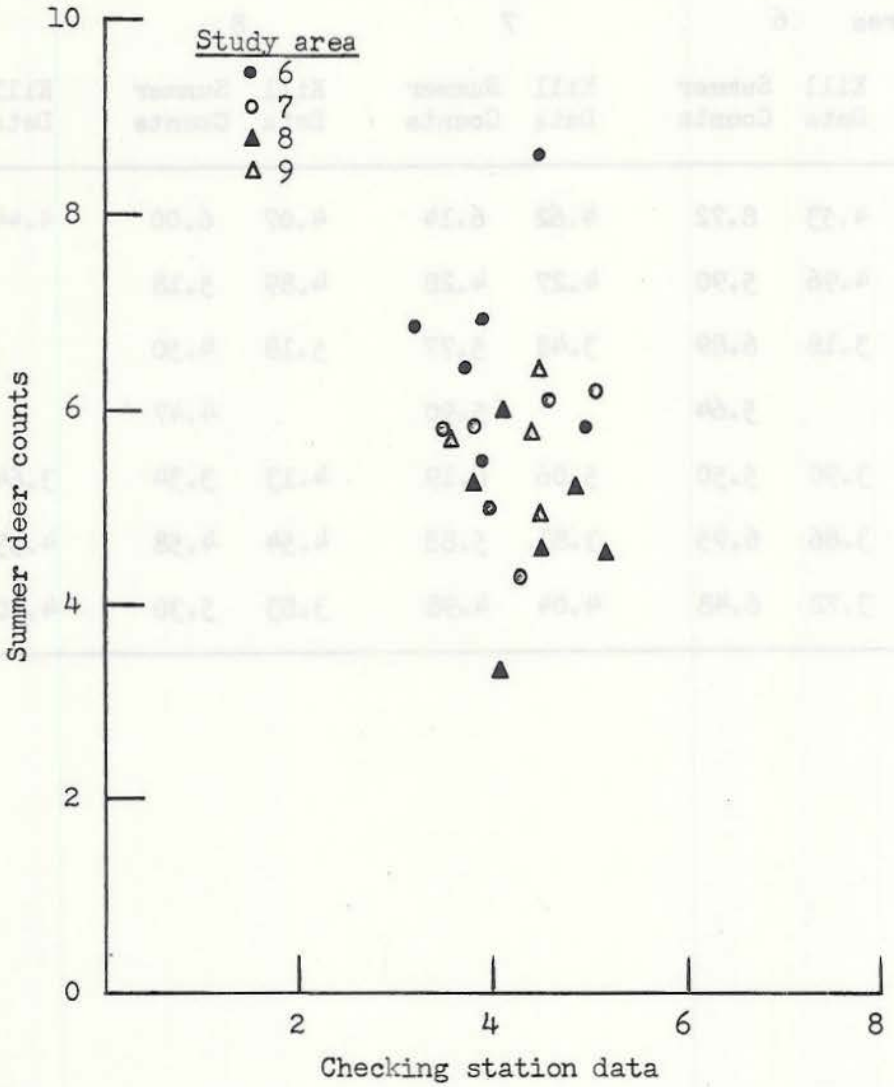


Figure 5. A comparison of annual ratios of antlerless deer to bucks as computed from two sources (see Table 6).

POPULATION ESTIMATES FROM KILL AND EFFORT DATA

Introduction. Although hunting success is commonly used in wildlife management as a measure of hunting conditions, its relationship to actual population level has seldom been considered for deer populations. Fisheries workers have made considerably more use of "catch-effort" relationships to estimate population levels. Ricker (1958) reviews the methods in use and gives various equations and examples. Probably the most comprehensive treatment, however, is still that of DeLury (1947, 1951), whose results are used here. He gives two equations, both of which require a knowledge of catch or kill by time periods and of the corresponding effort expended. The equations are as follows (using DeLury's notation):

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

$$\log_e C(t) = \log_e kN(0) - kE(t)$$

where:

$C(t)$ = kill or catch per unit of effort at time t.

$N(0)$ = initial population.

$K(t)$ = cumulative kill up to the t^{th} period of time.

k = a constant representing the proportion of the population taken per unit of effort.

DeLury (1947) develops the above equations from a differential equation representing the instantaneous relation between kill and effort, and alternatively, from a simple statistical model. As he points out (1947, p. 165), the distinction between a continuous and discrete model is unimportant so long as k is some very small fraction, as it will ordinarily be in the data discussed here. A difference from the basic situation treated by DeLury is that his development permits a single unit

of effort to take more than one unit of the population, while in deer hunting, a hunter presumably does not take more than one deer. In actual practice, of course, members of a hunting party sometimes do shoot more than one deer, but a model corresponding to the legal definition of deer hunting does result in a close approximation to DeLury's first equation (see appendix to this report).

DeLury does not consider the relationship between the constant, k, and the area or space in which the exploited population lives. Beverton (1954) includes the idea of area covered, and shows that population density per unit area is the essential consideration. All calculations and comparisons made here are standardized on a per-square-mile basis.

Nearly all of the records used here have been obtained from sample surveys by mail (involving responses from about 10,000 hunters each year), so the data are necessarily subject to sampling errors. Since the kill and effort data come from the same set of mail survey cards, there will not only be sampling errors in each of the variables used in the above equations, but the errors will also be correlated, presenting difficulties in estimation, including the possible attenuation of the regression coefficient (Yates, 1953) if the usual (DeLury, 1947, Ricker, 1958) practice of estimating k and N(0) through linear regression methods is followed. I have not made detailed attempts to do anything about this difficulty, since, as is shown in the balance of this section, the information thus far available is insufficient to produce a wholly satisfactory model for the estimation of populations through kill-effort relationships.

Sizable fractions of the population are taken in the first few days of the hunting season. Since data are available only on a daily basis, there is the further problem that the kill per unit effort will change

considerably during the day, and the value observed will be an average of C(t), rather than the instantaneous value used in development of the models. This difficulty is described by DeLury (1947, p. 162) and Ricker (1958, p. 146), and no satisfactory alternative seems to be available. The practice of grouping time periods together to give approximately equal amounts of effort should ordinarily minimize the effect, as is suggested by DeLury and by Ricker.

Uses of the data on kill and effort may be treated in several categories. One of these has already been considered in the section on buck population estimates, where hunting effort was used to adjust the adult buck population trend. It was also noted in that section that the constant, k, apparently differs among the major deer-hunting areas.

Estimating buck populations. DeLury (1947) recommends the first of the equations given above for estimating population sizes. The equation is "fitted" by linear regression methods, with K(t) taken as the cumulative kill up to the day on which C(t) is measured (DeLury, 1947, page 162). Using these procedures (and grouping days to give roughly equal amounts of effort), buck populations have been computed for each of the nine Districts in the major deer range (Figure 1) for the years 1953 to 1958. Records for the first day of the season were not used since the value of C(t) for this day is almost always out of line with the other days of the season.

In almost every case, the estimates of population size are markedly lower than those previously obtained (section above on population estimates from age and kill data), and are appreciably lower than the age data indicate to be possible. That is, if natural mortality is assumed to be non-existent, a minimal population can be computed by adding up the harvest

until the youngest age-class in some given year practically disappears from the kill (in 4 or 5 years in the Lower Peninsula). This procedure will give a maximal harvest estimate. These maximum harvest proportions are consistently less than those indicated by the kill-effort method, so it seems clear that the method underestimates the true population size.

These population estimates do, however, seem to follow population trends fairly well in the Lower Peninsula, as shown by their relation to the estimates from age and kill data (Figure 6). The position of the individual points with relation to a line of one-to-one correspondence (of population estimates) indicates that the kill-effort estimates almost always underestimate the other values. There also seems to be a rough grouping of areas, with Districts 6, 8, and 9 coming closest to agreement, Upper Peninsula Districts intermediate, and Districts 5 and 7 at the extreme.

Opening day hunting success. As mentioned above, opening day success is consistently higher than it should be to conform with the trend of the regression line. Graphs for several years are shown in Figure 7. When hunting success on the first day of the season is contrasted with population estimates from the age and kill data (Figure 8), there again seem to be consistent differences between areas of the state, with District 7 showing much lower success than is to be expected on the basis of population level.

Estimates of k from different sources. Average values of the proportion (k) of the population shot per hunter-day computed from the age-kill and kill-effort data appear closely related (Figure 9). Evidently k declines with increasing hunting pressure.

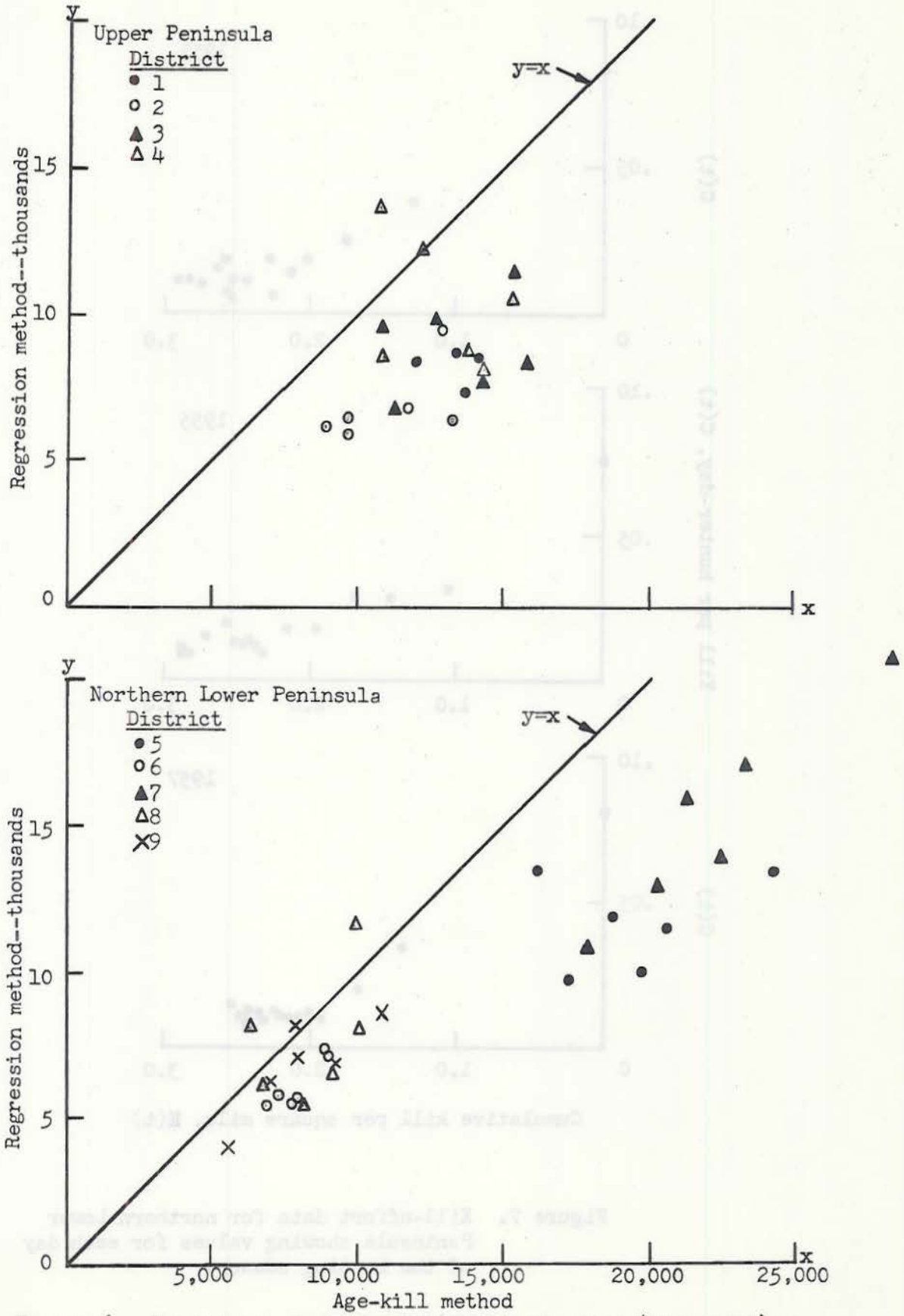


Figure 6. Comparison of buck population estimates (1953-1958) as obtained by two methods.

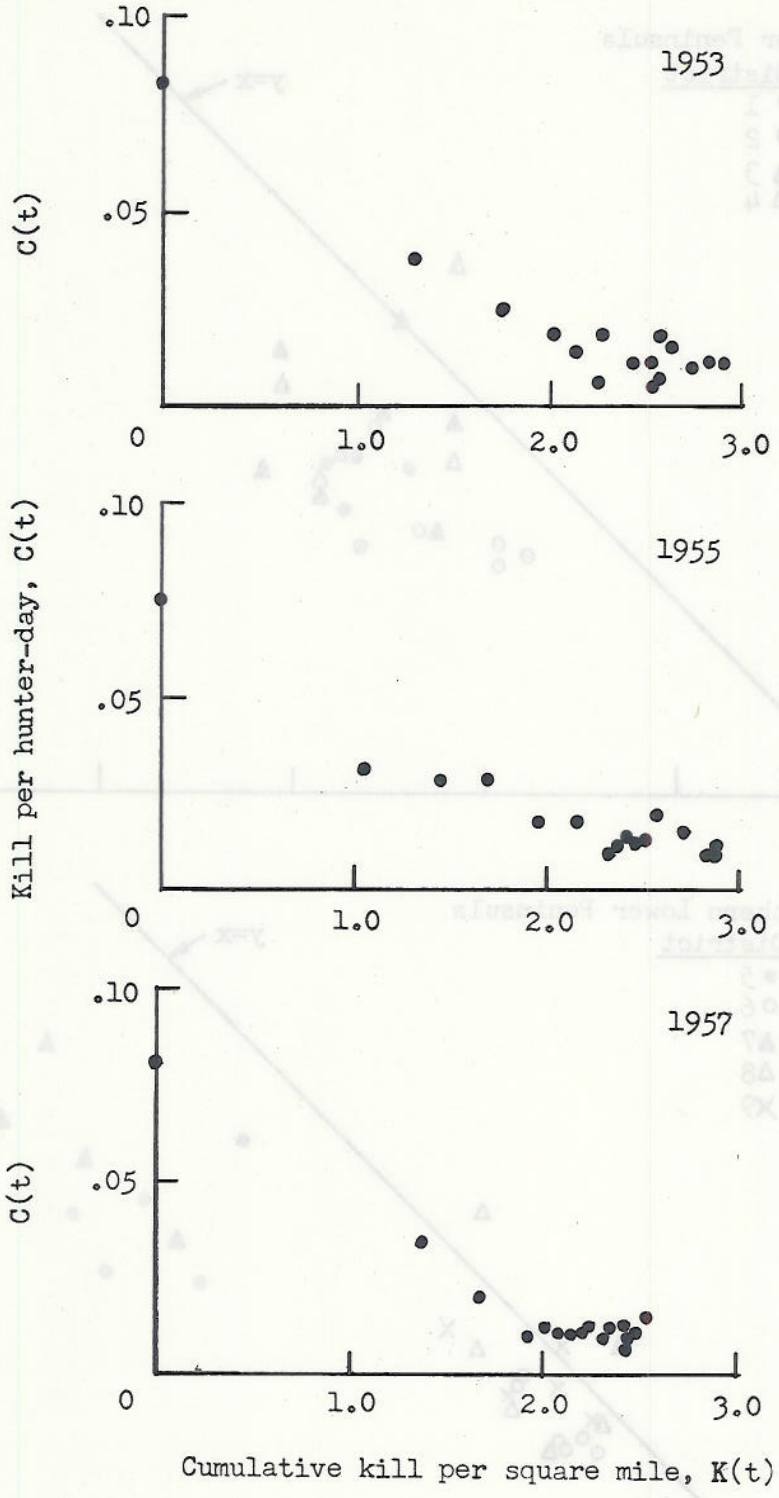


Figure 7. Kill-effort data for northern Lower Peninsula showing values for each day of the hunting season.

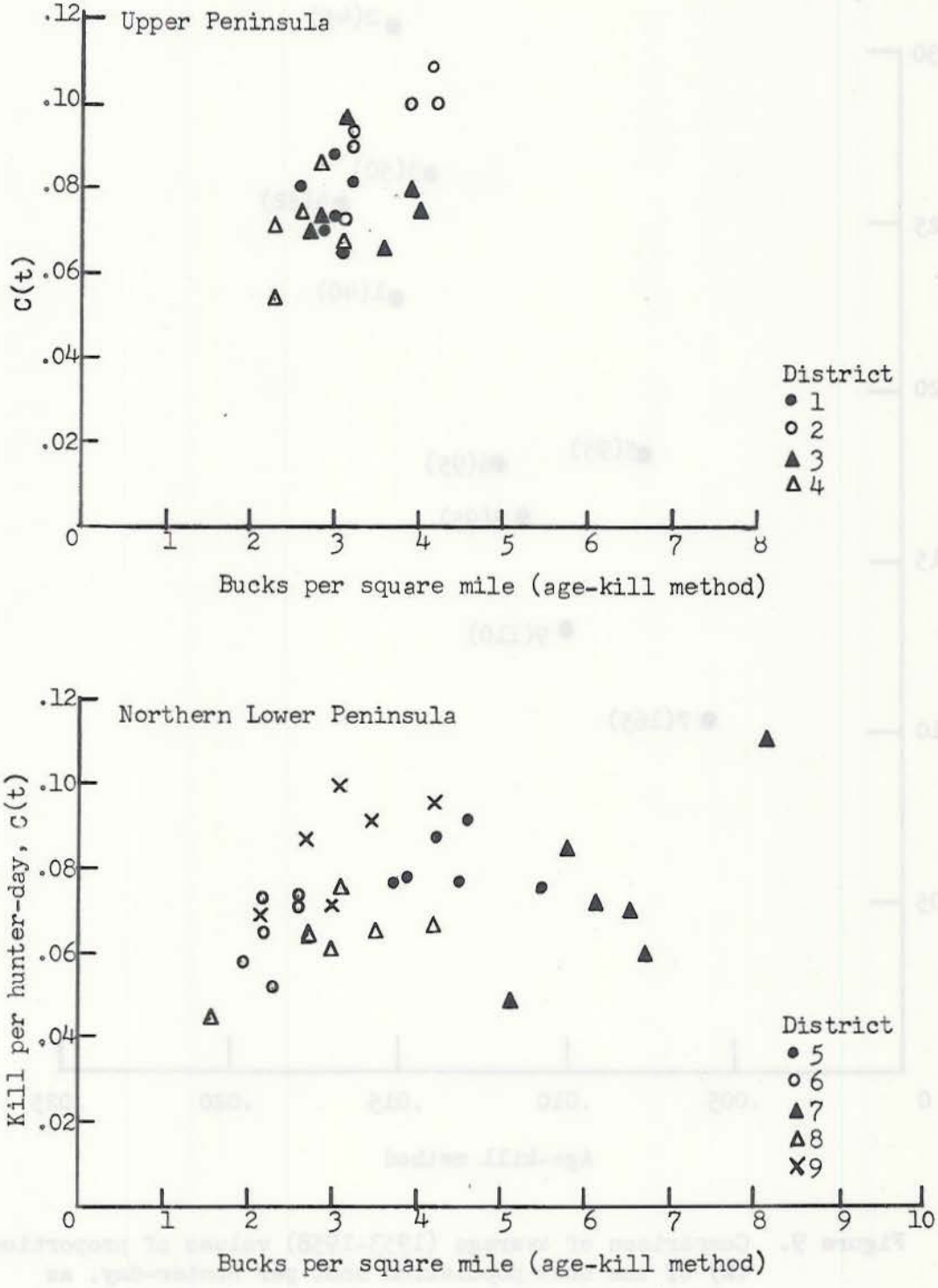


Figure 8. Kill per unit effort on opening day (November 15) vs. buck population level (1953-1958).

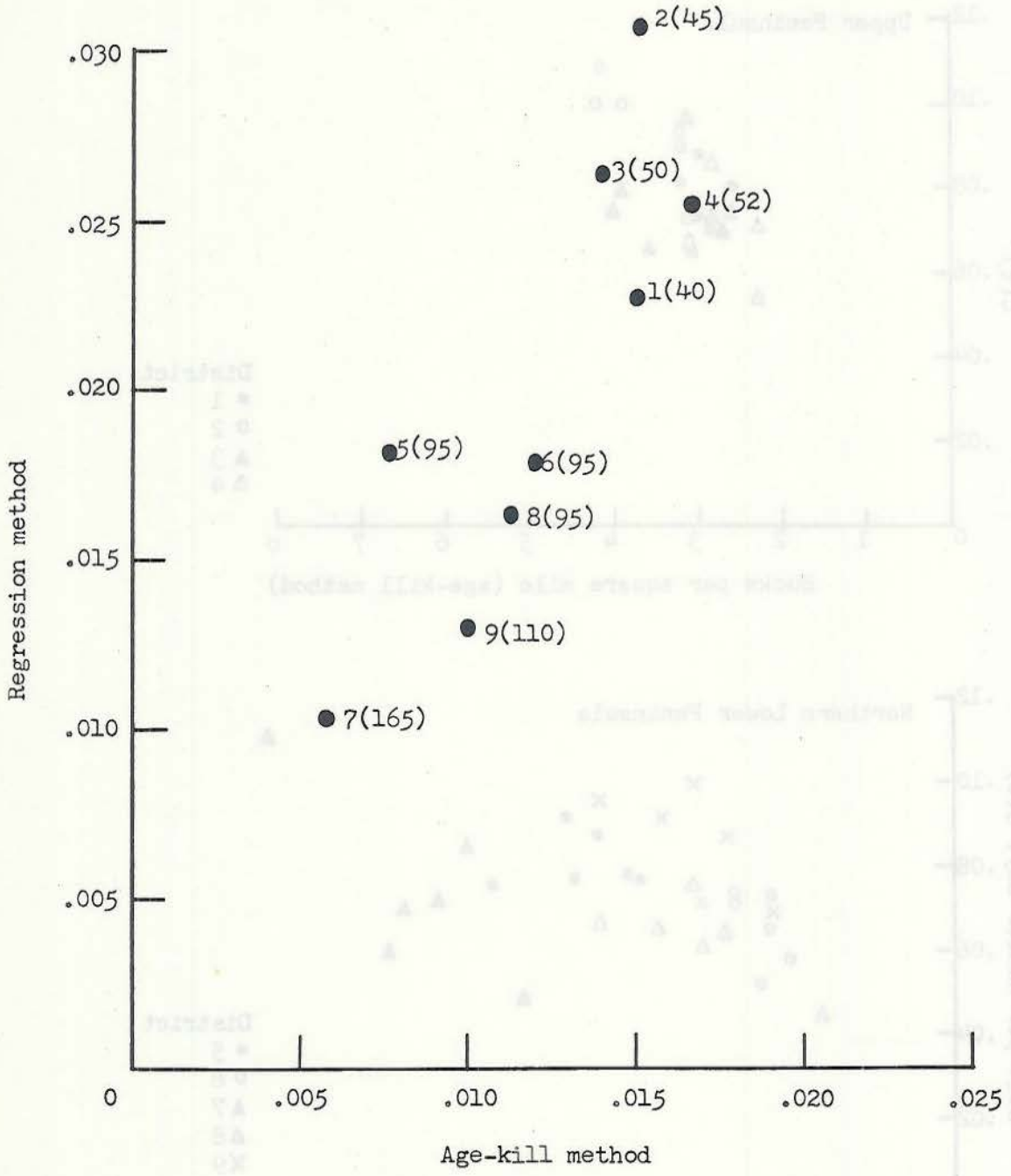


Figure 9. Comparison of average (1953-1958) values of proportion (k) of the buck population shot per hunter-day, as estimated through two methods. The first number at each point represents the Game Management District, while the number in parenthesis gives the median number (1953-1958) of hunter-days per square mile for the District.

Other factors possibly influencing the value of k are those associated with the difference in type of cover and in the types of hunting employed in the several areas. Many Lower Peninsula hunters depend on the presence of other hunters to keep the deer moving, but in most Upper Peninsula areas, only organized "drives" can be counted on for this purpose, and techniques of still-hunting and waiting by runways tend to be more important.

One might go to great lengths to ascribe the observed differences in k to variations in hunter ability, relative areas of dense swamp, and so on, but any really objective analysis will probably have to wait for careful field studies or controlled experiments. Such studies will be difficult at best, but will also be important as a check on the validity of hunter reports.

Some data is now available on two areas where trained observers keep daily hunting records. These are the fenced square-mile experimental area at the Cusino Wildlife Experiment Station, and the 7.5-square-mile Rifle River Area. Locations of these areas are shown in Figure 1; the Cusino area has been described by Van Etten (1957) and the Rifle River Area by Howe (1954). The Cusino area is maintained as an experimental area, where the herd is censused repeatedly to provide accurate population figures. Experimental hunts have been used to maintain the desired population levels since 1954, and three year's data on the results are given by Van Etten (1957). The small size of the area permits harvest of only a few deer each year, so precise measures of kill-effort relationships cannot be obtained there. Estimates of k computed from Van Etten's data are:

Year	Type of Season	Length of Season in Days	Hunter-days E(t)	Initial Population N(o)	Harvest K(t)	Estimate of k
1954	Any adult deer	4	25	21**	4**	.008
1955	Bucks only	7	54	10	7	.022
1955	Any-deer*	1	7	29	3	.016
1956	Bucks only	2	17	5	1	.013
1956	Any-deer*	4	25	25	9	.018

*Following buck hunting.
**Adult deer only; shooting of fawns stopped after 1st day.

The Rifle River Area is a Lower Peninsula area with extremely high hunting pressure, but exact census data are not available. Hunters must check in and out of the area, and since only one access road is for the general public, precise records on hunting pressure are obtained.

Estimates of k from eye-fitted regression lines are given for the Rifle River Area in Table 7. Hunting pressure figures used here are based on the number of daily permits issued, but the average daily length of hunt is about that observed at Cusino. The average value of k (.0078) for the Rifle River Area falls between those already estimated (Figure 9) for District 7, in which the area is located. This seems reasonable according to the relationship exhibited in Figure 9, since hunting pressure at the Rifle River Area is higher than in District 7 generally.

Changes in vulnerability. Results given above show that the regression method apparently seriously overestimates the proportion (k) of the population taken per unit of effort (hunter-day). The relationship (Figure 7) of the kill per unit effort, C(t), to the cumulative kill, K(t), seems to be more nearly curvilinear than straight, with a rapid drop early in the season and a tendency to level off as the season progresses. Since k is the slope of a line through the plotted points, it seems that k decreases as the hunting season advances.

TABLE 7

BUCK HUNTING DATA FROM THE RIFLE RIVER AREA

Year	Hunter-days Per Square Mile	Estimate of k	Hours Per Hunter Day
1945	167.6	.0086	5.4
1946	205.9	.0122	5.1
1947	193.8	.0080	4.8
1948	146.1	.0086	5.1
1949	159.3	.0077	4.8
1950	173.4	.0080	5.0
1951	119.0	.0098	4.4
1952	112.5	.0060	4.8
1953	282.7	.0060	5.8
1954	231.2	.0047	5.0
1955	196.9	.0066	4.9
Average	180.8	.0078	

Behavior of k as the season progresses may be shown more precisely by rewriting the first equation given in this section as:

$$k = \frac{C(t)}{N(0) - K(t)}$$

and using the buck population estimates from age-kill data for N(0), and the kill-effort records for C(t). A difficulty here is that since C(t) is actually a mean value for each day, the above equation tends to underestimate k. This may be demonstrated by obtaining a mean value of C(t) from the exponential relationship (DeLury, 1947):

$$C(t) = kNe^{-kE(t)}$$

Where N now represents the population at the beginning of the day, and E(t) represents the effort cumulated from the beginning of the day to some time, t, during the day. The mean value of C(t) is:

$$\bar{C}(t) = \frac{1}{E}\int_0^E kN\, e^{-kE(t)}\, dE(t) = \frac{N}{E}\left\{1-e^{-kE}\right\}$$

so that the estimate of k (now represented by k' to distinguish it as an estimate) is:

$$k' = \frac{\bar{C}(t)}{N(0) - K(t)} = \frac{1}{E}\left\{1-e^{-kE}\right\}$$

since $N(0) - K(t) = N$, the population at the beginning of the particular day of interest. When kE is small, k' is very close to k, as shown by the series expansion of $1 - e^{-kE} = kE - \frac{(kE)^2}{2!} + \frac{(kE)^3}{3!} - \ldots$; for small kE the power terms are negligible and k' is practically identical to k, but if kE is on the order of .1 to .3 (as it is in the first few days of the season), then k' becomes an underestimate of k. This means that values of k' obtained for the first several days of the season are appreciably lower than the true values, but later in the season kE becomes

small and k' approaches the true value.

Values of k' are shown in Figure 10 for the Upper and northern Lower Peninsulas. There is evidently a marked drop in vulnerability from opening day (November 15) to at least November 20th. Daily values of k' for the years 1953 to 1958 (Figure 11) show a definite tendency for k' to level off later in the season. Unfortunately, so little hunting occurs late in the season that the data are highly variable and offer little promise for population estimation. The leveling-off of values of k' provides further evidence that the initial decline in k' is not simply a consequence of overestimation of the population from the age-kill data. If the population were overestimated, k' would decline throughout the season, and conversely, if the population were underestimated, there would be a tendency for k to increase throughout the season (see beyond).

Appraisal of changes in vulnerability. The drop in k' evidently represents a decreasing vulnerability of surviving deer as the season advances. One possibility is that the youngest age group ($1\frac{1}{2}$-year-olds) may be more vulnerable than older deer, so that as these animals are shot off, overall vulnerability decreases. Such a situation would necessarily be accompanied by a decrease in the proportion of $1\frac{1}{2}$-year-olds in the harvest, but it has been shown (Table 1) that this evidently does not occur in any great degree.

Another possibility is that deer in relatively open areas are more vulnerable to hunting and are taken early in the season, and that late season hunting is largely confined to heavy cover, where deer are harder to shoot. Also, survivors of the first few days of hunting may tend to enter heavy cover and stay there during the daylight hours. There are

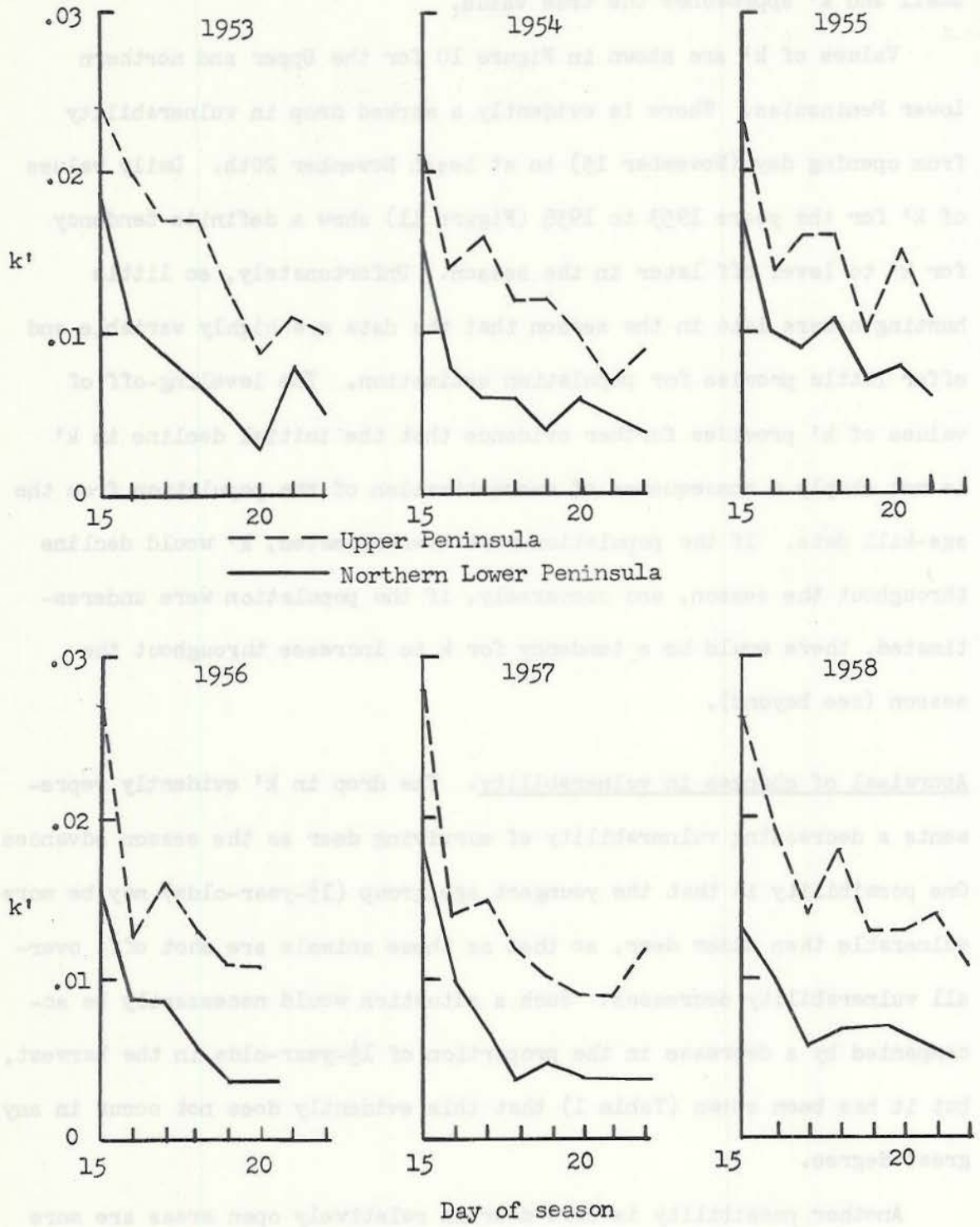


Figure 10. Daily estimates of proportion (k) of the buck population shot per hunter-day.

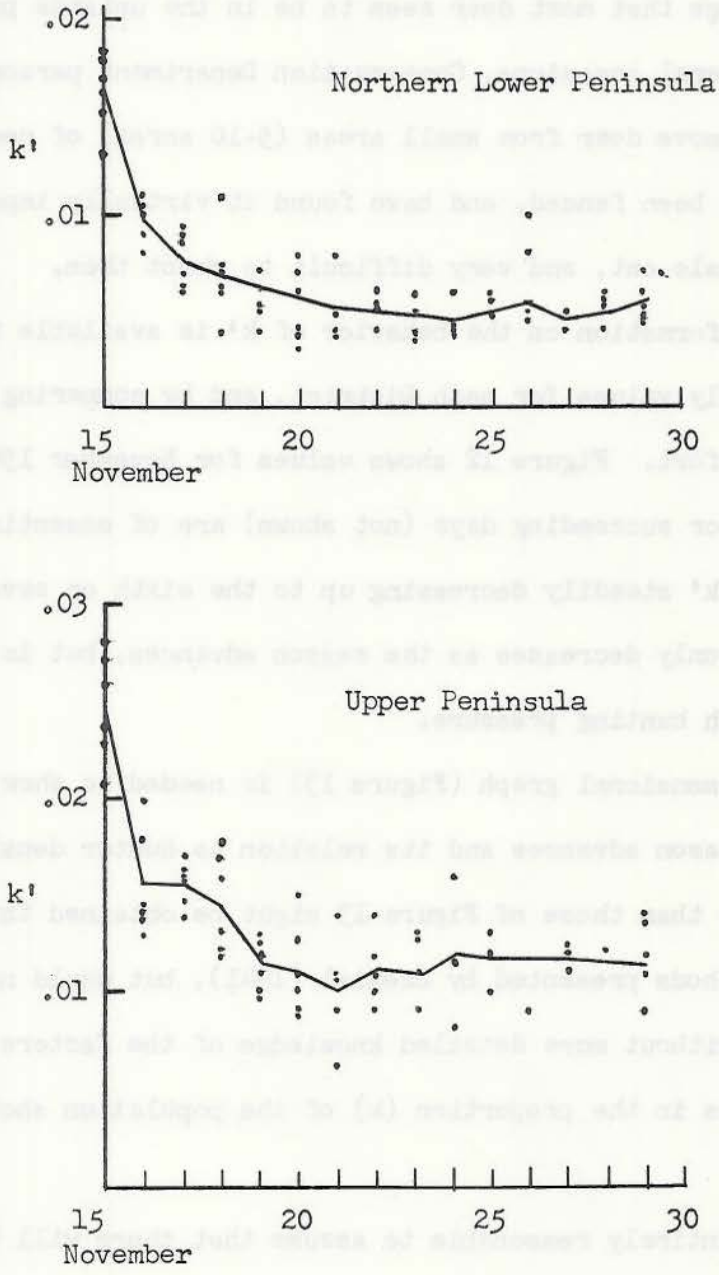


Figure 11. Combined (1953-1958) daily estimates of proportion (k) of the buck population shot per hunter-day. The curves were plotted from median values of k'.

few concrete data on deer behavior during the hunting season, beyond the general knowledge that most deer seem to be in the uplands prior to the season. On several occasions, Conservation Department personnel have attempted to remove deer from small areas (5-10 acres) of cedar swamp which have just been fenced, and have found it virtually impossible to drive such animals out, and very difficult to shoot them.

Further information on the behavior of k' is available through computation of daily values for each District, and by comparing these values with hunting effort. Figure 12 shows values for November 15th (opening day). Graphs for succeeding days (not shown) are of essentially the same form, but with k' steadily decreasing up to the sixth or seventh day. Evidently k' not only decreases as the season advances, but is also lower in areas of high hunting pressure.

A three-dimensional graph (Figure 13) is needed to show both behavior of k' as the season advances and its relation to hunter density. More precise results than those of Figure 13 might be obtained through use of some of the methods presented by Ezekial (1941), but would not be particularly useful without more detailed knowledge of the factors responsible for fluctuations in the proportion (k) of the population shot per unit of effort.

It seems entirely reasonable to assume that there will be a tendency for hunters to interfere with each other and reduce individual efficiency with increasing numbers of hunters per unit area, as suggested in Figure 13, but there is also a possibility that some of the observed differences in k' may be associated with relative amounts of dense cover in the various Districts, or be due to errors in estimating population level.

Maximum harvest rates. An important further consideration here is the

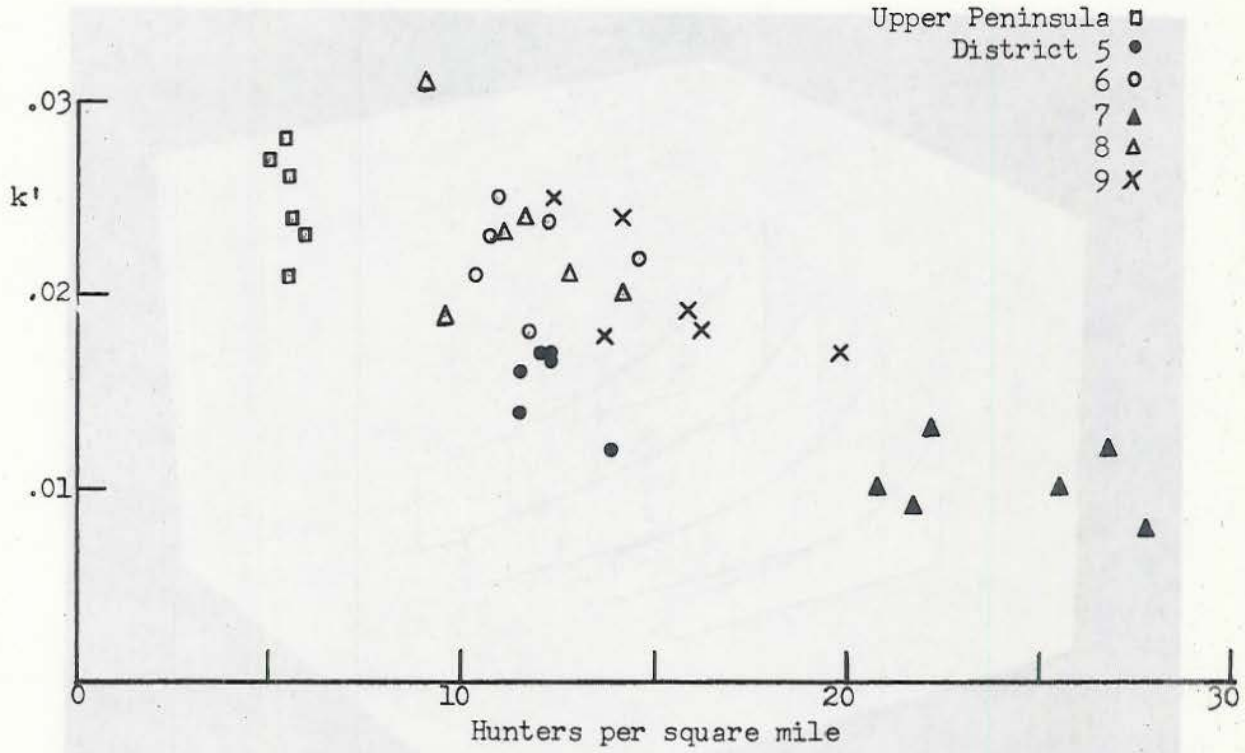


Figure 12. Estimates of the proportion (k) of the buck population shot per hunter-day on opening day of deer season (November 15) as compared to hunting pressure (1953-1958).

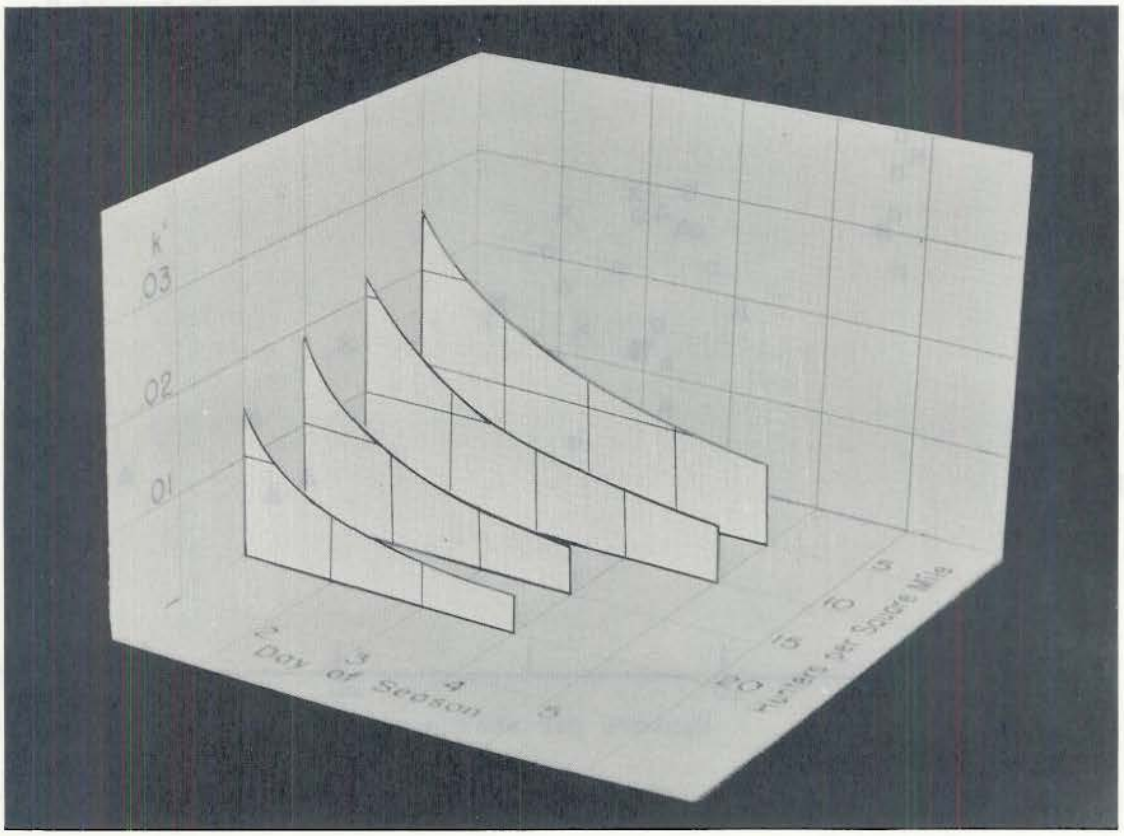


Figure 13. Joint effect of day of season and hunter density on k'.

point at which increasing hunter densities may cease to yield an increase in deer kill. Using the equation given previously (age-kill section):

$$1 - p = e^{-kE}$$

where p is the proportion of the population harvested, and plotting the product $k'E$ against hunting effort should indicate whether increasing effort will take an increasing fraction of the population. Since k' is a biased estimate of k (due to the use of an average value of C(t) obtained by dividing the kill for a given day by the effort expended in that day), the values plotted for $k'E$ (Figure 14) are, in fact, actually the proportion (p) of the available population harvested in that day rather than the exponential index (kE) of the equation above.

In any case hunting densities beyond about 15 hunters per square mile (Figure 14) apparently do not result in much increase in the proportion of the population harvested, the maximum proportion seeming to be about .30 on the first day of the season.

Effects of errors in estimating population size. The effects of errors in the estimation of population size on estimates of k may be examined rather simply if the bias in the estimator k' is disregarded for this purpose. The estimating equation is:

$$\hat{k} = \frac{C(t)}{N(0) - K(t)}$$

and, substituting N' as the estimate of N(0), and the defined value of C(t):

$$\hat{k} = \frac{k\{N(0) - K(t)\}}{N' - K(t)}$$

Further, let $B = \frac{\hat{k}}{k}$ = the ratio of the estimated value of k to the true value, p = proportion of the population shot at time t, and $R = \frac{N'}{N(0)}$ = ratio of estimated to actual population.

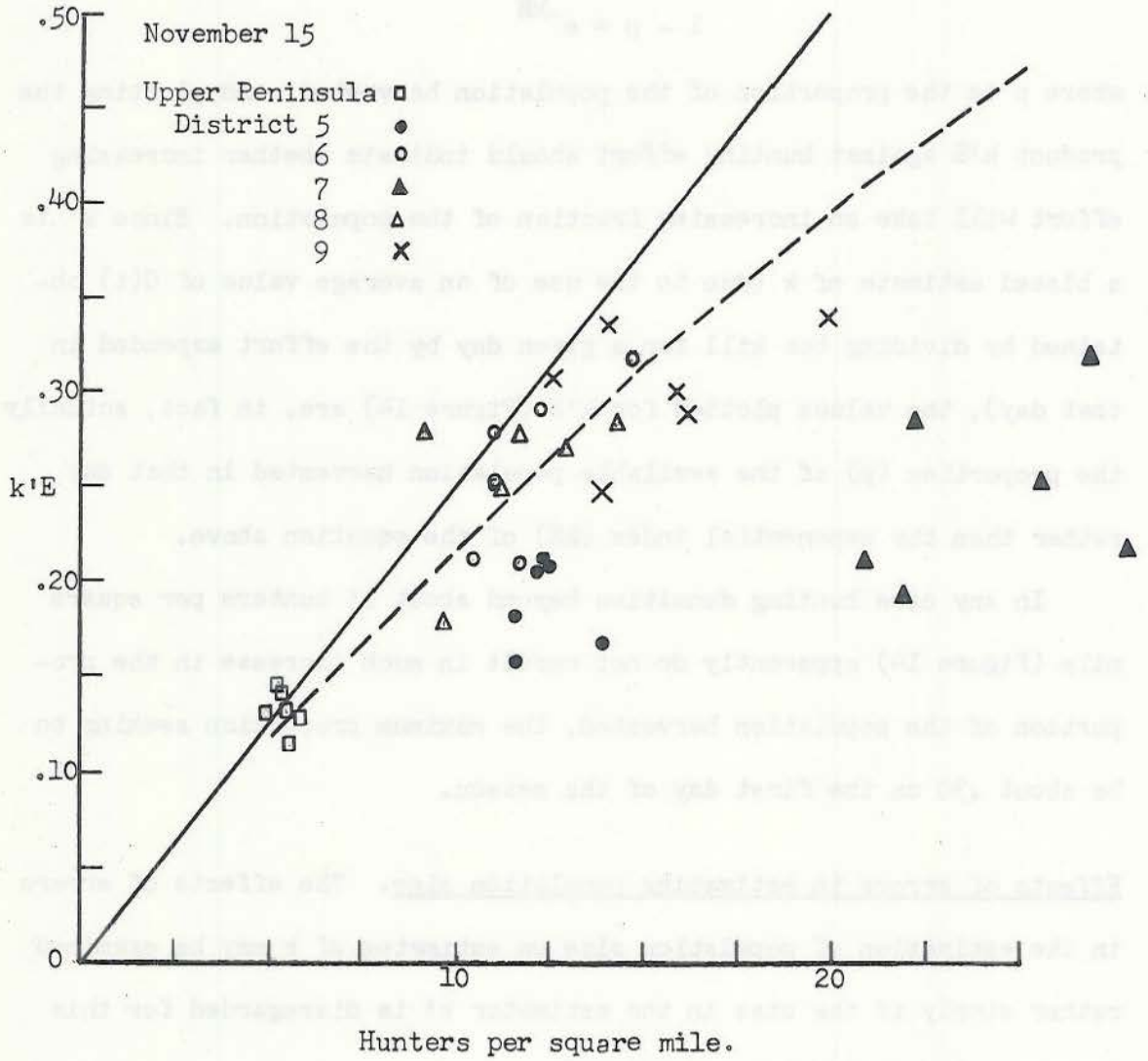


Figure 14. Proportion ($k'E$) of population harvested on opening day of hunting season (November 15) as compared to hunting pressure (1953-1958). The solid line shows the relationship to be expected for a true value of k, while the broken line represents the effect of using the biased estimate, k', of the same quantity (see page 61). Figure continued on next page.

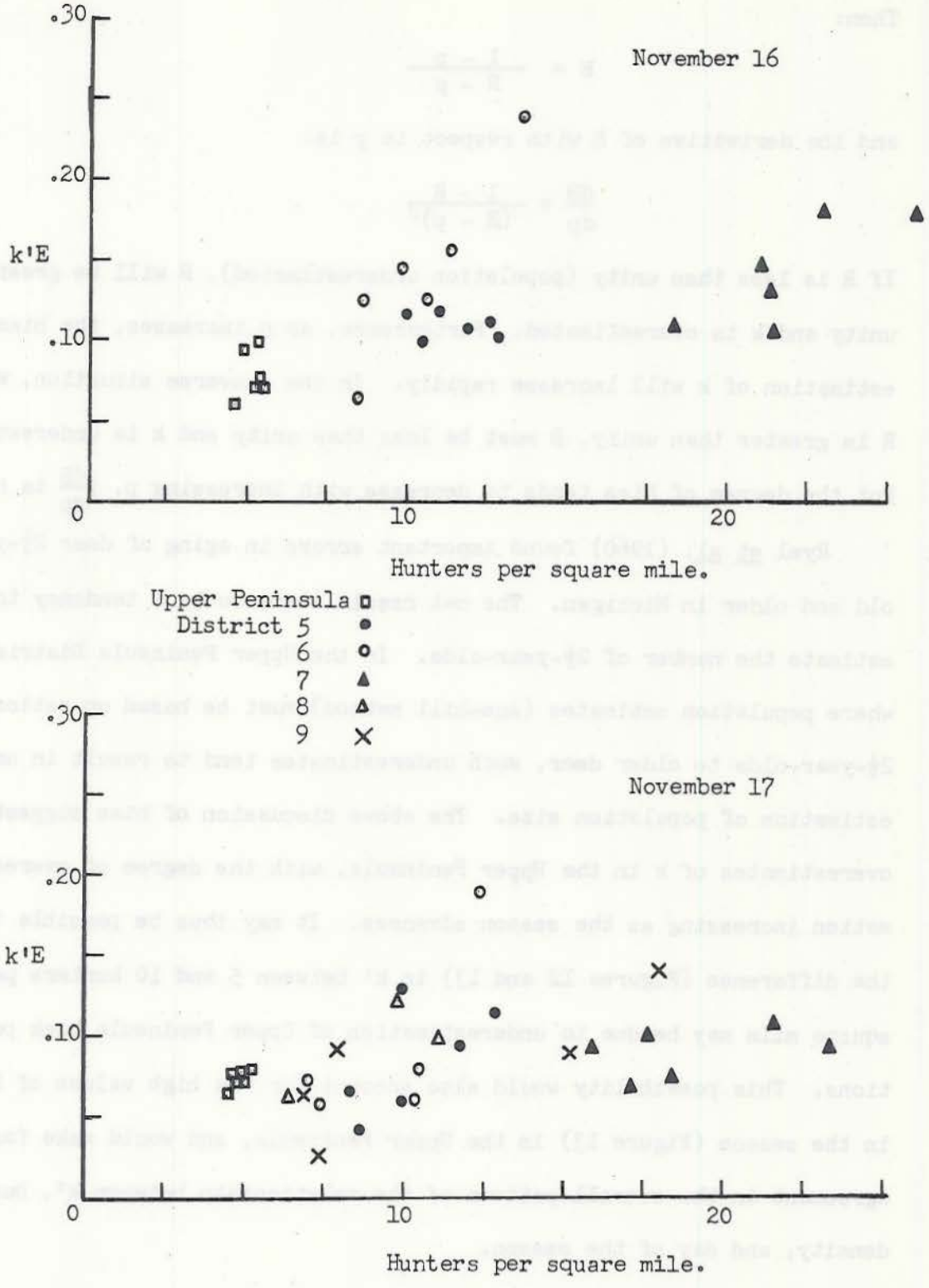


Figure 14 (continued). Data for November 16 and 17.

Then:

$$B = \frac{1 - p}{R - p}$$

and the derivitive of B with respect to p is:

$$\frac{dB}{dp} = \frac{1 - R}{(R - p)^2}$$

If R is less than unity (population underestimated), B will be greater than unity and k is overestimated. Furthermore, as p increases, the bias in estimation of k will increase rapidly. In the converse situation, where R is greater than unity, B must be less than unity and k is underestimated, but the degree of bias tends to decrease with increasing p. ($\frac{dB}{dp}$ is negative).

Ryel et al. (1960) found important errors in aging of deer $2\frac{1}{2}$-years-old and older in Michigan. The net result seems to be a tendency to underestimate the number of $2\frac{1}{2}$-year-olds. In the Upper Peninsula Districts, where population estimates (age-kill method) must be based on ratios of $2\frac{1}{2}$-year-olds to older deer, such underestimates tend to result in underestimation of population size. The above discussion of bias suggests overestimates of k in the Upper Peninsula, with the degree of overestimation increasing as the season advances. It may thus be possible that the difference (Figures 12 and 13) in k' between 5 and 10 hunters per square mile may be due to underestimation of Upper Peninsula buck populations. This possibility would also account for the high values of k' late in the season (Figure 13) in the Upper Peninsula, and would make for better agreement in the overall pattern of the relationship between k', hunter density, and day of the season.

Vulnerability as a function of time. The results given so far in this section show that vulnerability to hunting, represented as k or k', evidently changes drastically during the hunting season, making it impossible

to use the two equations given in the introduction to this section for population estimation. However, if the factors responsible for change in vulnerability can be sufficiently identified, it seems to me that a method of obtaining unbiased population estimates from kill-effort data can be devised. We do not, at present, know just why vulnerability declines rapidly early in the season, so attempts at deriving a method for population estimation must be based on some sort of empirical relationship. Also, since hunter efficiency apparently is greater at lower levels of hunter density, evidently there are two factors operating in opposite directions--a declining vulnerability as the season advances, but an increasing hunter efficiency as fewer and fewer hunters remain afield. Attempts to consider both of these factors as separate entities in an estimating equation lead to considerable complications, due in large part to the highly variable nature of the kill-effort data. I have therefore considered only cases where the proportion of the population killed per unit effort, k, is taken as a function of time (t), represented by day of the season, numbering the first day as 1, and so on to the 16th day.

There are, of course, a very large number of functions that might be used here. Because k apparently drops off very rapidly early in the season, and then seems to level off to a constant value, one might logically consider a function of the form:

$$k = a + \frac{b}{t^c}$$

where a, b, and c are constants. Such a function will "fit" the estimates, k', very nicely, but direct estimation of the constants from kill-effort data requires a very complex analysis.

Two simpler equations for k are:

(1) $$k = \frac{b}{t^a}$$

(2) $$k = ba^{\frac{1}{t}}$$

and the equation:

$$C(t) = k\{N(0) - K(t)\}$$

may be rewritten with the above substitutions for k. Fitting such representations to actual data (using least-squares methods) still leads to equations which are difficult to solve, and I have confined the investigations here to use of arbitrarily chosen values of the constant a, so that ordinary multiple regression methods may be used.

Using equation (1) and $a = \frac{1}{2}$ (i.e., vulnerability decreases as the reciprocal of the square-root of day of the season), the general equation becomes:

$$C(t) = bN(0)t^{-\frac{1}{2}} - bt^{-\frac{1}{2}}K(t)$$

and least-squares methods may be used to estimate b and N(0) (the "normal" equations are equivalent to those of multiple regression without corrections for the means).

Using this equation, population estimates for the six years of available data in the Lower Peninsula may be compared with those from the age-kill method (Figure 15). While averages of these estimates are close to those of the age-kill method, there are evidently some wide deviations, with extreme cases in 1955 and 1958. There was less of a drop in k' early in the season in 1955 and 1958 (Figure 10), and behavior of the cumulative kill, K(t), (Figure 16) is also different for these years, with a low kill early in the season being made up in the next few days, so that it seems some change in deer- or hunter-behavior may have changed the functional relation between k and t. Weather records show that the opening day (November 15) of 1955 was particularly cold and rainy, and there

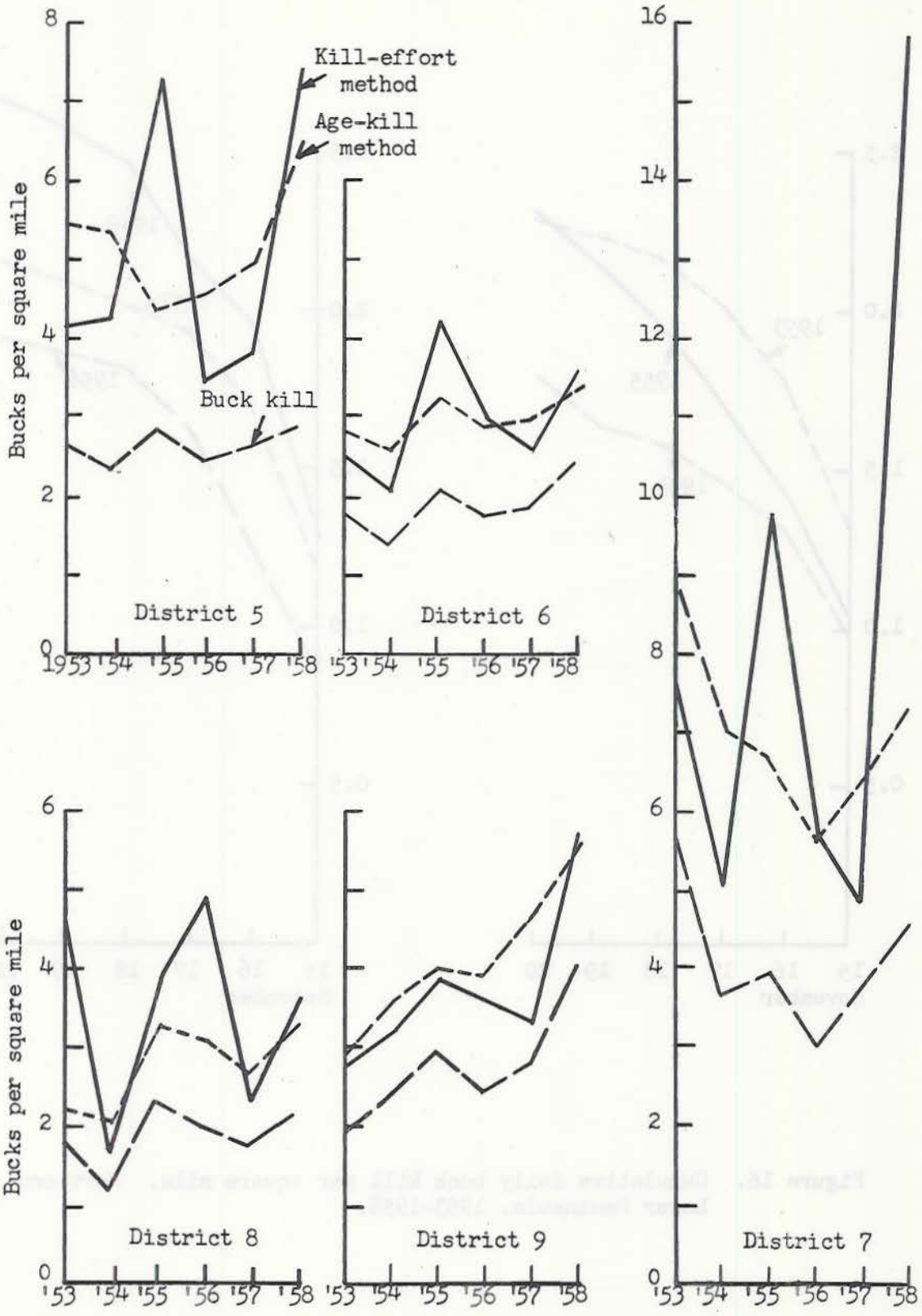


Figure 15. District buck population estimates from kill-effort and age-kill methods.

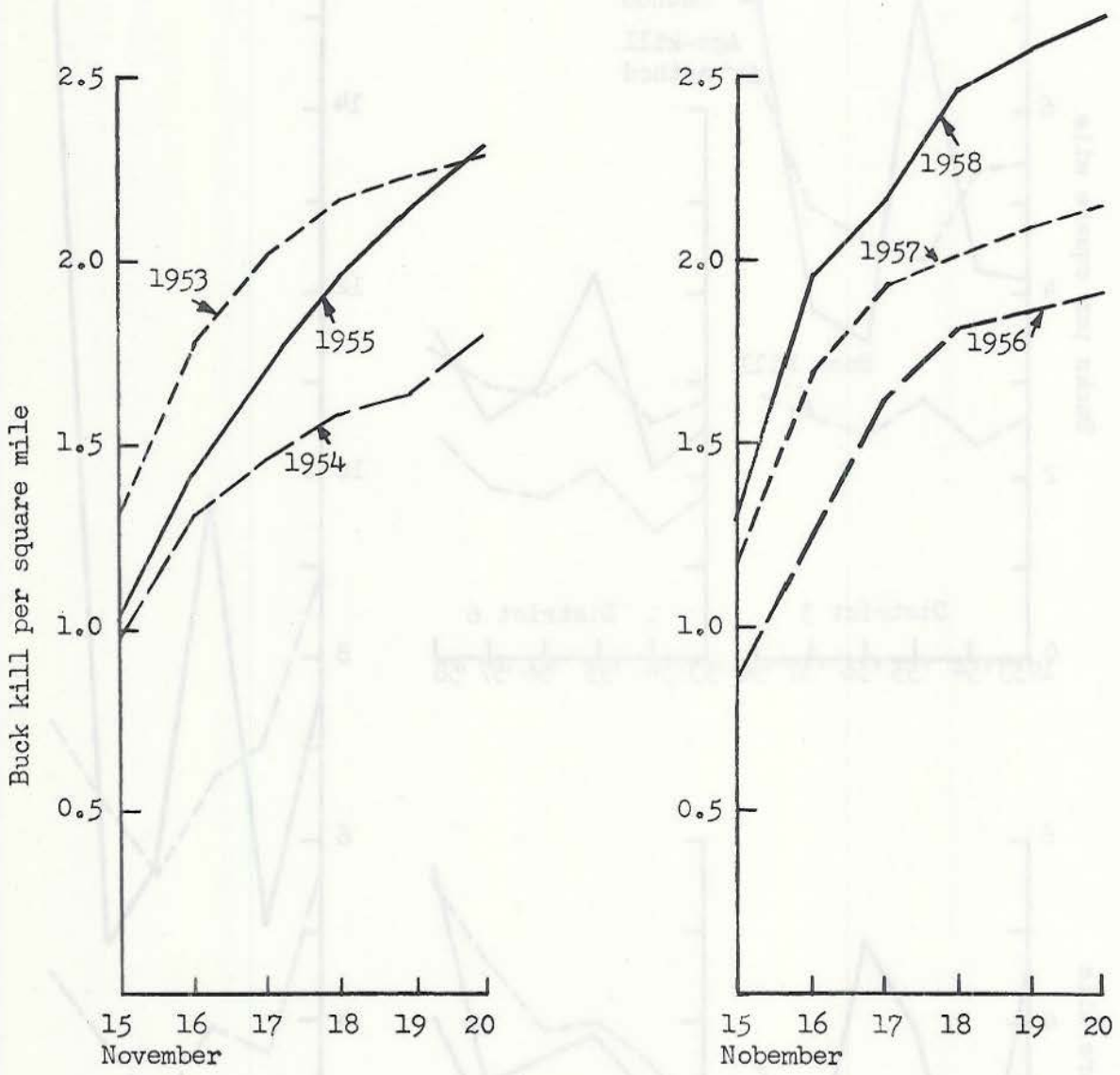


Figure 16. Cumulative daily buck kill per square mile. Northern Lower Peninsula, 1953-1958.

were strong winds and heavy snow from the afternoon of the 16th to the morning of the 17th, so that hunter efficiency may well have been low on these days. There was also rain during the opening days of the 1958 season, but temperatures were milder than in 1955, and conditions then apparently were not less satisfactory than in 1956 or 1957.

Using a = 3 in equation (2) yields results similar (Figure 17) to those obtained with equation (1). They conform a little more closely to the age-kill estimates, but are not entirely satisfactory.

Values of k determined from the two equations and compared with estimates (k') obtained from the age-kill method do conform in a general way (Figure 18) to the observed change in vulnerability, but it seems likely that no one arbitrary function may accurately represent the actual situation for all areas and years.

When some better notion of the actual situation becomes available from field studies, further analysis of these relationships may be worthwhile. Three items especially need further consideration:

(1) I have used arbitrary values for the constant, a, in the equations, but least-squares equations can be derived which permit the estimation of values of the constant directly from kill-effort data. Solution of such equations requires laborious computation, and use of an electronic computer may be advisable if a number of years and areas are to be studied.

(2) No attempt has been made here to adjust for the bias due to C(t) being actually an average, rather than an instantaneous value.

(3) If possible, the decrease in hunter density as the season advances should be taken into account in further studies.

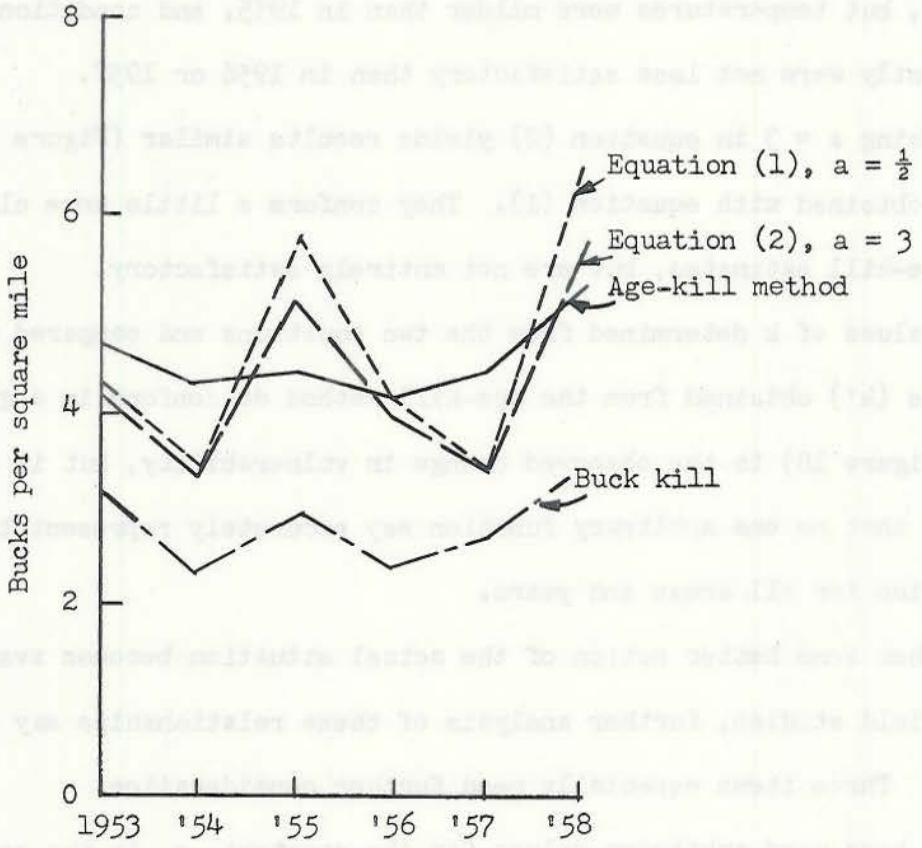


Figure 17. Buck population estimates for northern Lower Peninsula as estimated from age-kill method and two forms of kill-effort method.

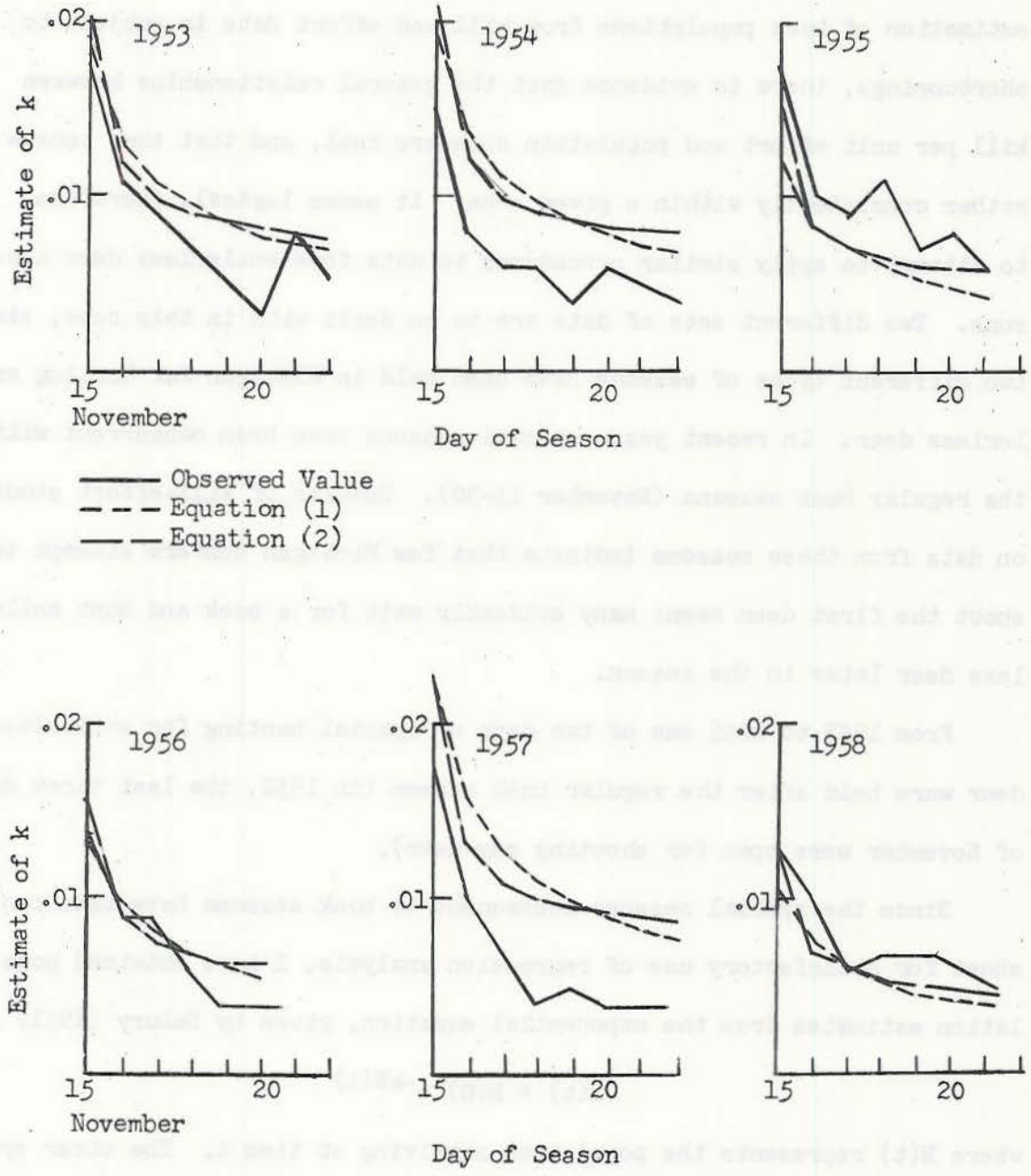


Figure 18. Estimates of proportion (k) of buck population shot per hunter-day for northern Lower Peninsula. The estimates are based on two equations representing decreasing vulnerability to hunting (page 66) and a direct measure of k (Figure 10).

Estimating antlerless populations from kill and effort data. While the estimation of buck populations from kill and effort data is subject to shortcomings, there is evidence that the general relationships between kill per unit effort and population size are real, and that they behave rather consistently within a given area. It seems logical, therefore, to attempt to apply similar procedures to data from antlerless deer seasons. Two different sets of data are to be dealt with in this case, since two different types of seasons have been held in Michigan for hunting antlerless deer. In recent years special seasons have been concurrent with the regular buck seasons (November 15-30). Results of kill-effort studies on data from these seasons indicate that few Michigan hunters attempt to shoot the first deer seen; many evidently wait for a buck and hunt antlerless deer later in the season.

From 1953 to 1956 one or two days of special hunting for antlerless deer were held after the regular buck season (in 1952, the last three days of November were open for shooting any deer).

Since the special seasons subsequent to buck seasons have been too short for satisfactory use of regression analysis, I have obtained population estimates from the exponential equation, given by DeLury (1951) as:

$$N(t) = N(0)\ e^{-kE(t)}$$

where N(t) represents the population surviving at time t. The other symbols are as previously defined. If mortality from causes other than legal harvest is disregarded, then $N(t) = N(0) - K(t)$, and the equation may be rewritten as:

$$N(0) = \frac{K(t)}{1-e^{-kE(t)}}$$

If values of k are available, the equation may be used to estimate the initial population, N(0).

To facilitate comparisons with pellet-group counts, population estimates from the "subsequent" special season data have been made only for the Study Areas (Figure 1). Values of k used here are those obtained from the buck population estimates (age-kill method) made on the same areas. Since it was shown earlier in this section that k changes (decreases) during the season, it is worthwhile here to consider what value was actually obtained for k.

If the value of k for a particular day of the season is represented as k(t) (assuming that k(t) is constant through the day, or that a mean value for the day is used), and if e(t) represents the effort expended on that day, then the surviving population after the season is:

$$N(t) = N(0)e^{-k(1)e(1)}\ e^{-k(2)e(2)}\ \ldots\ e^{-k(16)e(16)}$$

$$= N(0)\ e^{-\sum k(i)e(i)}$$

where $\sum$ denotes summation from i = 1 to i = 16.

The estimate of k was actually obtained in this report from the equation:

$$\frac{N(t)}{N(0)} = e^{-kE(t)} \text{ where } E(t) = \sum e(i)$$

so that k was estimated as:

$$k = \frac{-\log_e \frac{N(t)}{N(0)}}{\sum e(i)}$$

but under the assumption of changing k, the estimate becomes:

$$k = \frac{\sum k(i)e(i)}{\sum e(i)}$$

which is a weighted average of the daily values of k, the weights being the daily values of hunting effort.

The "subsequent" special season areas have varied in size, and regulations have changed over the period studied (Figure 19). Hunting regulations in 1952 and 1953 did not limit the number of hunters. In later years

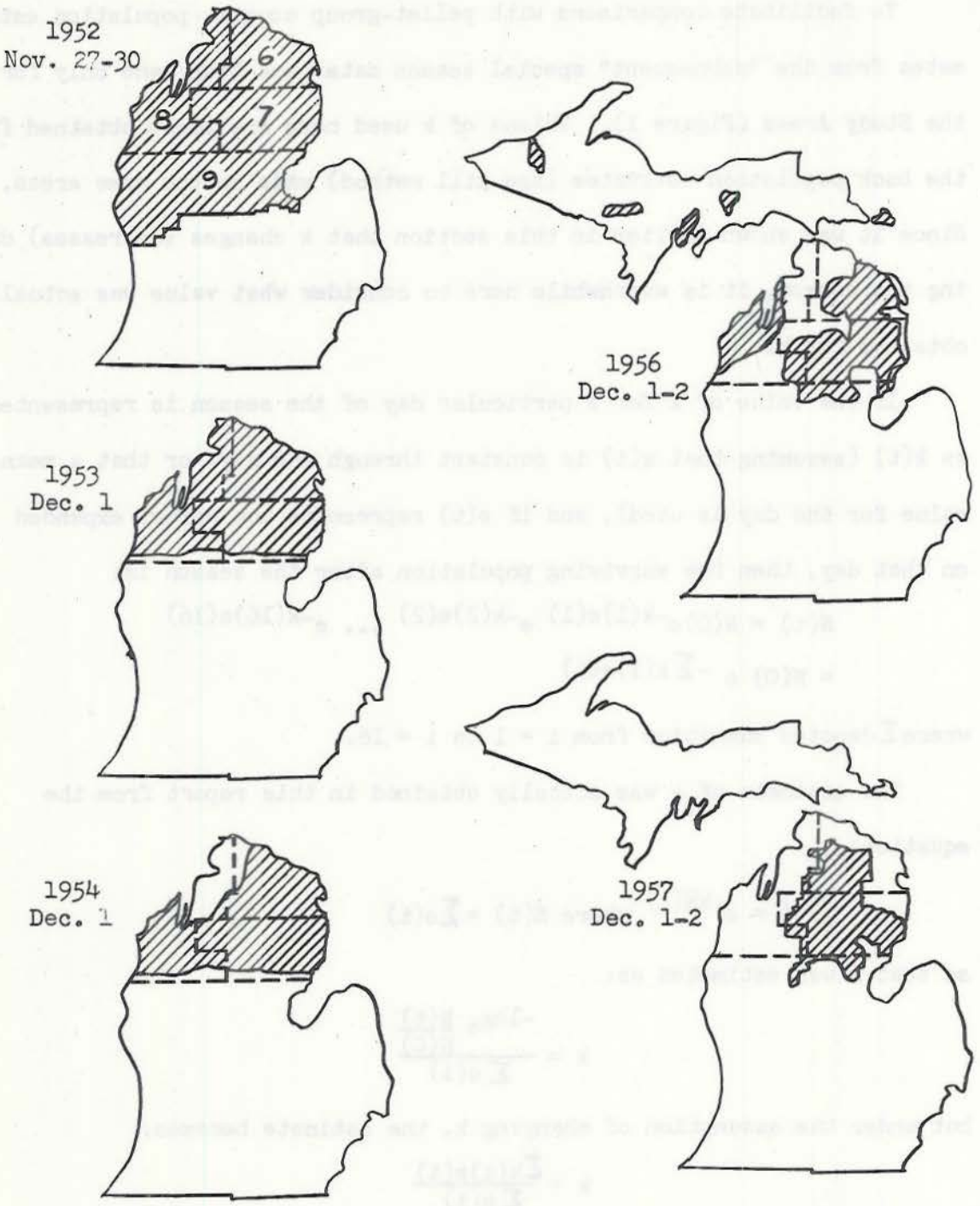


Figure 19. Areas in which "subsequent" special seasons were held, 1952-1957. Dates given are those on which the seasons were held. Broken lines show boundaries of Study Areas (Figure 1).

hunting was by permit only, and limited numbers of permits were issued for each specific area. The 1952 results are of uncertain value since our mail questionnaire was not designed to give hunting effort data in the same manner as in the years after 1952.

Population estimates obtained here are presumably those pertaining to the deer population alive at the end of the regular season. The legal buck kill has been added to give a total pre-season population, which, however, tends to be an underestimate by whatever losses of antlerless deer occur through illegal shooting in the regular season, and by any crippling losses.

Comparison with other population estimates. Results are compared graphically with population estimates from the sex-age-kill method and with the pellet-group count estimates in Figures 20 and 21, and summarized in Table 8. Close correlations among the several sources are evident, particularly with the sex-age-kill method. Some of the discrepancies are no doubt due to the fact that the special season areas do not exactly fit the Study Areas geographically (Figure 19). Some parts of the Study Areas are not covered by special-season units, and some of the special season units overlap two or more study areas. Most significant, however, is the fact that the kill-effort estimates generally exceed those from the other two sources. The chief exception seems to be Area 8, and this is explicable on the basis that the special season areas used for these estimates (kill-effort) excluded some of the higher population areas.

The apparent overestimation of population level by this method suggests that the values of k applying to these subsequent special seasons should be higher. This seems entirely reasonable if antlerless deer behave towards hunting in the same manner as do bucks, so that k is highest

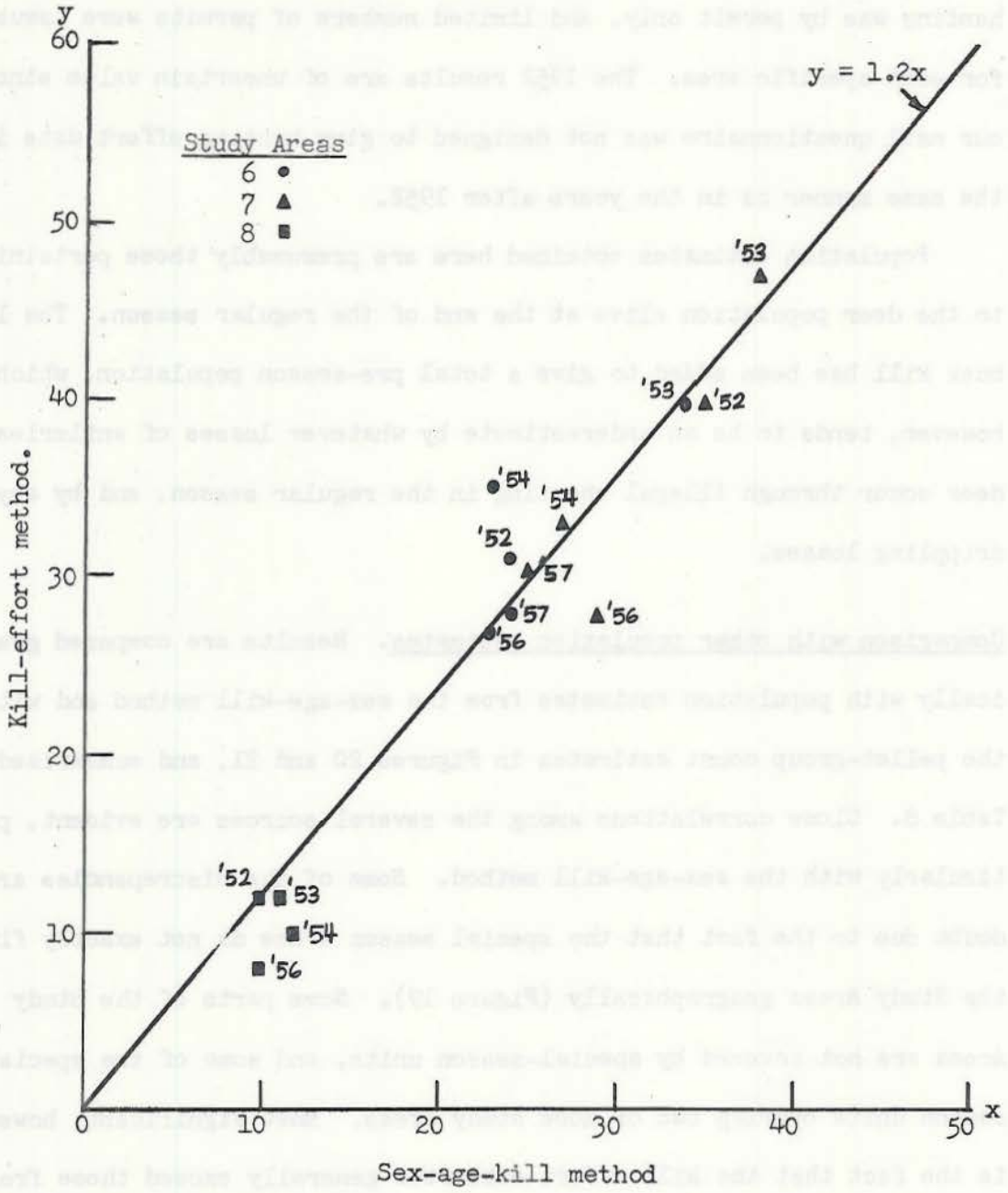


Figure 20. A comparison of Study Area deer population estimates from kill-effort and sex-age-kill methods (page 75). Figures are deer per square mile. Ratio line "eye-fitted".

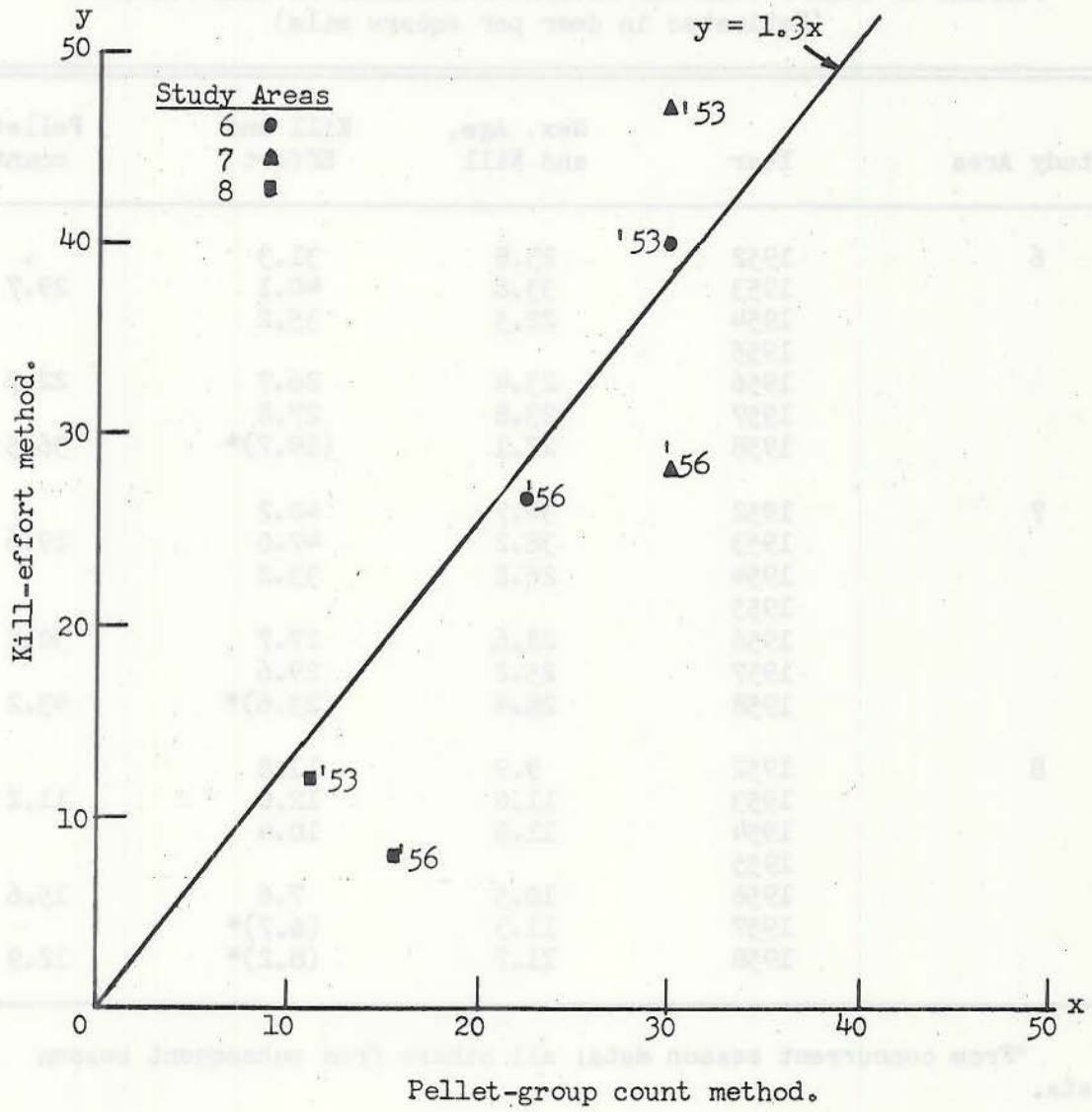


Figure 21. A comparison of deer population estimates from kill-effort and pellet-group count methods. Figures are deer per square mile. Ratio line "eye-fitted."

TABLE 8

SUMMARY OF DEER POPULATION ESTIMATES OBTAINED BY THREE METHODS
(Estimates in deer per square mile)

Study Area	Year	Sex, Age, and Kill	Kill and Effort	Pellet-count
6	1952	23.8	31.3	
	1953	33.6	40.1	29.7
	1954	22.5	35.2	
	1955			
	1956	23.4	26.7	22.7
	1957	23.8	27.8	
	1958	27.1	(19.7)*	36.5
7	1952	34.7	40.2	
	1953	38.2	47.0	29.6
	1954	26.8	33.2	
	1955			
	1956	28.6	27.7	30.2
	1957	25.2	29.6	
	1958	28.4	(23.6)*	43.2
8	1952	9.9	11.8	
	1953	11.0	12.0	11.2
	1954	11.8	10.4	
	1955			
	1956	10.5	7.6	15.6
	1957	11.3	(6.7)*	
	1958	11.7	(8.2)*	12.9

*From concurrent season data; all others from subsequent season data.

early in the season and drops off thereafter. Since the subsequent seasons are of only one to three days duration, it seems that the average value of k applicable here will be higher than that resulting from data collected over the entire buck season.

The values of k used here for estimating populations are a little higher than those used for buck populations, inasmuch as these latter values were based on square miles of deer range, in an attempt to compensate for areas of farmland with few deer and low hunting pressure in some of the Districts. Since figures on areas of deer range are not available for the individual special season areas, the values of k were recomputed for total land areas involved. Such changes are generally minor, relative to the other differences noted.

Without more data on behavior of k, and on illegal kills of antlerless deer in the buck seasons, it does not seem worthwhile at present to attempt further refinement of the population estimates from subsequent special season data. The close correlation with estimates from other sources provides good support for the notion that the estimates are reliable measures of deer population levels, but the recent change to concurrent special seasons means that such methods will not be currently useful unless a similar relationship exists in the concurrent seasons.

Population estimates from concurrent special season data. Kill-effort population estimates from concurrent special season data are markedly lower than those from the sex-age-kill method (Figure 22), and thus indicate a lower vulnerability to hunting. This is a reversal of the apparent situation in the subsequent special seasons. Evidently hunters in the concurrent seasons have not been taking antlerless deer as readily as bucks in the years covered here.

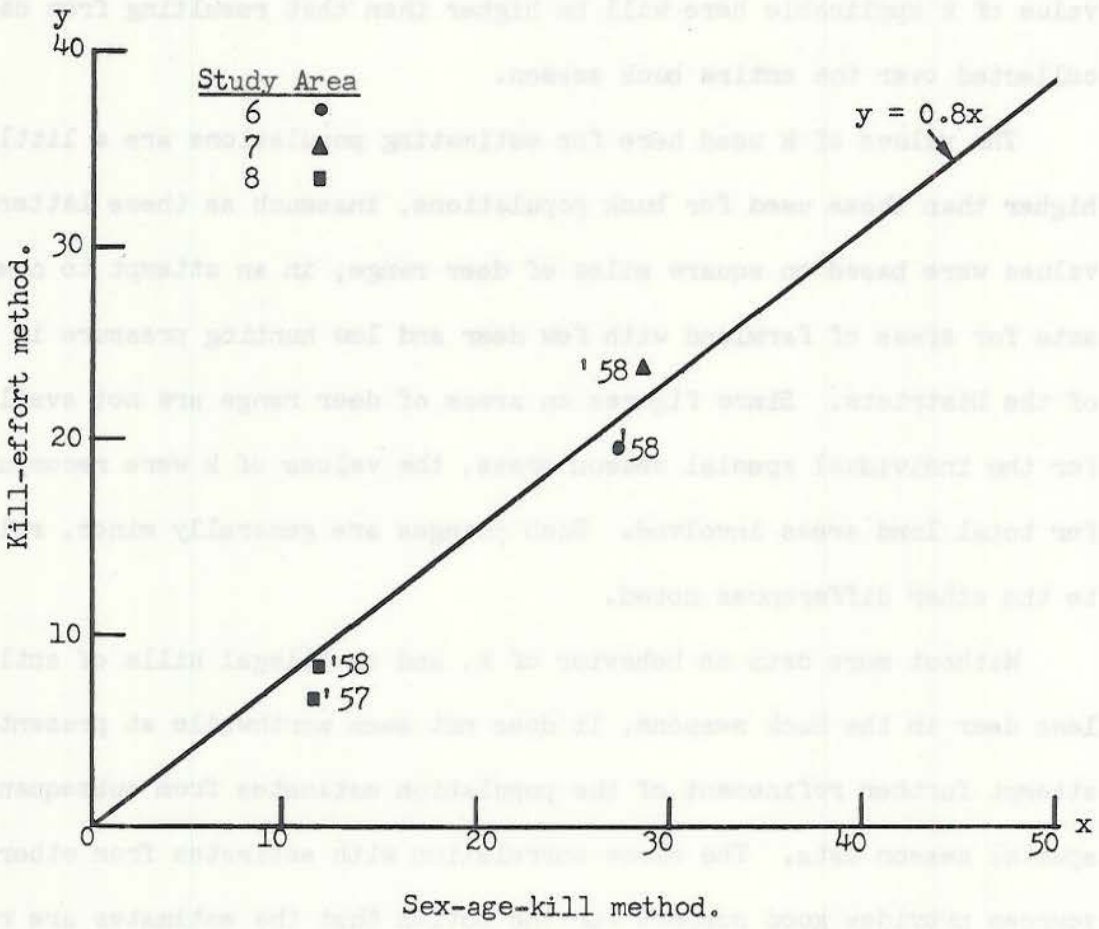


Figure 22. A comparison of deer population estimates from kill-effort method (concurrent special season data) and sex-age-kill method. Figures are deer per square mile. Ratio line "eye-fitted."

INDICES TO DEER POPULATION LEVELS

Introduction. Our experience has been that no single method is available to estimate extensive deer population levels reliably and directly. The pellet-group count may well approach direct and reliable estimates (within sampling error) when carefully used, but it is also true that this method is expensive, and it is also subject to both known and unknown sources of bias. There are, then, two reasons for attempting to use several indices or direct estimates of deer populations: (a) cost, and, (b) uncertainty about biases.

In most usages, an index is expected to measure relative population levels between areas as well as changes in time (trends). If an index is to do these things satisfactorily, it must be directly proportional to the actual population level and therefore can theoretically be transformed into a direct estimate of population density. Since most indices of deer population levels depend on kill figures or sight records, such things as changes in hunter numbers, differences in vegetation, and weather conditions, along with a number of human factors, may cause the index values to vary in their relation to the actual population densities. Nonetheless, it remains true that the basic data are often collected for other purposes, frequently at a relatively low cost. Also, records that may provide index values are usually available for large areas and over long spans of time, while direct estimates of populations may be too expensive to permit annual use on a number of areas.

In the present case the problem is to make maximal use of several sources of data which can be reasonably expected to vary with deer population densities. Probably optimal use of the indices (i.e., getting the maximum amount of information) can be achieved only through a very detailed

study, including much field work and dealing with several factors which probably cannot be reliably evaluated without extensive data on population levels.

Indices used in this report. The indices considered in this section are listed below along with descriptions of their sources.

(1) July deer counts. These counts are essentially roadside counts, made in the course of other duties, and are presumably recorded only during work in deer areas. The counts have been maintained in all Michigan deer range since the early 1930's. Records are kept by nearly all Conservation Department personnel whose duties carry them regularly through the deer country. The counts are actually made for the four months of July through October, and there are evidently real differences between months, with the July records seeming to show the closest correlation with populations as estimated from pellet-group counts. An additional reason for using here only the counts made in July is that they are available just before hunting regulations are set (in August).

The chief advantage to the counts other than their timeliness and the fact that they are readily understood by the general public, is the large volume, averaging around 5,000 deer actually tallied in July alone. Possible sources of bias are easily conceived, including differences in vegetation, roads, observers, weather, and so on. Some field workers keep the records conscientiously, while others undoubtedly keep none at all, but fill out a form at the end of each month and submit it as required.

In earlier years these counts served as virtually the only available measure of deer population levels, but in more recent years we

have attempted to restrict their use to measures of long-term trends on large areas.

(2) Archery kill. Some 30,000 to 40,000 archers annually take about 2,000 deer in Michigan. Their hunting success (about 6 per cent) is low but rather consistent, and archers seem, by and large, to be persistent hunters. Nearly all counties are open to the taking of antlerless deer, as well as bucks, with bow and arrow, so the kill may vary in closer relation to the population than in seasons where only adult males may be taken. The usual problems of weather conditions, different hunting conditions, etc., apply here, too, but the long season (October 1 to November 5) may tend to cancel out such effects. For purposes of this report only the total kill per 100 square miles has been used. It seems desirable to make some adjustment for hunter numbers, but my attempts to do so have not significantly increased the correlation with pellet-group counts.

(3) Highway kills. In recent years, rather complete records have been kept of deer accidentally killed on Michigan highways. The care with which such records are kept varies from area to area, and not all deer killed by cars are reported to the Conservation Department. Also, there are obviously marked differences in the likelihood of deer being struck by automobiles in the various areas in the major deer range of Michigan, and highway traffic volume has been increasing steadily over recent years. In spite of these difficulties, a correlation between deer accidentally killed and deer populations evidently does exist. Again, attempts to include supplementary data, such as traffic volume, have not increased the correlation between deer killed per unit area and pellet-group counts, but I believe a more detailed study may yield a means of improvement. Here, I will

use deer killed per 100 square miles as index values.

(4) Camp kill. Under Michigan laws, any four hunters occupying a "camp" (with definition of "camp" uncertain) may obtain a special license to take one deer for camp use, over and above the one-deer-per hunter regulations. Current regulations restrict hunters to taking only a buck with three-inch antlers or better on camp permits. These licenses have not been very popular, averaging under 1,000 sold annually for the years 1952-56, and dropping sharply in 1957 with an increase in the fee. Unless the regulations are changed, the camp kill cannot be expected to yield much information on deer populations; it is included here for its historical value and in the expectation that the regulation may well be changed in the future, quite possibly to make any kind of deer legal for camp licenses. Again, adjustments for hunter numbers seem worthwhile, but preliminary investigations have not shown enough improvement to justify corrections for present purposes. Figures used here are camp kill per 100 square miles.

Areas used for comparison. A unit of at least county size is indicated for comparisons, inasmuch as some of the records are kept only on a county basis. Sampling variations seem to indicate that a unit of size larger than a county is necessary, and the District (Figure 1) seems useful as such a unit. While ecological and herd management criteria may suggest units which do not follow District boundaries exactly, administrative use of such units and the convenient geographic arrangement make them preferable here.

The question of criteria. The major problem, here, and throughout this

report, is one of finding criteria for judging potential measures of population level. In essence, the only real criterion is the actual population density, either as an average or as an instantaneous value. We do not, however, have any immediate prospect of obtaining exact measures of deer populations, and one of the chief reasons for spending much time on these several indices is to use them as independent measures of population level.

One obvious criterion for judging the value of index measures is to compare them with the pellet-group counts, and such comparisons are shown below. We cannot, however, be sure that the pellet-group counts are not biased, and this uncertainty argues against using them as a base for combining the several indices into one measure. That is, we might use regression or correlation methods to determine some sort of weights for each index and thus combine the several sources. Such combinations lack the desirable property of independence; biases in the pellet-group counts may be introduced into the combined index and effectively prevent any fair comparison of the end-products. A further difficulty exists in the fact that the various indices are based on different measures--the kills of deer by archers, automobiles, and "gun" hunters cannot be expected to be in the same ratio to the true population level, and roadside counts are in altogether different units (deer seen per 100 hours).

If the indices were directly proportional to population level, the problem would be resolved into a search for correction factors which would adjust each index to the density of deer population per unit area (with the further necessity for weighting according to reliability). I suspect that the relationship between index and population is not that of a simple proportion, and that the true relation is likely to be curvi-

linear. However, I assume here that portions of the curves can be approximated reasonably well by straight lines. If the true relationship is curvilinear, the linear regression of index on population will have a "y-intercept" which does not pass through the origin. The assumption of a straight-line relationship between index and population permits linear transformations of the indices without changing anything except the scale of measurement. An illustration of the idea basic to transformations is the conversion of temperatures from one scale (Centigrade, Fahrenheit, Kelvin, etc.) to another. Degrees Centigrade may be converted to Fahrenheit by multiplying by the factor 1.8 and adding 32; this implies no change in the length of the mercury column, but is simply a change of scale.

Under the assumption of linearity, the several indices are all presumed to be measures of the same quantity (deer populations) but in different units or on a different scale. A further feature is implied by the idea that the several indices are not equally reliable. This may be taken to mean that the indices are sampling results and that "sample sizes" vary between indices. In actual fact, this is evidently not strictly true, as various sorts of bias have been described above, but in the absence of suitable supplementary data, about all that can be done is to lump all of these sources of variation in one "error" category and attempt to devise suitable weights which will favor the indices with smallest fluctuations from true deer population levels.

It seems desirable to derive the weights independently of the transformation (change of scale) inasmuch as a poor choice of weights will not in general bias the results, but will simply give less precise combined index values. The effects of failure to transform values to exactly the same scale are much less certain, and since it seems evident from the

beginning that the relationship of the indices to true populations is not exactly linear, one cannot very well expect to get a transformation to precisely the same scale. The best I hope to do here is to make a start--a good deal more study and some rather more complicated mathematics will be necessary for full evaluation of the possibilities.

If weights are chosen independently of the transformations, they need to be essentially based on "dimensionless" measures. These might include the correlation coefficient, coefficient of variation (variation relative to the mean) and sample sizes. These three items are at least roughly independent of the units of measurement (and hence "dimensionless"). An alternate possibility would be available if actual population levels could be measured, since it would then be possible to consider weights in terms of regression or least-squares relationships of the indices to true population levels. One such measure is given here with the pellet-group counts used as "true" population levels.

Some possible criteria for combining indices. Several possible bases for comparisons of the indices are described in the following paragraphs.

(1) Sample size. I do not believe the indices used here are likely to have a common variance, so their reliability probably cannot be judged accurately from the size of samples obtained. However, the following items should yield rough measures of reliability:

Index	Unit Used	Average Number	Square Root	Weight
July count	Number of deer seen	5,000	70.0	.409
Archery kill	Number of hunters in samples	2,000	44.7	.258
Camp kill	Number of parties in samples	200	14.1	.081
Highway kill	Number of deer tallied	1,900	43.6	.252
				1.000

The weights shown above are proportional to the square root of the average number tallied, in accordance with the principle that the standard error of an estimate decreases as the square root of the sample size increases.

Probably more reasons can be proposed for not using the above "sample sizes" than can be arrayed in defense of the choice. The simplest defense is that the only wholly valid criterion would be comparison with actual deer populations; without this, the only recourse is to use such measures as can be shown to have a bearing on the fluctuations of the index.

(2) Coefficient of variation. Complete sets of data for the four indices are available for all nine Districts for six years (1953-1958). Deer populations unquestionably vary from District to District and, in at least some Districts, vary among the years covered. I have therefore used the analysis of variance technique to attempt to remove variation due to these differences (between Districts and years) and consider the deviations or "error" component as a measure of the sampling variability not accounted for by these two sources. Actually, in terms of the analysis of variance, there will no doubt be a significant "interaction." However, we do not have independent samples within a given District in a particular year and thus cannot obtain a measure of interaction. Its presence seems to be a simple consequence of the fact that population levels vary in different manners in different Districts; in at least one District (District 7) there has been a persistent downward trend in the earlier years covered here, while several of the other Districts show little evidence of change of population level. Again, the best I can do now is to consider such variation as is known to exist and is accessible. Also, the error mean-square here does not necessarily measure sampling

variation exactly; one could probably find a number of measures with smaller error terms over the area and years considered, but with little or no relation to deer populations.

Results of the analysis are shown in Table 9 along with coefficients of variation, computed as the square root of the error mean-square divided by the mean value of the index.

(3) Mean-square deviations from regression. Simple linear regressions of pellet-group counts on the indices provide a means of measuring variability of the indices in terms of agreement with the pellet-group count results on certain areas. Results are in terms of the same scale of measurement (deer per square mile) since the deviations-mean-square from regression used here is the average of vertical deviations squared.

Results of that analysis are shown along with those of the coefficient of variation in Figure 23. Both measures are plotted against the square root of "sample size," since both should be expected to decrease in proportion to true sample size. I have already mentioned several reasons for not expecting particularly good agreement, and the results are perhaps a little better than one might expect. The principal difficulty seems to be the reversal of the position of the Highway and Archery kill indices between the two criteria.

Since an important purpose of the present analysis is to construct an independent measure of population size, I believe the variance about regression should not be used for weighting purposes.

(4) Correlation coefficients. Recent trends in statistical work (Tukey,

TABLE 9

ANALYSES OF VARIANCE OF INDEX DATA
1953-1958

Source	Degrees of Freedom	July Count		Archery Kill		Highway Kill		Camp Kill	
		Sum of Squares	Mean Square	Sum of Squares	Mean Square	Sum of Squares	Mean Square	Sum of Squares	Mean Square
Total	53	12,164.05		2,765.87		397.89		41.05	
Districts	8	10,060.05	1,257.50	2,608.15	326.02	271.00	33.88	22.32	2.790
Years	5	304.07	60.81	43.50	8.70	86.20	17.24	10.09	2.02
Deviations	40	1,799.93	44.998	114.22	2.856	40.69	1.017	8.64	.216
Means		28.487		6.091		5.420		1.037	
Coefficients of variation		.187		.277		.186		.448	

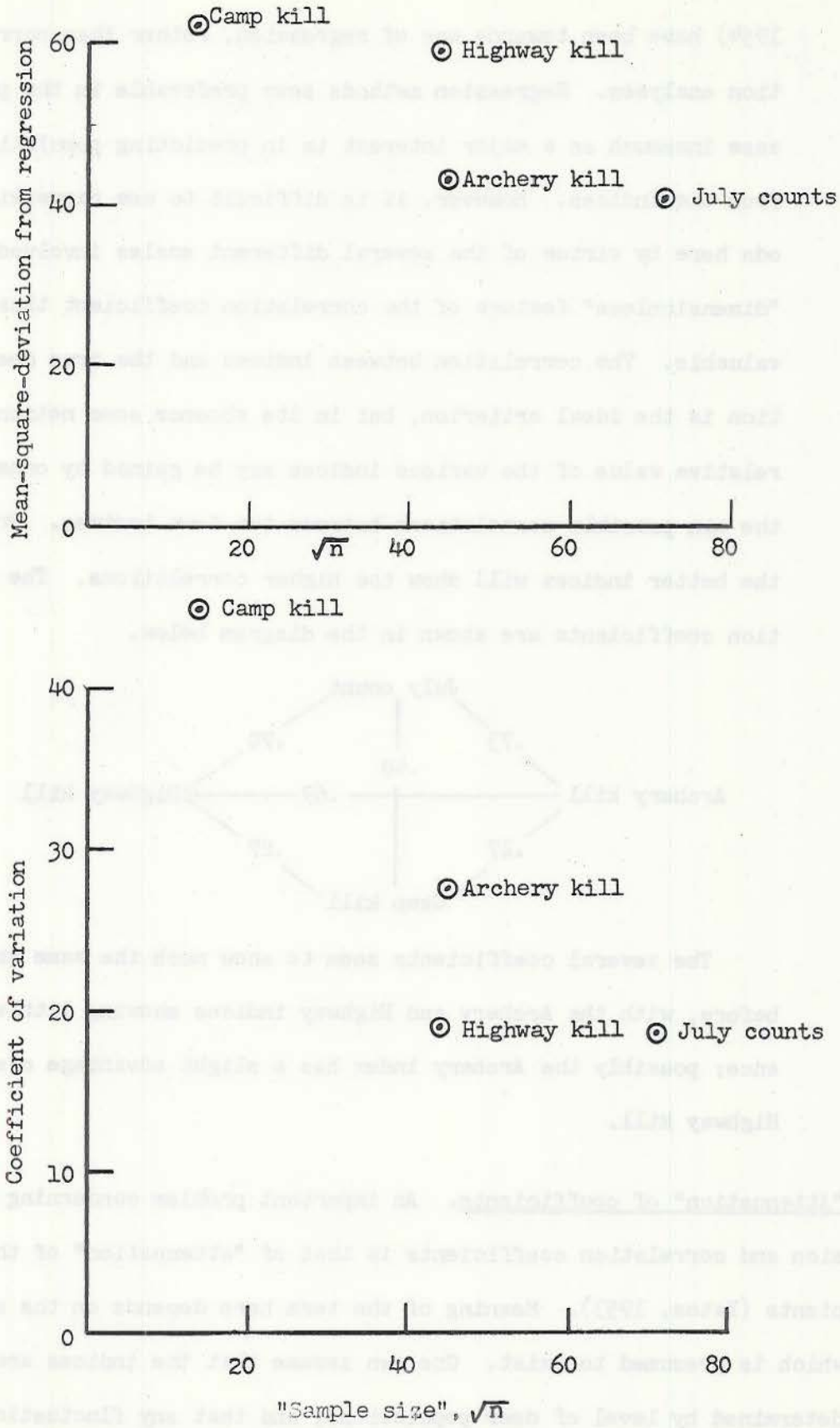
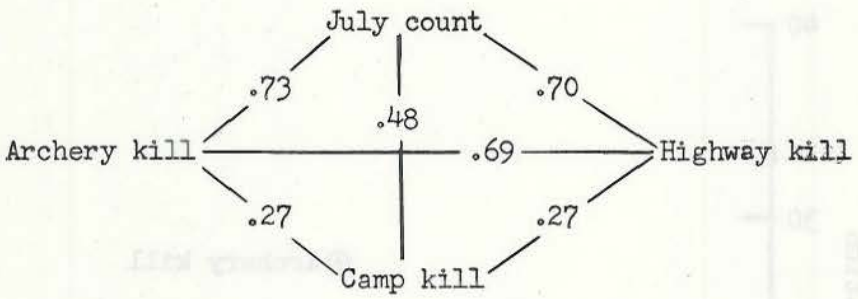


Figure 23. A comparison of two measures of variation in deer population indices.

1954) have been towards use of regression, rather than correlation analyses. Regression methods seem preferable in the present case inasmuch as a major interest is in predicting population level from the indices. However, it is difficult to use regression methods here by virtue of the several different scales involved, and the "dimensionless" feature of the correlation coefficient thus becomes valuable. The correlation between indices and the true deer population is the ideal criterion, but in its absence some notion of the relative value of the various indices may be gained by considering the six possible correlations between the four indices. Presumably the better indices will show the higher correlations. The correlation coefficients are shown in the diagram below.



The several coefficients seem to show much the same ranking as before, with the Archery and Highway indices showing little difference; possibly the Archery index has a slight advantage over the Highway kill.

"Attenuation" of coefficients. An important problem concerning the regression and correlation coefficients is that of "attenuation" of the coefficients (Yates, 1953). Meaning of the term here depends on the situation which is presumed to exist. One can assume that the indices are completely determined by level of deer populations, and that any fluctuations are due solely to sample sizes, or that various other factors affect the index so

that no matter how large the sample, the correlation will never approach unity. In the latter case, the model usually adopted is that of the bivariate normal distribution, in which the correlation coefficient appears as a parameter (fixed constant) in the distribution. In the problem dealt with here the following model seems more realistic:

$$Y = AU + e$$

$$X = BU + d$$

where:

Y = value of one index.

X = value of a second index.

U = true deer population per unit area.

A and B = constants transforming the true population level to the scale of the index (fraction of the population killed, etc.).

e and d = random error components of the same or different magnitude, but both assumed to have zero means.

Mathematical expectations of the usual computations needed for regression and correlation coefficients are:

$$E\left\{s_y^2\right\} = A^2\sigma_u^2 + \sigma_e^2$$

$$E\left\{s_x^2\right\} = B^2\sigma_u^2 + \sigma_d^2$$

$$E\left\{s_{xy}\right\} = AB\sigma_u^2$$

so that:

$$r = \frac{s_{xy}}{\sqrt{s_x^2 \, s_y^2}} = \frac{AB\sigma_u^2}{\sqrt{(A^2\sigma_u^2 + \sigma_e^2)(B^2\sigma_u^2 + \sigma_d^2)}}$$

$$b = \frac{s_{xy}}{s_x^2} = \frac{AB\sigma_u^2}{B^2\sigma_u^2 + \sigma_d^2} = \frac{A}{B + \frac{\sigma_d^2}{B\sigma_u^2}}$$

Under the above model, the correlation coefficient (r) approaches unity only when the sampling errors are small relative to the variability of true population values, and the poorer indices necessarily show the lower correlations. A similar situation exists with regard to the regression coefficient--if sampling error is small then the coefficient measures what it is supposed to; otherwise it is "attenuated," and this may prevent the regression line from passing through the origin as it should if the two measures are proportional expressions of exactly the same quantity. There is thus the uncertainty about whether the relations are truly curvilinear, or whether attenuation of the regression coefficient makes them appear to be so.

These difficulties cannot be resolved absolutely without a knowledge of true deer populations. For the present the fair degree of concord among the data as to relative value of the four indices may suffice. Since the relative value of the Highway and Archery indices is not completely clear, I have chosen to weight them equally, and it seems that the "sample size" values provide such an equal weighting and place the indices in approximate accord with the other measures of reliability. The step remaining is to bring the four indices to a common scale, as suggested before.

Transformation to a common scale. Choice of a scale is largely a matter of convenience. I have used 10 as the mid-point here, and prefer units sufficiently small so as to avoid confusion with deer per square mile; larger units (say mid-point of 100) might achieve this purpose more surely, but may also imply a false sense of reliability.

In terms of the thermometer example mentioned before, I have here chosen a "zero" point (10). It seems inappropriate to use a transformation which may yield negative or zero values.

The remaining task is to bring the indices to the same range of values. I have arbitrarily chosen to transform the available data to have a common variance, but other criteria might be used (e.g., requiring that a certain proportion of the transformed values fall within a fixed range).

Ideally, the transformations ought to be based on the same set of data for all indices (same years and areas), but the Highway kill figures are not available by District for 1952. I have, however, included the 1952 data for the other indices, in order to use the combined index in reference to that year.

The actual transformations proceed as follows:

To transform a distribution with frequencies $f(x)$, mean $\bar{x}$, and variance, s^2 to one with mean $\bar{z}$ and variance S^2:

Let: $z = Bx + A$

$\bar{z} = B\bar{x} + A$

Then: $$\frac{\sum(z - \bar{z})^2}{n - 1} = S^2 = \frac{\sum(Bx + A - B\bar{x} - A)^2}{n - 1} = \frac{B^2\sum(x - \bar{x})^2}{n - 1}$$

$S^2 = B^2 s^2$

$$\boxed{B = \frac{S}{s}}$$

$\bar{z} = B\bar{x} + A$

$$\boxed{A = \bar{z} - B\bar{x} = \bar{z} - \frac{S}{s}\bar{x}}$$

The quantities in boxes above are those necessary for the actual transformation, where x represents the index value and z the transformed value. The mean has already been selected as 10 for the transformed variable and the variance is taken as 9 for arithmetic convenience, and to give a moderate range of transformed values.

The necessary computations and tabulations of original index values

and transformed values are given in Tables 10 to 13. Values of the constants A and B are:

	A	B
July count	4.3457	0.1947
Archery kill	7.5634	0.4057
Highway kill	4.0652	1.0949
Camp kill	6.2504	3.4738

Frequency distributions of the transformed values are shown in Figure 24. A final step is to combine the four indices by weights proportional to the square roots of "sample size"; the results are shown graphically in Figure 25.

Appraisal of results. While the ultimate appraisal of the results depends on comparisons with other measures of deer populations, some subjective criteria may be mentioned as follows:

(1) Stability of deer population levels is generally to be expected, and these combined index values (Figure 25) do not show the erratic fluctuations that might be expected if they were not following population levels.

(2) Differences between Districts correspond to other population information.

(3) The heavy harvest of 1952 in the Lower Peninsula is reflected by the index for all Districts in this area, and the gradual increase in populations in subsequent years (except District 7) is about what we believe has gone on. The continued decrease in District 7 up to 1957 is also evident from other data presented later in this report.

(4) The gradual increase in three of the Upper Peninsula Districts up to 1956 is quite likely the result of recovery from the severe winter

TABLE 10

HIGHWAY KILL PER 100 SQUARE MILES

	Kill per 100 square miles						Transformed values					
District	1953	1954	1955	1956	1957	1958	1953	1954	1955	1956	1957	1958
1	2.8	2.8	3.0	3.8	3.7	3.8	7.13	7.13	7.35	8.22	8.12	8.22
2	4.0	6.2	6.7	7.2	9.9	7.1	8.44	10.85	11.40	11.95	14.90	11.84
3	1.8	5.5	5.9	8.4	5.7	5.9	6.04	10.09	10.52	13.26	10.30	10.52
4	2.5	5.0	7.1	11.0	6.9	7.3	6.80	9.54	11.84	16.11	11.62	12.06
5	3.9	3.7	5.3	6.4	6.5	7.1	8.34	8.12	9.87	11.07	11.18	11.84
6	2.1	2.5	4.2	4.7	4.2	4.7	6.36	6.80	8.66	9.21	8.66	9.21
7	8.6	9.2	9.1	11.5	12.0	12.6	13.48	14.14	14.03	16.66	17.20	17.86
8	2.1	2.5	3.9	4.7	4.3	4.2	6.36	6.80	8.34	9.21	8.77	8.66
9	1.2	1.8	3.9	3.5	4.0	4.3	5.38	6.04	8.34	7.90	8.44	8.77

Computations for transformation

$s^2 = 7.5073$ $\quad n = 54$

$s = 2.7400$ $\quad B = \frac{S}{s} = \frac{3.0000}{2.7400} = 1.0949$

$\bar{x} = 5.4204$ $\quad A = 10 - 1.0949\ (5.4204) = 4.0652$

Check on transformation

$s^2 = 9.0001$

$\bar{z} = 9.9991$

TABLE 11

CAMP KILL PER 100 SQUARE MILES

	Kill per 100 square miles							Transformed values						
District	1952	1953	1954	1955	1956	1957	1958	1952	1953	1954	1955	1956	1957	1958
1	2.3	2.0	2.9	2.1	2.1	0.6	0.8	14.24	13.20	16.32	13.55	13.54	8.33	9.03
2	2.2	3.1	2.1	1.6	2.7	0.4	0.5	13.89	17.02	13.54	11.81	15.63	7.64	7.99
3	1.1	2.4	2.2	1.4	1.2	0.4	0.6	10.07	14.59	13.89	11.11	10.42	7.64	8.33
4	1.4	1.5	1.0	1.2	1.6	0.3	0.2	11.11	11.46	9.72	10.42	11.81	7.29	6.94
5	1.2	1.2	1.4	1.1	0.9	0.8	0.8	10.42	10.42	11.11	10.07	9.38	9.03	9.03
6	0.6	0.8	0.4	0.6	0.3	0.4	0.1	8.33	9.03	7.64	8.33	7.29	7.64	6.60
7	2.2	3.1	1.6	1.9	2.0	1.0	1.2	13.89	17.02	11.81	12.85	13.20	9.72	10.42
8	0.7	0.1	0.4	0.1	0.3	0.1	0.0	8.68	6.60	7.64	6.60	7.29	6.60	6.25
9	0.3	0.2	0.0	0.0	0.2	0.1	0.0	7.29	6.94	6.25	6.25	6.94	6.60	6.25

Computations for transformation

$s^2 = .74585$ $\quad n = 63$

$s = .8636$ $\quad B = \frac{S}{s} = \frac{3.0000}{.8636} = 3.4738$

$\bar{x} = 1.0794$ $\quad A = 10 - 3.4738\ (1.0794) = 6.2504$

Check on transformation

$s^2 = 9.001$

$\bar{z} = 9.999$

TABLE 12

JULY DEER COUNTS

	Deer seen per 100 hours							Transformed values						
District	1952	1953	1954	1955	1956	1957	1958	1952	1953	1954	1955	1956	1957	1958
1	18.4	16.4	29.5	19.3	20.7	17.6	17.1	7.93	7.54	10.09	8.10	8.38	7.77	7.68
2	23.9	29.4	34.8	29.5	37.0	30.9	40.3	9.00	10.07	11.12	10.09	11.55	10.36	12.19
3	30.9	35.1	37.1	35.2	33.9	32.8	35.5	10.36	11.18	11.57	11.20	10.95	10.73	11.26
4	27.8	27.4	42.5	26.5	37.0	30.1	30.5	9.76	9.68	12.62	9.50	11.55	10.21	10.28
5	43.6	32.8	28.1	30.4	29.8	32.9	35.0	12.83	10.73	9.82	10.26	10.15	10.75	11.16
6	39.7	11.3	16.6	8.5	13.7	11.5	13.2	12.08	6.54	7.58	6.00	7.01	6.58	6.92
7	71.4	78.6	77.8	58.2	38.1	43.2	59.7	18.25	19.65	19.49	15.68	11.76	12.76	15.97
8	20.6	13.1	14.2	14.0	18.9	16.9	24.8	8.36	6.90	7.11	7.07	8.02	7.64	9.17
9	15.0	12.2	13.2	9.9	16.8	22.1	16.7	7.27	6.72	6.92	6.27	7.62	8.65	7.60

Computations for transformation

$s^2 = 237.315$, $n = 63$

$s = 15.405$, $B = \frac{S}{s} = \frac{3.000}{15.405} = .1947$

$\bar{x} = 29.041$, $A = 10 - .1947\ (29.041) = 4.3457$

Check on transformation

$s^2 = 8.9991$

$\bar{z} = 10.0002$

TABLE 13

ARCHERY KILL PER 100 SQUARE MILES

	Kill per 100 square miles							Transformed values						
District	1952	1953	1954	1955	1956	1957	1958	1952	1953	1954	1955	1956	1957	1958
1	0.9	0.8	1.6	2.5	1.8	1.7	0.8	7.93	7.89	8.21	8.58	8.29	8.25	7.89
2	0.7	0.6	5.1	3.9	2.8	1.3	6.1	7.85	7.81	9.63	9.14	8.70	8.09	10.04
3	1.0	2.8	3.4	4.0	4.7	3.6	2.1	7.97	8.70	8.94	9.19	9.47	9.02	8.42
4	1.3	2.0	3.2	3.3	3.1	3.0	6.5	8.09	8.37	8.86	8.90	8.82	8.78	10.20
5	6.9	9.5	9.1	12.1	12.2	8.7	12.9	10.36	11.42	11.26	12.47	12.51	11.09	12.80
6	2.7	3.9	1.7	0.6	4.9	1.2	3.6	8.66	9.14	8.25	7.81	9.55	8.05	9.02
7	28.2	23.6	18.2	28.5	25.1	22.8	28.1	19.00	17.14	14.95	19.12	17.75	16.81	18.96
8	1.7	2.3	1.4	1.4	4.0	1.0	3.5	8.25	8.50	8.13	8.13	9.19	7.97	8.98
9	6.1	1.9	4.4	2.0	3.5	2.7	3.4	10.04	8.33	9.35	8.37	8.98	8.66	8.94

Computations for transformation

$s^2 = 54.686$ $\quad n = 63$

$s = 7.395$ $\quad B = \frac{S}{s} = \frac{3.000}{7.395} = .4057$

$\bar{x} = 6.006$ $\quad A = 10 - .4057\ (6.006) = 7.5634$

Check on transformation

$s^2 = 8.9991$

$\bar{z} = 9.9995$

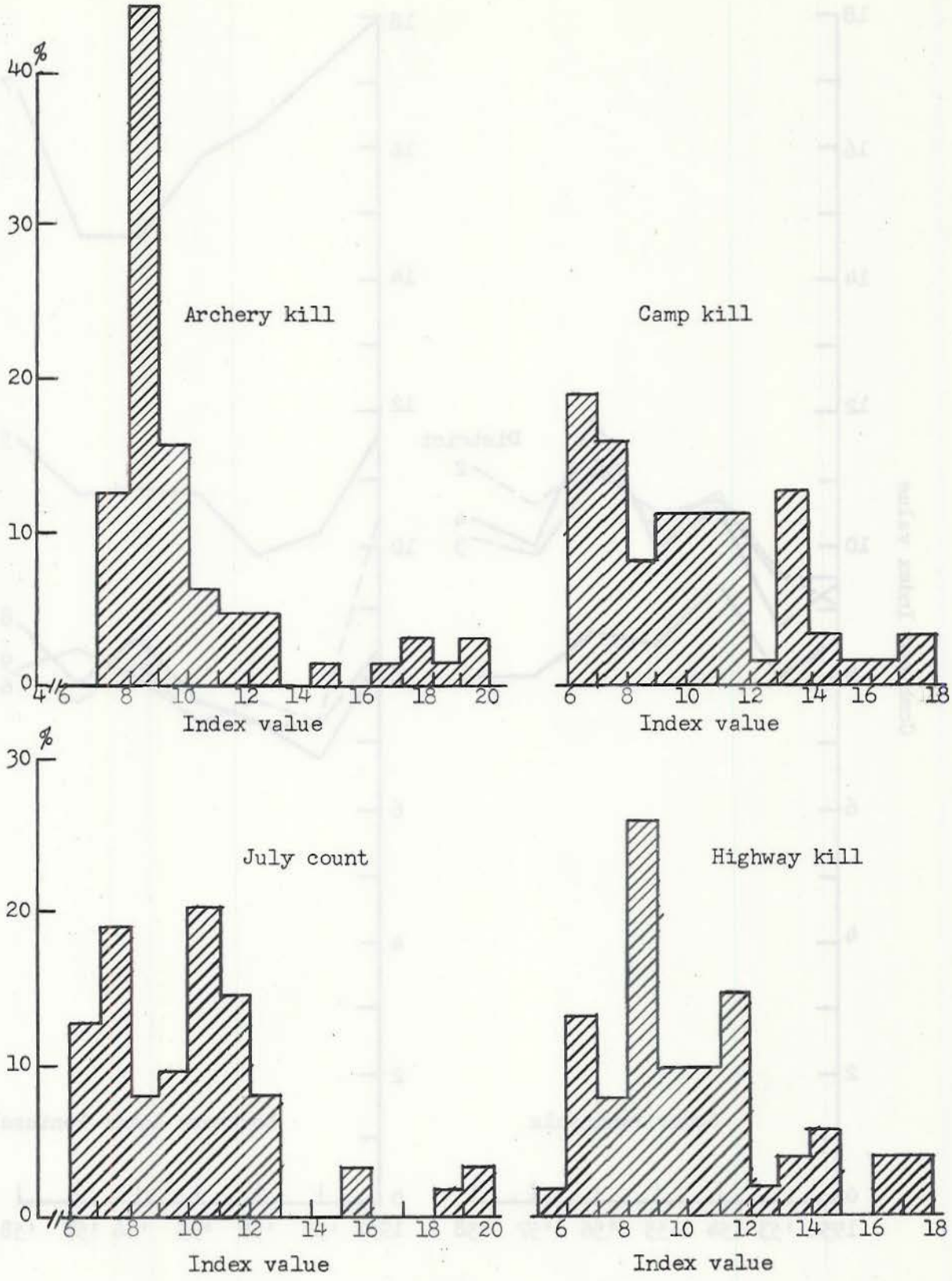


Figure 24. Frequency distribution of transformed variates.

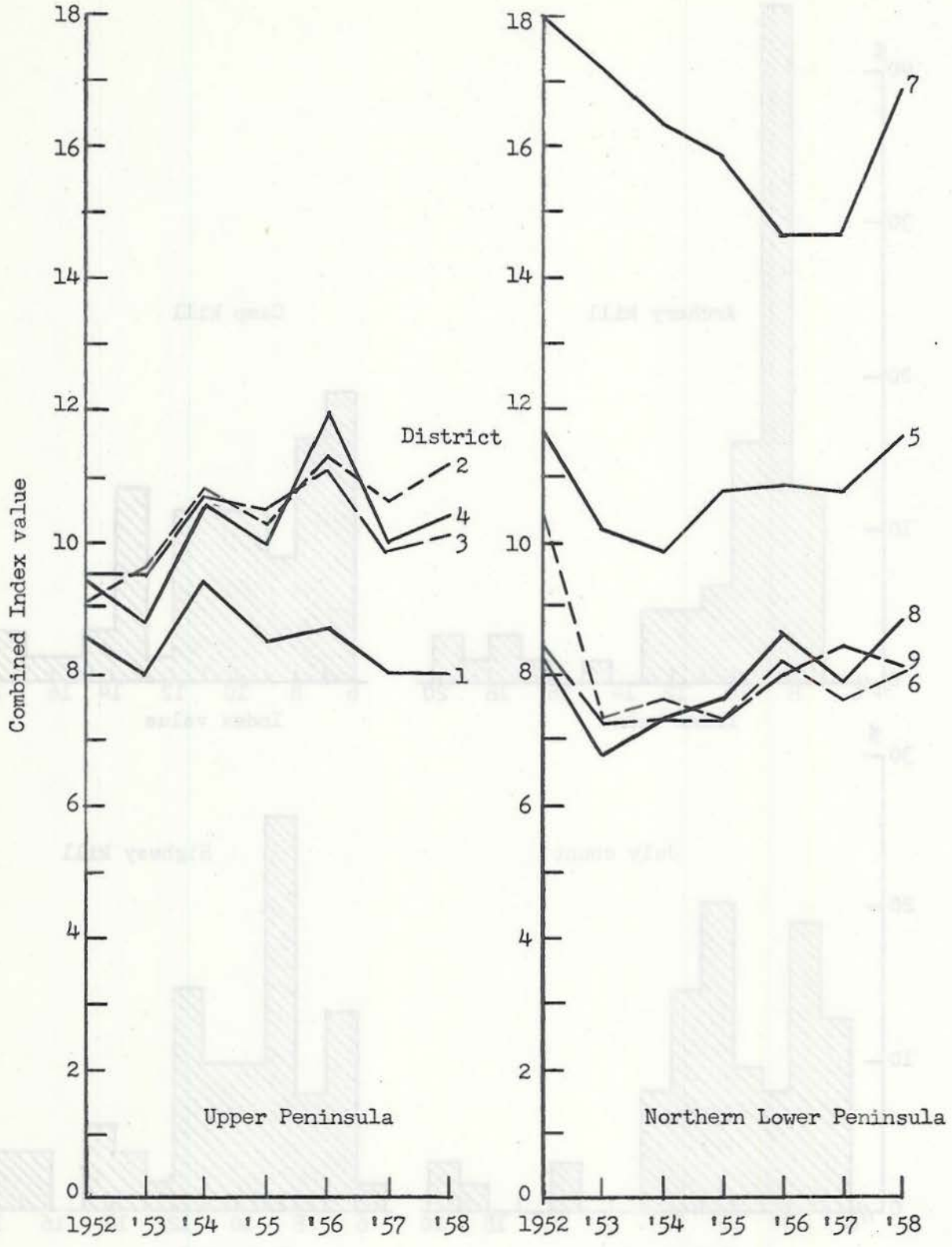


Figure 25. Combined deer population indices by Game Management District and year.

conditions of 1950-51, and the drop in 1957 may be a delayed consequence of heavy over-winter losses in 1956 (Eberhardt, 1956a). The somewhat different behavior of District 1 may be due to the fact that severe winter conditions seem to be more or less chronic there. In general, the index values seem to follow the pattern of deer populations as we know them from other sources.

III. COMPARISON OF THREE METHODS OF ESTIMATING POPULATION LEVELS

Introduction. The three independent methods of estimating relative deer population levels described in earlier sections of this report are:

(1) Pellet-group counts.

(2) The sex-age-kill method.

(3) Combined index--a composite of several measures.

The first two of these measures are expressed as deer per square mile, and the third (index) as a relative measure, not directly translatable to absolute population levels. All three are here used as fall (pre-hunting) populations.

Experience with the pellet-group count on areas of known populations suggests that it may provide reliable estimates of actual population levels, but there are clearly possibilities of error (bias) other than that due to sampling fluctuations (Figure 2). Use of the method on large areas is often hampered by inadequate knowledge of mortality losses during the period covered by the counts.

We have not had an opportunity to check the other two methods in a similar manner, and must therefore depend on comparisons among the three measures for their evaluation. Since no one of the methods has been demonstrated to be unbiased, I cannot very well determine with certainty which is "best," unless some arbitrary criteria are accepted as standards.

Independence. It is important to note here that the three estimates are independent in most senses of the word. The pellet-group counts are field

surveys and are related to the other methods only by allowances for the legal kill. The estimates from sex, age, and kill data depend on mail survey figures for legal gun kill and on biological data obtained at roadside checking stations during the hunting seasons. The index data are based on two mail survey sources (archery and camp kills) which are unrelated to the regular gun kill surveys, and on two measures which have no connection with the mail surveys (summer deer counts and highway kill).

A fourth method of estimating populations (from kill and effort data) is not included in the comparisons in this section because the estimates are not independent of the other measures of population level (see section on kill-effort data).

Sampling errors. The manner in which the index values and the sex-age-kill estimates are constructed makes it very difficult to obtain any useful direct measure of sampling error, but certainly the individual estimates are subject to such errors, and comparisons among the set of observations will thus be subject not only to various biases, but also to chance errors.

Comparison by correlation analysis. There are 20 individual population estimates for which results from all three methods can be compared. These cover all of the northern Lower Peninsula and extend over the period from 1952 to 1958. The values for these areas are given in Table 14, and comparisons between the three pairs of estimates are shown in Figure 26.

Correlation coefficients among the three measures are:

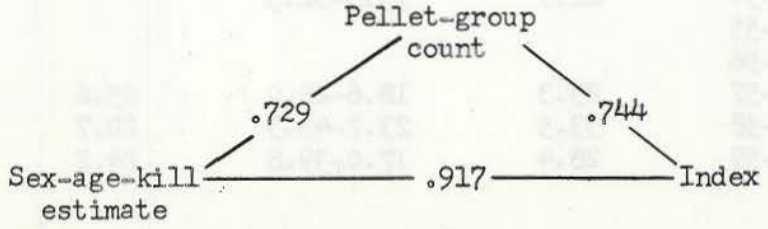


TABLE 14

POPULATION DATA FROM THREE SOURCES

Study Area	Year	Pellet Counts (Deer per sq. mile) Spring Estimate Plus Legal Harvest	Approx. Confidence Limits	Sex, Age and Kill (Deer per sq. mile)	Index Values
6	1952-53			23.8	13.6
	1953-54	29.7	17.3-42.1	33.6	13.0
	1954-55			22.5	12.1
	1955-56	26.2	10.6-41.8		12.1
	1956-57	22.7	15.6-29.8	23.4	11.9
	1957-58			23.8	11.8
	1958-59	36.5	26.9-46.1	27.1	12.8
7	1952-53			34.7	17.8
	1953-54	29.6	15.7-43.5	38.2	16.4
	1954-55			26.8	16.8
	1955-56	33.3	13.3-53.3		14.7
	1956-57	30.2	25.8-34.6	28.6	14.4
	1957-58			25.2	14.0
	1958-59	43.2	31.7-54.7	28.4	14.8
8	1952-53			9.9	8.2
	1953-54	11.2	6.0-16.4	11.0	6.8
	1954-55			11.8	7.2
	1955-56	14.8	6.8-22.8		7.5
	1956-57	15.6	10.7-20.5	10.5	8.3
	1957-58			11.3	7.8
	1958-59	12.9	8.1-17.7	11.7	8.3
9	1952-53			11.8	7.0
	1953-54	9.0	3.8-14.2		6.7
	1954-55				7.0
	1955-56	12.3	7.9-16.7		7.0
	1956-57	12.4	8.5-16.3	12.9	7.9
	1957-58			13.1	8.0
	1958-59	17.2	12.9-21.5	15.9	8.1
Lake Co.	1952-53	33.8	10.8-56.8	40.6	17.3
	1953-54	22.9	13.3-32.5		10.6
	1954-55				11.2
	1955-56				13.1
	1956-57	23.3	18.6-28.0	25.6	13.1
	1957-58	33.5	23.7-43.3	20.7	10.0
	1958-59	28.4	17.0-39.8	24.2	12.8

TABLE 14--Continued

POPULATION DATA FROM THREE SOURCES

Study Area	Year	Pellet Counts (Deer per sq. mile) Spring Estimate Plus Legal Harvest	Pellet Counts (Deer per sq. mile) Approx. Confidence Limits	Sex, Age and Kill (Deer per sq. mile)	Index Values
Mio Ranger District	1952-53	45.0	32.7-57.3	54.0*	16.2
	1953-54	31.1	15.9-46.3	39.0*	14.5
	1954-55			36.0*	12.4
	1955-56				14.5
	1956-57	27.3	19.7-34.9	20.6*	11.2
	1957-58	50.6	41.2-60.0	25.0*	12.3
	1958-59	46.3	26.8-65.8	41.6*	15.8

*Oscoda County Only

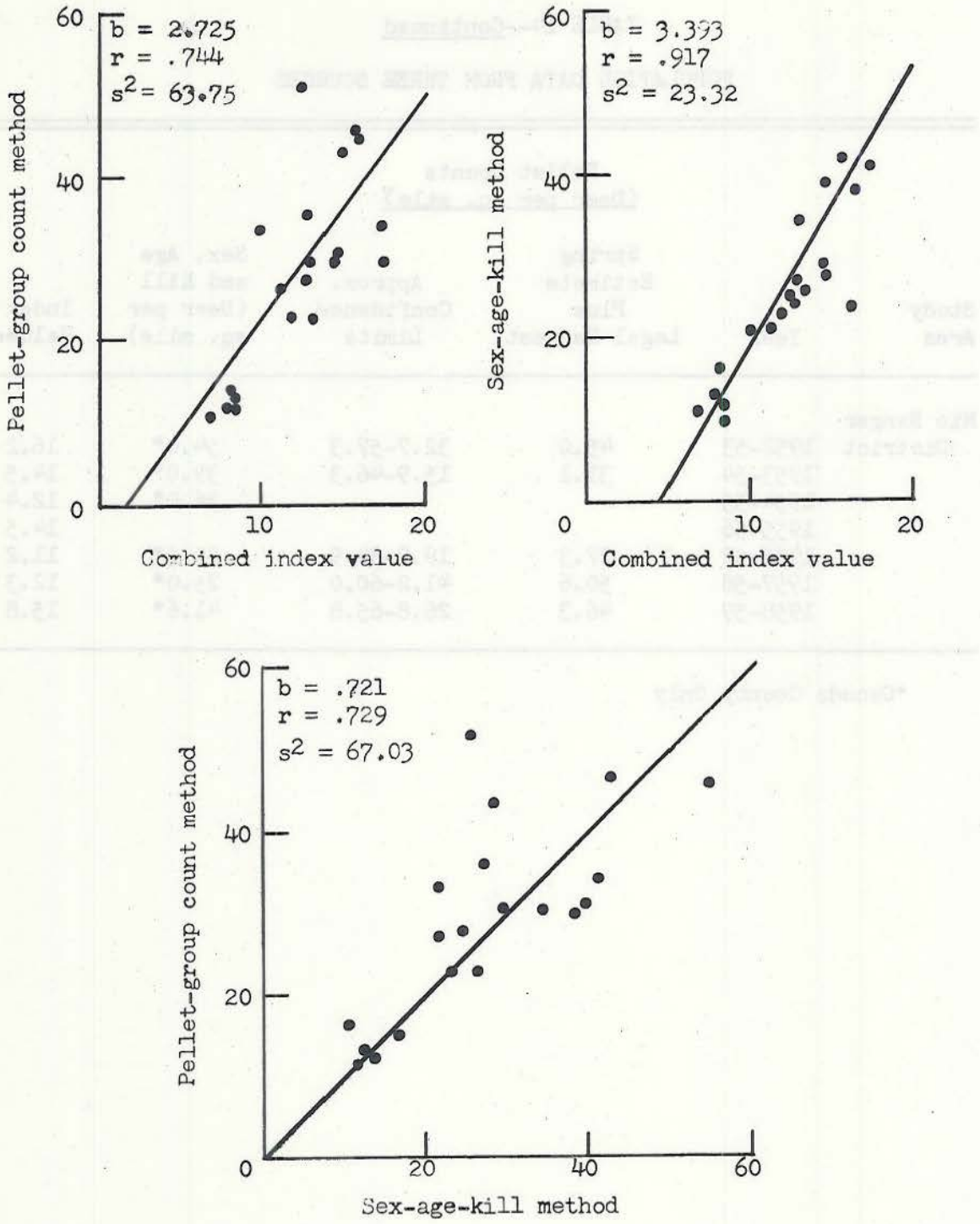
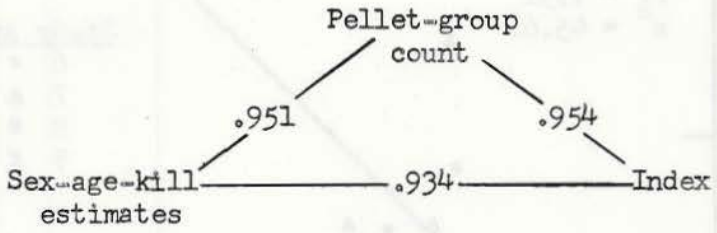


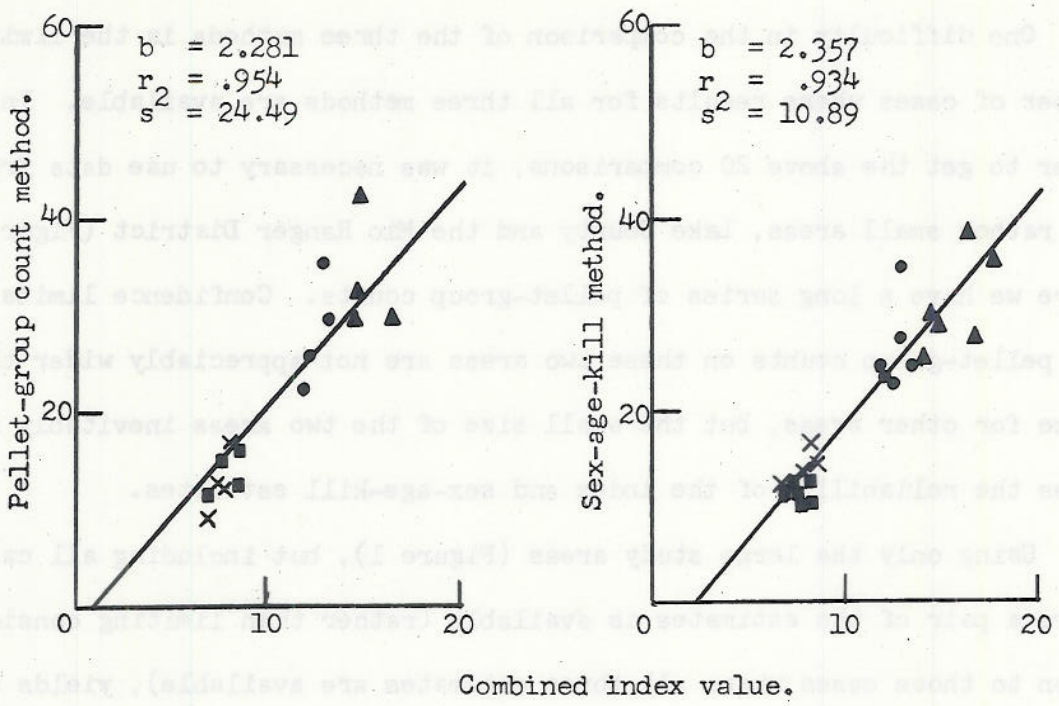
Figure 26. A comparison of measures of deer population levels obtained by three methods on six areas. Limited to cases where data are available for all three methods.

One difficulty in the comparison of the three methods is the limited number of cases where results for all three methods are available. In order to get the above 20 comparisons, it was necessary to use data from two rather small areas, Lake County and the Mio Ranger District (Figure 1), where we have a long series of pellet-group counts. Confidence limits on the pellet-group counts on these two areas are not appreciably wider than those for other areas, but the small size of the two areas inevitably reduces the reliability of the index and sex-age-kill estimates.

Using only the large study areas (Figure 1), but including all cases where a pair of the estimates is available (rather than limiting consideration to those cases where all three estimates are available), yields better agreement among all three measures (Figure 27). Correlation coefficients for the measures are as follows:



Comparison by regression analysis. Considering the problem as one of predicting deer populations from these measures yields some further notion of their relative value. A serious shortcoming should be mentioned first--the presence of sampling errors in all three variables prevents labeling any one as an independent measure in the sense of the usual "normal" regression theory, and a choice of two possible regression lines (Winsor, 1946) thus exists for each pair to be studied. A selection may be made, however, by regarding the ultimate goal as one of direct estimation of population numbers. The index values then become the independent variables in two cases. I have used the pellet-group counts as the dependent



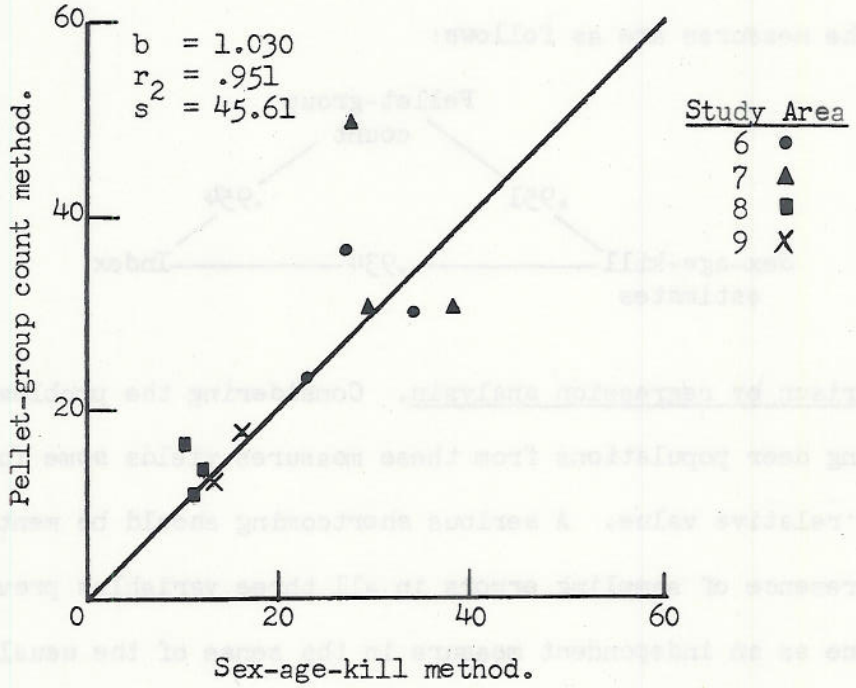


Figure 27. A comparison of measures of deer population levels obtained by three methods on four major Study Areas.

variable in the third case because there is evidence as to the validity of this measure as a direct estimate of population level.

Using the above arrangement of variables, the deviations-mean-square from regression may be computed for each set of data. Under normal regression theory, the square root of this quantity is roughly equivalent to one standard error of a prediction (made from an observed value of the independent variable).

The several measures of relationships among the three population indices (Figures 26 and 27) are:

(1) The regression slope (b).

(2) The correlation coefficient (r).

(3) Deviations-mean-square from regression (s^2).

Since the principal purpose here is one of prediction (estimating population level), it seems that the most useful measure for comparison is the variance about regression (s^2).

A summary of the two criteria (correlation and regression) is:

		Correlation Coefficient(r)		Deviations-mean-square (s^2)	
Dependent variable (y)	Independent variable (x)	Twenty Areas	Study Areas	Twenty Areas	Study Areas
Pellet-group count estimate	Sex-age-kill estimate	.729	.951	67.03	45.61
Sex-age-kill estimate	Index	.917	.934	23.32	10.89
Pellet-group count estimate	Index	.744	.954	63.75	24.49

Even the lowest deviations-mean-square from regression (10.89) is large enough to indicate limits (two standard errors) on predictions of about $\pm$ 7 deer per square mile. It is important, however, that this is

a prediction of the value of another variable measure and that limits on the prediction of true populations will presumably be narrower, but the degree of reduction in limits cannot be determined without measures of internal variance for each method.

Without a knowledge of the sampling errors involved here, it is impossible to say how much of the deviations are due to this source, and how much may be due to biases. An adjustment for attenuation (Yates, 1953) would increase the correlation coefficients.

Comparison by sequence in time. While the measures of population size used in the correlation and regression analyses are independent in the sense of collection of data, they are nevertheless related, since there is a continuity of deer population levels in any one area. Considering the three population measures in terms of the time sequence of population levels (Figure 28) demonstrates good agreement as to population trend, with the pellet-group counts again showing more erratic behavior than the other two methods. Some points of importance concerning Figure 28 are:

(1) The index values are not adjusted to correspond with the other two measures other than by the arrangement of the scales. Also, the relative position of index points and the other two measures varies between areas, probably by virtue of the failure of a line relating index values to the other measures to go through the origin (see section on index values and Figures 26 and 27).

(2) The values of the sex-age-kill estimates for Areas 6, 7, and 8 are higher in 1953 than in 1952, and this does not seem logical in view of the very high antlerless deer harvest of 1952, which we believe definitely reduced the deer population in most northern Lower Peninsula areas. The cause for this anomaly may be an error (of uncertain

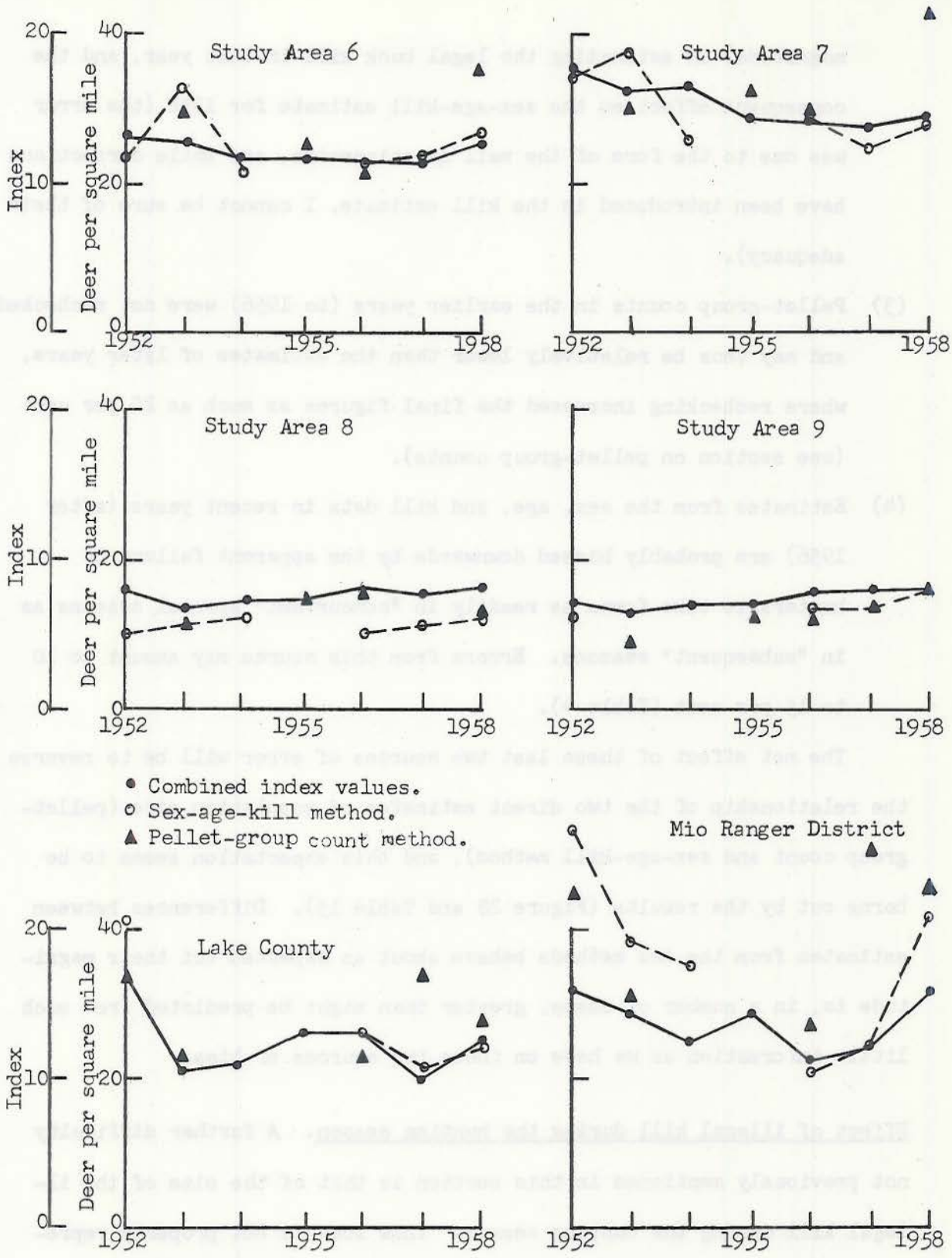


Figure 28. Deer population trends on six areas as shown by three measures of population level.

magnitude) in estimating the legal buck kill in that year, and the consequent effect on the sex-age-kill estimate for 1952 (the error was due to the form of the mail questionnaire, and while corrections have been introduced in the kill estimate, I cannot be sure of their adequacy).

(3) Pellet-group counts in the earlier years (to 1956) were not rechecked, and may thus be relatively lower than the estimates of later years, where rechecking increased the final figures as much as 20 per cent (see section on pellet-group counts).

(4) Estimates from the sex, age, and kill data in recent years (after 1956) are probably biased downwards by the apparent failure of hunters to take fawns as readily in "concurrent" special seasons as in "subsequent" seasons. Errors from this source may amount to 10 to 15 per cent (Table 4).

The net effect of these last two sources of error will be to reverse the relationship of the two direct estimates of population size (pellet-group count and sex-age-kill method), and this expectation seems to be borne out by the results (Figure 28 and Table 15). Differences between estimates from the two methods behave about as expected but their magnitude is, in a number of cases, greater than might be predicted from such little information as we have on these two sources of bias.

Effect of illegal kill during the hunting season. A further difficulty not previously mentioned in this section is that of the size of the illegal kill during the hunting season. This loss is not properly represented in the pellet-group estimates (it makes them too low) and may have some unknown effect on the sex-age-kill estimates, although since these depend principally on the ratio of $1\frac{1}{2}$-year-old to older does and on pre-

TABLE 15

DIFFERENCE BETWEEN PELLET-GROUP COUNT AND SEX-AGE-KILL POPULATION ESTIMATES

DIFFERENCE IN DEER PER SQUARE MILE

	Area 6	Area 7	Area 8	Area 9	Lake	Mio
1952-53					- 6.8	- 9.0
1953-54	- 3.9	- 8.6	+ 0.2			- 7.9
1954-55						
1955-56						
1956-57	- 0.7	+ 1.6	+ 5.1	- 0.5	- 2.3	+ 6.7
1957-58					+12.8	+25.6
1958-59	+ 9.4	+14.8	+ 1.2	+ 1.3	+ 4.2	+ 4.7

DIFFERENCE AS PROPORTION OF PELLET-COUNT ESTIMATE

	Area 6	Area 7	Area 8	Area 9	Lake	Mio
1952-53					- .20	- .20
1953-54	- .13	- .29	+ .02			- .25
1954-55						
1955-56						
1956-57	- .03	+ .05	+ .33	- .04	- .10	+ .24
1957-58					+ .38	+ .50
1958-59	+ .26	+ .34	+ .09	+ .08	+ .15	+ .10

season populations of adult bucks there is no clear evidence for an effect from illegal kill on the estimates. There is, of course, also a weakness in that the sex-age-kill estimates depend on an assumed "natural" mortality rate for adult bucks which cannot be very accurately checked with the data at hand.

Discussion. From the results given above, it seems that the index and the sex-age-kill estimates are most closely correlated, and one might infer from this that these are the best measures of population level. Such an inference depends strongly on the notion of independence and of a logical relationship to deer populations; presumably both could be spurious measures of population level and still be highly correlated. In view of the sources of the data, and of the general behavior of these measures, the logical inference seems to be that these are valid measures of deer population levels.

Some further support for the validity of these three sources as measures of true deer population levels may be drawn from the fact that the points representing the pellet-group-count and sex-age-kill estimates are about evenly divided by lines of equal population levels (Figures 26 and 27), although the more extreme deviations seem to be those of "high" pellet-group count estimates. Approximate confidence limits on the pellet-group-count estimates (Table 14) show that 4 out of 20 sets of limits fail to include the sex-age-kill estimate. This does not, of course, take into account the possible sampling error of the sex-age-kill estimates, which will also affect the agreement of the two sources.

While there is a great deal yet unexplained and unknown about the results summarized here, there seems to be good agreement in three independent sources of data on population level. Apparently the pellet-group

count results are sharply off in a few recent cases, and further investigation of possible causes seems essential, along with a continuation of the other methods as checks.

The possibility of bias in the pellet-group-count results makes any scheme for combining the three measures to get one single estimate of population level an uncertain procedure, and the fact that the index values are on a different scale further compounds the problem. Transforming the index to a deer-per-square-mile scale requires the adoption of one of the other two methods as a standard, and there is an additional complication in the lack of measures of sampling error for all but the pellet-group counts.

For the present, it seems to me best to make a more or less subjective choice of population levels for any given area by taking into account the known shortcomings of the three methods.

IV. SURVIVAL AND MORTALITY

The problem. Obtaining reliable estimates of survival rates may well be one of the most difficult and important problems facing persons responsible for deer herd management. The difficulties, in fact, are such that very few serious attempts have yet been made. Most of the efforts to date are either from limited areas or are "rules of thumb" derived largely from reproductive rates and sex ratios.

It must be granted that statements to the effect that a buck law can at most result in harvesting 10 per cent of the herd, or that a healthy herd can withstand a mortality of 40 per cent, have their place and utility. They do not, however, provide any degree of precision in setting harvest regulations, and may be downright misleading. If we are to make optimum use of the deer herd that can be sustained in any given area, it seems necessary to harvest adult bucks at a higher rate than adult does, and this ordinarily implies a higher buck mortality rate.

Herd composition and sampling problems. If survival rates for major individual segments of the population (generally adult males, adult females, and juveniles) are to be obtained, it is necessary to use estimates of the composition of the herd. Two or three general sources of data on composition may be considered: sight records, legal kill, and possibly deer accidentally killed on highways. Such data from sight records as are available on large areas of Michigan are not compatible with those collected in the hunting seasons; so the first source does not seem usable unless the

data are carefully collected by experienced biologists (see section on the sex-age-kill method).

Use of age and sex data obtained from samples of the legal kill is complicated by sampling and other problems, few of which are subject to any clear analytical solutions. Roadside checking stations in Michigan have been operated at points where it would be possible to sample the southward flow of deer. Two complications are that some 40 per cent of the deer killed each season are taken by residents of the areas in which the deer are killed and are not sampled, and that roadside checks are dependent on voluntary cooperation of the hunters. Hunters who take small deer may elect not to stop at the stations, and thus bias the samples. This point may not be serious since many hunters do not seem to realize that the checks are not compulsory.

Several attempts have been made in Michigan to check deer directly in the field, but the results have always been completely unsatisfactory in terms of numbers examined for a given expenditure of manpower. It seems to me that the present roadside system will have to be continued but we probably should attempt to institute special samplings to check on the validity of the data. These methods might include attempts to stop segments of traffic and interview hunters and the introduction of "marked" deer or cars into the flow of traffic above the checking stations.

If the checking station records are accepted as representative samples of the actual deer kill, there remain two further questions. The first difficulty is that, with the exception of 1952, Michigan seasons on antlerless deer have been so restricted that we have examined far more adult bucks than antlerless deer. I have attempted to avoid this problem by working with the two large herd segments (adult bucks and antlerless deer) separately, and by making the assumption that the $1\frac{1}{2}$-year-old class

of bucks and does is of equal size at the start of the hunting season.

The second problem is that the various age classes may not be equally vulnerable to hunting, or equivalently, that hunters show some selection in shooting deer. The principal difficulty is that hunters apparently do not take fawns in proportion to their numbers. Maguire and Severinghaus (1954) have presented evidence to show that "yearlings" are more vulnerable than older deer. Their methods of testing the change in age structure of the sample as the season progresses (which seems to be the only available measure of differential harvest) are questionable, but Chi-square tests on the data which they present seem to bear out the notion of a differential in some of the New York areas.

Results of Chi-square tests on Michigan data (Tables 1 and 16) are ambiguous, suggesting real changes in ratios in some cases, but not in others. Also, there is an important distinction between the cases (Tables 1 and 16) in which these tests have been applied. The harvest of adult bucks amounts to from 50 to 70 per cent of the population (Table 2), so that any important difference in vulnerability of the different age-classes can be expected to show up as a marked change in daily age-ratios. The harvest rates for antlerless deer are much lower, amounting to perhaps 5 to 10 per cent of the population (not counting illegal kills), so even a sizable difference in vulnerability may not result in a detectable shift in kill age composition. The 1952 season is an exception, inasmuch as a fairly large fraction of the antlerless herd was harvested in that year, and there was a definite change in the ratio of adult does to fawns during the three-day season. The 1952 data show (Figure 29) a linear relationship between the logarithms of adult:fawn ratios and cumulative hunting effort, as is to be expected from differ-

TABLE 16

RESULTS OF CHI-SQUARE TESTS OF HETEROGENEITY--COMPOSITION OF ANTLERLESS KILL BY DAY OF SEASON (NORTHERN LOWER PENINSULA)

Comparison	Year	Number of Deer Examined	Chi-square Value	Degrees of Freedom	Probability of Chi-square Value
$1\frac{1}{2}$-year-olds vs. older does	1957	1,258	7.63	9	$.50<p<.70$
	1958	2,499	18.31	10	.05
Fawns vs. adult does	1957	2,044	10.25	10	$.30<p<.50$
	1958	4,215	35.20	13	$p<.001$

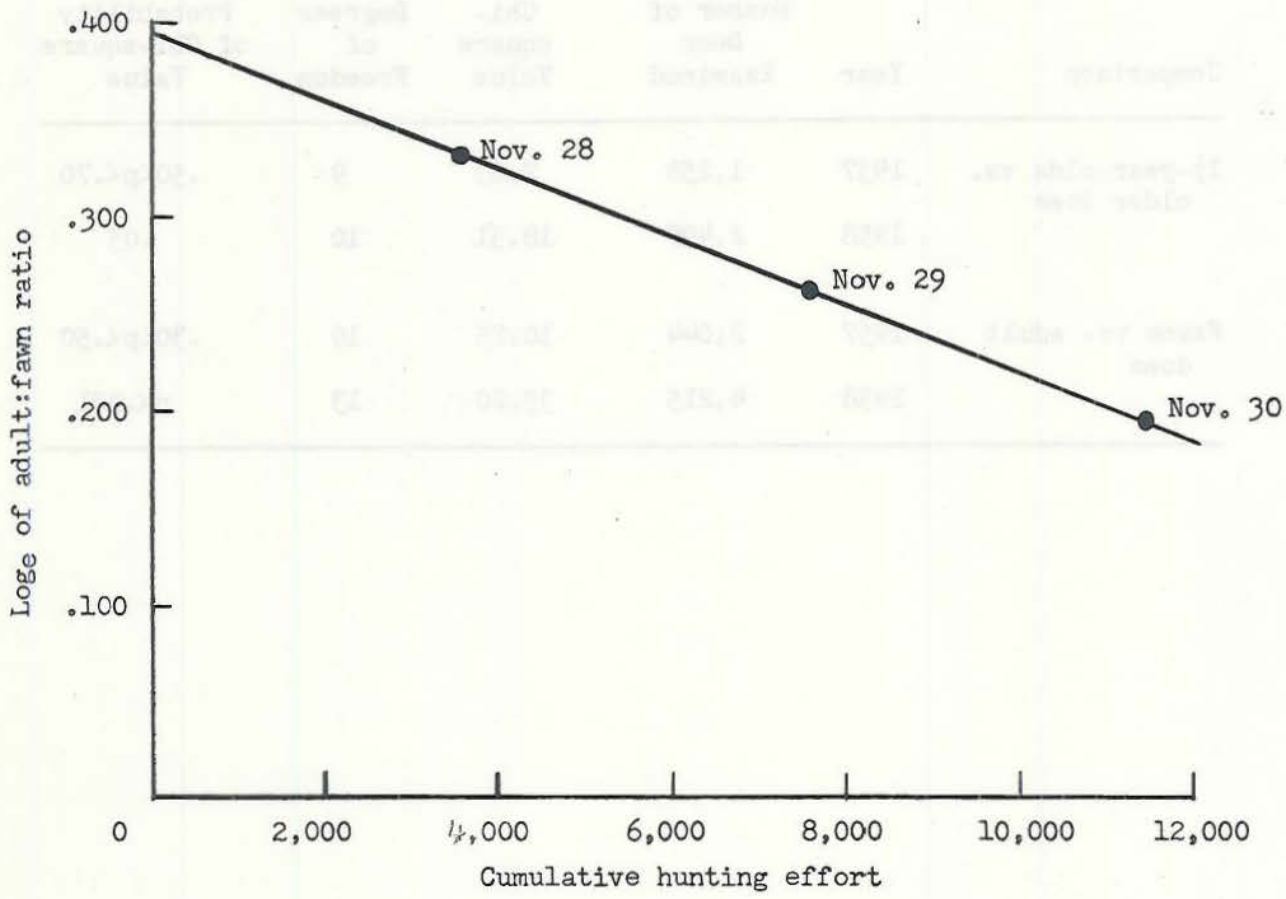


Figure 29. Adult:fawn ratios in 1952 special deer season compared to cumulative hunting effort reported on mail survey questionnaires.

ential vulnerability rates (Eberhardt and Blouch, 1955). There did not, however, seem to be any change in the ratio of adult bucks to adult does or of buck to doe fawns in the 1952 season.

Further evidence on the question of fawn:doe ratios is given later in this report; so far as adults are concerned, I believe that the $1\frac{1}{2}$-year-olds are slightly more vulnerable to hunting than are older deer, but adjustments for such an effect are complicated (Eberhardt and Blouch, 1955) and will not be attempted here.

Age determination. The deer-aging technique developed by Severinghaus (1949) may be subject to important errors of classification (Ryel et al., 1960). We are reasonably sure, however, that fawns and $1\frac{1}{2}$-year-olds can be identified with high accuracy. Errors no doubt increase proportionately with increasing age of the deer. Results of aging tests given more or less routinely to Michigan biologists show something of the reliability of the method, but the tests are given under laboratory conditions, while field conditions often leave much to be desired in the way of lighting and comfort, and ready access to key age criteria. Some rather extensive data on variations in the appearance of jaws of known age are given by Severinghaus (1949), and we are also building up a collection of "known-age" jaws which may throw some further light on the situation in Michigan (Ryel, et al., 1960).

As far as possible, I have limited the computations used here to fawn:adult and $1\frac{1}{2}$-year-old:older-deer ratios. While this restriction is desirable to avoid biases, it also results in the loss of information, because the ratios between successive age classes may provide a means of tying years together in a matrix of links, rather than the single chain provided by using only an annual ratio of $1\frac{1}{2}$-year-olds to all older deer.

Methods of estimating survival and mortality. The necessary ingredients for estimating survival rates are measures of population size and a knowledge of the sex and age composition. There are available in this report two principal sources of extensive population data--the index values and estimates from the sex-age-kill method. Pellet-group-count estimates might also be used, but are available on a much more limited basis.

Survival rates may also be estimated from age distributions alone, by measuring the rate of decline of successive age-groups. Application of this method has been described for deer by Hayne and Eberhardt (1952), but the original and most extensive use of the method is that of fisheries workers, and a detailed description is given by Ricker (1958) and others. As Ricker and also Beverton (1954) point out, the method is not very satisfactory unless some supplemental data are available, since the basic assumption of a constant recruitment rate is so seldom met in practice. The method does seem to agree fairly well with results from other sources insofar as buck populations are concerned, but its use for female deer is complicated by the fact that the female segment is the producing portion of the herd. Unless the female herd remains absolutely constant, it seems that the ratios used to estimate survival will actually be a composite of survival and reproductive rates, and thus of uncertain value. Consequently, little use will be made here of estimates from the age structure alone.

Rates obtained by comparison of the age structure and measures of population size at two successive points in time do not provide any information on the relative magnitude of losses from different causes. It would be possible to attempt to estimate survival for periods shorter than one year, but the appropriate data are lacking except on an annual basis.

Information on losses from specific causes is available, but usually only in the form of numbers of deer lost. Such data exist for Michigan as estimates of deer harvested legally in the hunting seasons, and from the results of a few extensive field surveys. Since such figures are available as specific numbers of deer, and the overall mortality may be available only as a rate, it is apparent that the total population size must also be known for effective use of both sources of information.

Survival rate calculations are reported here for deer populations by District, since most of the population and kill data are available on that basis and because much Michigan herd management is geared to the District mechanism.

Survival estimates based on index population data. Estimates utilizing the combined index data (for population level in successive years) are given here in three steps (Table 17). The technique consists of: (1) estimating the composition of the herd from the kill data, using the assumption of equal numbers of $1\frac{1}{2}$-year-old does and bucks to tie together the antlered and antlerless segments of the herd, (2) prorating the index value for a given year among the several classes of interest, and, (3) determining survival estimates from the ratio of a particular class to the same group one year earlier.

As an illustration, the survival of adult does was computed (Table 17) for 1952-53 in District 5 as follows: The combined index value for all adult does in 1952 was determined to be 5.22, and the value for $2\frac{1}{2}$-year-old and older does in 1953 as 3.23. The ratio of these two values, .62, is the estimated survival of adult does from early November of 1952 to the same date in 1953.

TABLE 17

SURVIVAL ESTIMATES FROM INDEX DATA

PART A: Herd Composition (proportions)

District	Year	Adult Bucks	1½-Year-Old Does	2½-Year-Old and Older Does	Buck Fawns	Doe Fawns
5	1952	.185	.112	.334	.206	.163
	1953	.172	.124	.317	.204	.183
	1954	.234	.148	.330	.139	.148
	1955*					
	1956	.203	.115	.395	.112	.175
	1957	.197	.126	.355	.128	.195
	1958	.215	.149	.341	.157	.138
6	1952	.179	.118	.308	.197	.198
	1953	.170	.132	.309	.193	.194
	1954	.171	.128	.378	.171	.150
	1955*					
	1956	.180	.116	.358	.180	.166
	1957	.186	.129	.357	.168	.159
	1958	.201	.145	.299	.208	.147
7	1952	.173	.116	.331	.208	.172
	1953	.200	.162	.310	.162	.166
	1954	.224	.146	.369	.149	.111
	1955*					
	1956	.182	.104	.405	.150	.158
	1957	.215	.138	.343	.165	.139
	1958	.196	.134	.352	.176	.142
8	1952	.174	.133	.298	.205	.189
	1953					
	1954					
	1955*					
	1956	.206	.149	.378	.151	.115
	1957	.217	.146	.344	.169	.123
	1958	.205	.156	.303	.189	.147
9	1952	.176	.118	.340	.194	.171
	1953					
	1954					
	1955*					
	1956	.190	.146	.366	.151	.146
	1957	.152	.109	.420	.188	.130
	1958	.190	.138	.333	.201	.138

*No special season in northern Michigan in 1955.

TABLE 17--Continued

PART B: Index values assigned to various classes

District	Year	Index Value	1½-Year-Olds	2½-Year-Old and Older Does	Total Does	Doe Fawns	Buck Fawns
5	1952	11.7	1.31	3.91	5.22	1.91	2.41
	1953	10.2	1.26	3.23	4.49	1.87	2.08
	1954	9.9	1.46	3.27	4.73	1.46	1.38
	1955	10.8					
	1956	10.9	1.25	4.30	5.55	1.91	1.22
	1957	10.8	1.36	3.83	5.19	2.11	1.38
	1958	11.6	1.73	3.96	5.69	1.60	1.82
6	1952	10.5	1.24	3.23	4.47	2.08	2.07
	1953	7.3	.96	2.26	3.22	1.42	1.41
	1954	7.6	.97	2.87	3.84	1.14	1.30
	1955	7.3					
	1956	8.2	.95	2.94	3.89	1.36	1.48
	1957	7.6	.98	2.71	3.69	1.21	1.28
	1958	8.0	1.16	2.39	3.55	1.18	1.66
7	1952	18.0	2.09	5.96	8.05	3.10	3.74
	1953	17.2	2.79	5.33	8.12	2.86	2.79
	1954	16.4	2.39	6.05	8.44	1.82	2.44
	1955	15.9					
	1956	14.7	1.53	5.95	7.48	2.32	2.20
	1957	14.7	2.03	5.04	7.07	2.04	2.42
	1958	16.8	2.25	5.91	8.16	2.38	2.96
8	1952	8.4	1.12	2.50	3.62	1.59	1.72
	1953	7.2					
	1954	7.3					
	1955	7.6					
	1956	8.6	1.28	3.25	4.53	.99	1.30
	1957	7.9	1.15	2.72	3.87	.97	1.34
	1958	8.8	1.37	2.67	4.04	1.29	1.66
9	1952	8.2	.97	2.79	3.76	1.40	1.59
	1953	6.8					
	1954	7.3					
	1955	7.3					
	1956	8.0	1.17	2.93	4.10	1.17	1.21
	1957	8.4	.92	3.53	4.45	1.09	1.58
	1958	8.1	1.12	2.70	3.82	1.12	1.63

TABLE 17--Continued

PART C: Balance of index data and survival estimates

District	Year	Index Values: $2\frac{1}{2}$-Year-Old and Older Bucks	Index Values: Total Adult Bucks	Survival Rates: Adult Does	Survival Rates: Doe Fawns	Survival Rates: Adult Bucks	Survival Rates: Buck Fawns
5	1952	.85	2.16	.62	.66	.23	.52
	1953	.49	1.75	.73	.78	.48	.70
	1954	.85	2.32				
	1955						
	1956	.96	2.21	.69	.71	.35	
	1957	.77	2.13	.76	.82	.36	
	1958	.76	2.49				
6	1952	.64	1.88	.50	.46	.15	.46
	1953	.28	1.24	.89	.68	.27	.69
	1954	.33	1.30				
	1955						
	1956	.52	1.48	.70	.72	.29	.66
	1957	.43	1.41	.65	.96	.32	.91
	1958	.45	1.61				
7	1952	1.03	3.11	.66	.90	.21	.74
	1953	.65	3.44	.74	.84	.23	.86
	1954	.78	3.67				
	1955						
	1956	1.15	2.68	.67	.88	.42	.92
	1957	1.13	3.16	.84		.33	.93
	1958	1.04	3.29				
8	1952	.34	1.46				
	1953						
	1954						
	1955						
	1956	.49	1.77	.60		.32	.88
	1957	.56	1.71	.69		.25	
	1958	.43	1.80				
9	1952	.48	1.44				
	1953						
	1954						
	1955						
	1956	.44	1.52	.86	.78	.24	.76
	1957	.36	1.28	.61		.33	.71
	1958	.42	1.54				

Survival estimates from the sex-age-kill method. Survival rates may also be determined (Table 18) from population sizes estimated by the sex-age-kill method. Only adult females are considered here, inasmuch as survival estimates have already been given for adult bucks (Table 2), and estimates for fawns seem seriously biased. Essentially the same scheme applies as for the index population data, but estimates of total population numbers are used rather than index values. The principal advantage is that these numerical estimates of total losses may be compared directly with results of "dead deer" surveys. A disadvantage seems to be the rather erratic fluctuations of these estimates in comparison to those from index values. I have no way of being sure which of the two situations is actually occurring in the herd; possibly survival may fluctuate considerably from year to year, but rather smooth population trends seem more realistic under most conditions.

Survival estimates from age distributions alone. A third possibility for estimating annual survival rates is that of analysis of the age structure. The estimates (Table 19) are based on the ratio of $2\frac{1}{2}$-year-old and older does to all adult does in a given year, as described by Hayne and Eberhardt (1952). Presumably estimates might also be prepared from other combinations of the age data, but I have used only the separation between $1\frac{1}{2}$-year-old and older deer due to the uncertain accuracy of the aging techniques. Comparison of the survival estimates for adult females from the three sources (Figure 30) shows considerable fluctuation, but fairly good overall agreement between the sex-age-kill and combined index data. The estimates from age structure alone do not seem to agree very well with the other sources and seem to hold rather closely to an average value (about .70). As previously mentioned, these estimates

TABLE 18

ADULT DOE SURVIVAL ESTIMATES FROM DISTRICT POPULATION DATA

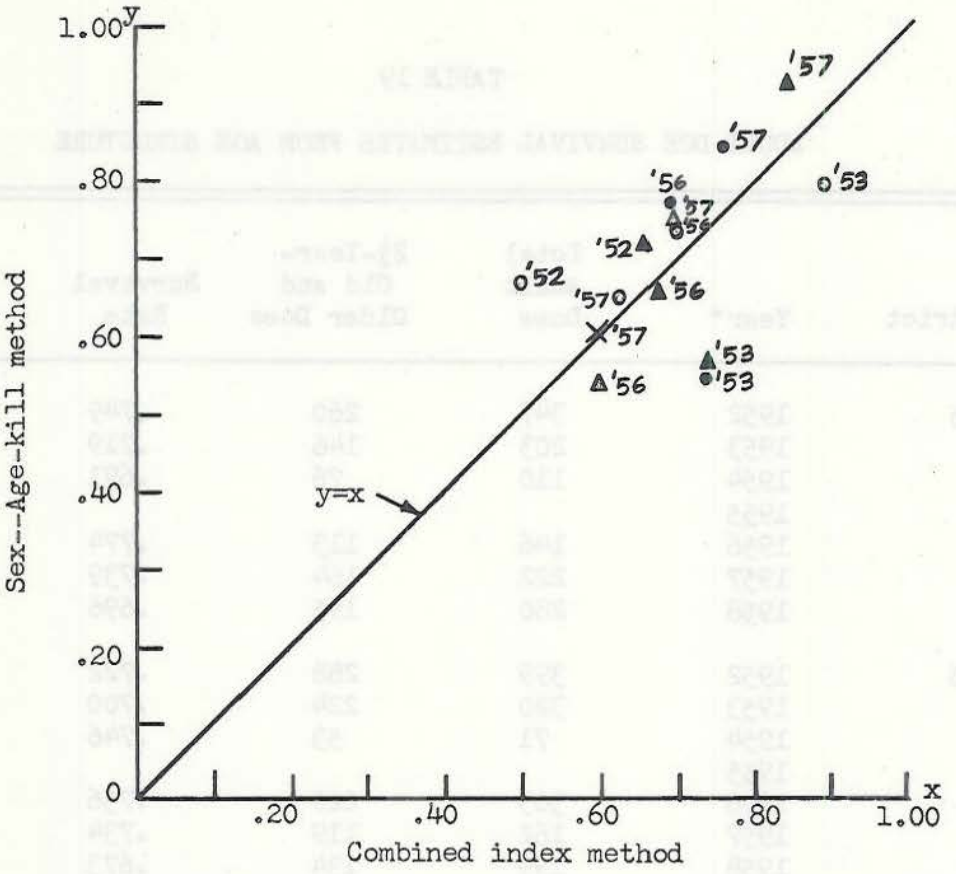
District	Year	1½-Year-Old Does	2½-Year-Old and Older Does	Total Doe Population	Survival Rate	District Average
5	1952	9,260	27,590	36,850		
	1953	14,800	37,830	52,630	.535	
	1954	12,390	28,150	40,540		
	1955					.718
	1956			43,300	.775	
	1957	11,850	33,550	45,400	.844	
	1958	16,640	38,310	54,950		
6	1952	5,530	14,340	19,870	.669	
	1953	5,720	13,290	19,010	.802	
	1954	5,010	15,250	20,260		.714
	1955					
	1956	4,960	15,380	20,340	.739	
	1957	5,460	15,040	20,500	.647	
	1958	6,470	13,260	19,730		
7	1952	15,760	45,200	60,960	.716	
	1953	22,700	43,680	66,380	.557	
	1954	14,640	36,990	51,630		.707
	1955					
	1956	10,170	39,660	49,830	.649	
	1957	12,920	32,320	45,240	.917	
	1958	15,820	41,470	57,290		
8	1952	6,960	15,490	22,450		
	1953					
	1954					
	1955					
	1956	6,670	16,940	23,610	.541	
	1957	5,400	12,780	18,180	.811	.676
	1958	7,570	14,750	22,320		
9	1952	5,310	15,340	20,650		
	1953					
	1954					
	1955					
	1956	5,900	14,900	20,800		
	1957	6,520	24,700	31,220	.602	
	1958	7,650	18,810	26,460		

TABLE 19

ADULT DOE SURVIVAL ESTIMATES FROM AGE STRUCTURE

District	Year*	Total Adult Does	2½-Year-Old and Older Does	Survival Rate	District Average
5	1952	347	260	.749	
	1953	203	146	.719	
	1954	110	76	.691	
	1955				.728
	1956	146	113	.774	
	1957	222	164	.739	
	1958	280	195	.696	
6	1952	399	288	.722	
	1953	320	224	.700	
	1954	71	53	.746	
	1955				.722
	1956	303	229	.756	
	1957	162	119	.734	
	1958	199	134	.673	
7	1952	1,183	877	.741	
	1953	841	553	.658	
	1954	380	272	.716	
	1955				.725
	1956	357	284	.796	
	1957	399	285	.714	
	1958	580	420	.724	
8	1952	1,164	804	.691	
	1953				
	1954				.692
	1955				
	1956	1,008	723	.717	
	1957	709	498	.702	
	1958	574	379	.660	
9	1952	595	442	.743	
	1953				
	1954				.740
	1955				
	1956	105	75	.714	
	1957	73	58	.794	
	1958	82	58	.707	

*Year in which age samples were collected; survival rates actually apply to previous year.



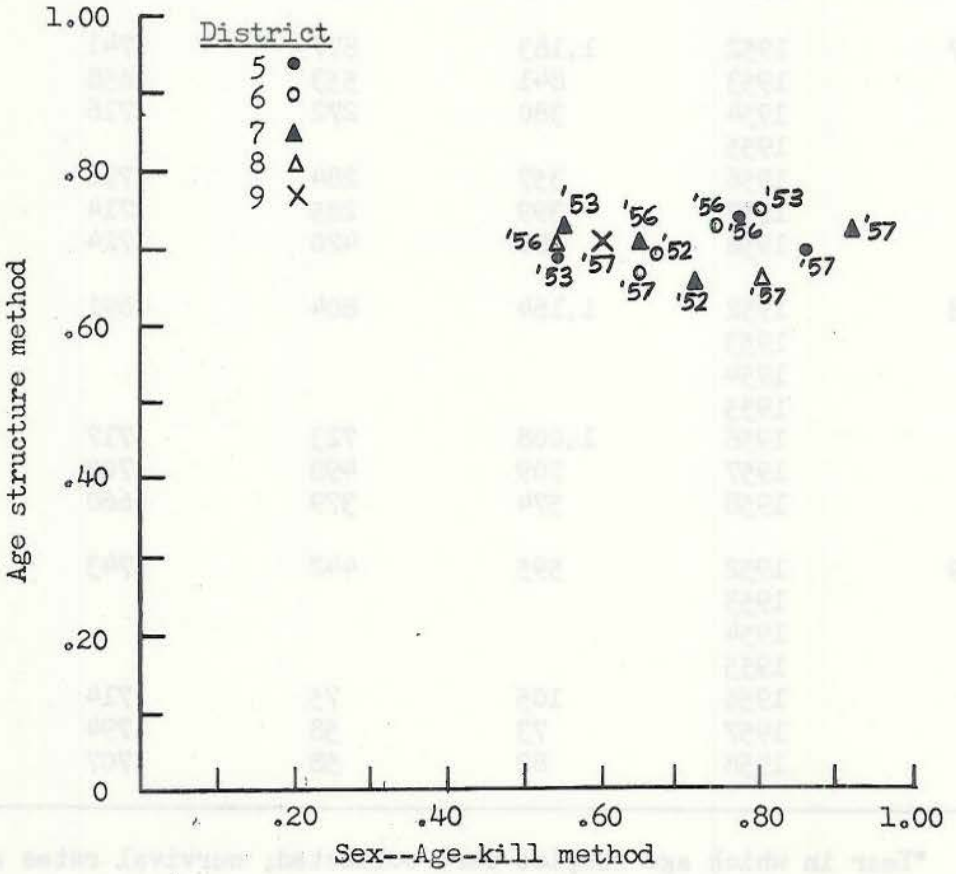


Figure 30. A comparison of estimates of adult doe survival rates as obtained by three methods.

from age structure alone are based on doubtful assumptions and perhaps can be expected to approximate only roughly the average rate of survival over a series of years, provided the population does not fluctuate greatly.

Adult buck survival rates. A comparison of buck survival estimates from two sources (index data and buck population data) demonstrates (Figure 31) a reasonably close relationship, but the estimates from buck population data tend to be higher than those from the index data. Reasons for the difference are not clearly evident. One might suppose that the natural mortality rate assumed in the buck population estimates was too low, but it can be shown (see section on buck population estimates) that the survival estimates there depend on the "recruitment" rates and not on the assumed natural mortality rates (the effect of using a different natural mortality rate is to change the estimated population size).

Another possibility is the likelihood that fawns are under-represented in the age composition data. The effect of under-representation of fawns will be to raise the index values assigned to other segments of the population in Table 17. Overestimation of the relative size of the buck population will not, however, necessarily have any effect on the survival estimates. If the bias is a constant factor, no effect will be exerted on the survival estimates.

The average difference (Table 20) between the two estimates is about .02, and a "t" test suggests that the difference is real (significant at 5 per cent level). I have been unable to arrive at any satisfactory explanation of the difference, but we can probably tolerate an error of this magnitude in the present state of our information. Certainly the overall agreement indicates that these survival rates have a sound factual

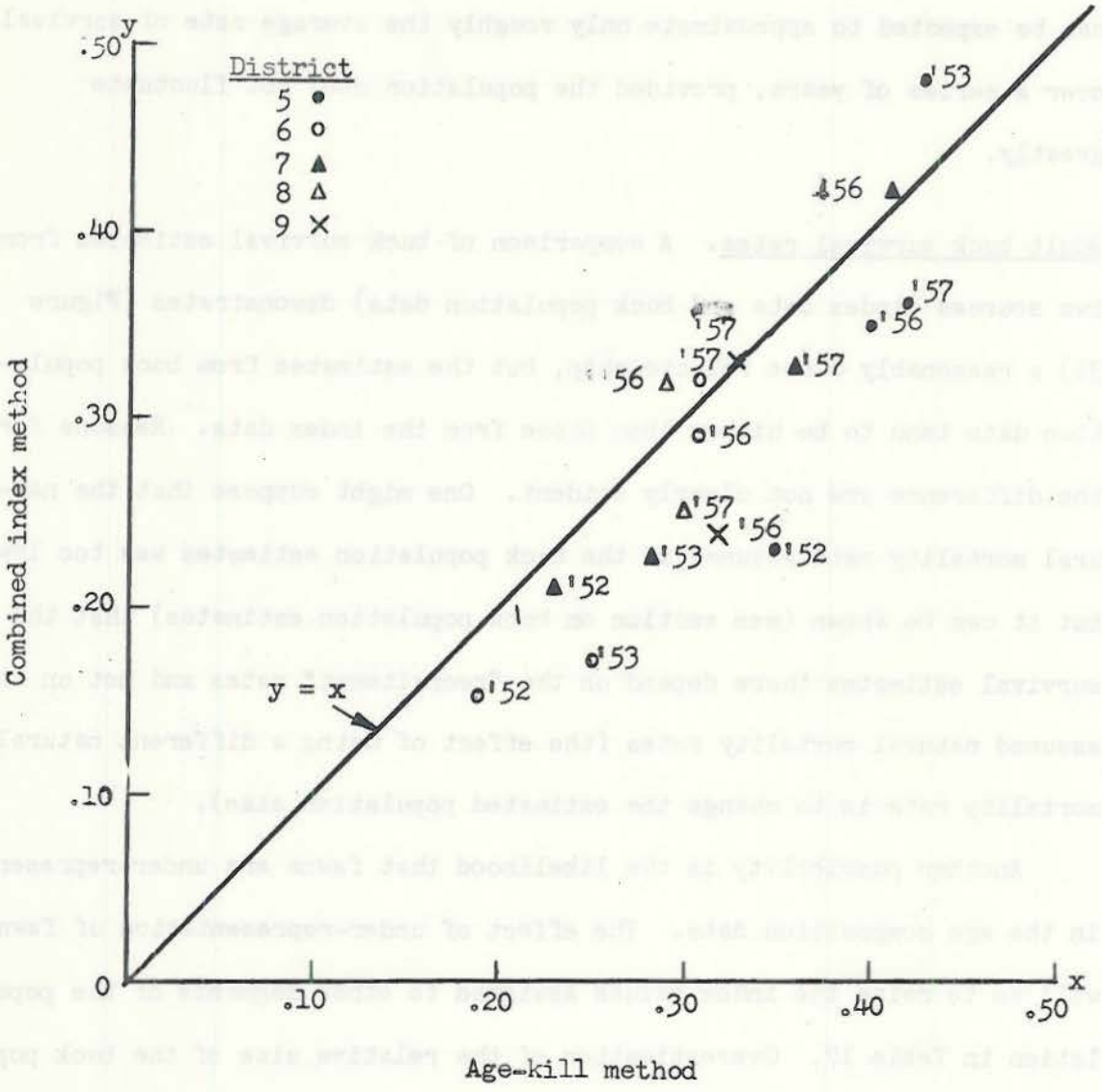


Figure 31. A comparison of estimates of adult buck survival rates as obtained by two methods.

TABLE 20

COMPARISON OF ADULT BUCK SURVIVAL ESTIMATES FROM TWO SOURCES

District	Year	From Index Data	From Age-Kill Data	Differences
5	1952	.23	.35	-.12
	1953	.48	.43	.05
	1956	.35	.40	-.05
	1957	.36	.42	-.06
6	1952	.15	.19	-.04
	1953	.27	.25	.02
	1956	.29	.31	-.02
	1957	.32	.31	.01
7	1952	.21	.23	-.02
	1953	.23	.28	-.05
	1956	.42	.41	.01
	1957	.33	.36	-.03
8	1956	.32	.29	.03
	1957	.25	.30	-.05
9	1956	.24	.32	-.08
	1957	.33	.33	0
Sums		4.78	5.18	-.40
Means		.299	.324	-.0250

Variance of differences = .001947

Standard error = .01103

$$t = \frac{.025}{.0110} = 2.27$$

basis as measures of the population characteristic under consideration.

In general, the estimates of survival seem reasonably satisfactory, excepting the unknown effect of the under-representation of fawns. In Figures 30 and 31, estimates for 1952 and 1953 show the greatest deviations. This may be a consequence of the relatively large proportion of the herd harvested in 1952 (followed by the second largest antlerless harvest in 1953). Also, most of the procedures on which these estimates depend were first put into full scale operation in 1952--in any such situation, some time is no doubt needed to develop a routine leading to consistent information.

Components of mortality. So far, only overall survival rates have been considered. While these rates are essential to any useful analysis of deer population dynamics, a maximum management value is possible only if the information can be used to determine procedures leading to fullest utilization of the deer herd. This process will require a knowledge of the component causes of herd losses. Not enough information is now available to do this accurately, but an attempt is made here to provide a rough notion of the general situation.

Survival rates and hunting effort. Fisheries workers (Ricker, 1958, Beverton, 1954) have used estimates of overall survival and fishing effort to compute fractions of mortality assignable to fishing and to "natural" causes (all losses other than fishing). If natural mortality takes a constant fraction of the population, and if fishing effort fluctuates considerably from year to year, a plot of logarithms of total mortality coefficients against fishing effort should show approximately a linear relationship (Beverton, 1954, pp. 103-105). As will be shown later in

this section, there is reason to believe that illegal kill in the hunting season is a major cause of adult doe mortality. One might then expect that such losses would vary from year to year in accordance with hunting effort. Plotting the logarithms of mortality coefficients against hunting effort data (Figure 32) does not, however, show a consistent behavior. Possibly total hunting effort is not a good criterion for measurement of the force of mortality from illegal kill. Alternatively, doe mortality from other causes (natural mortality) may not be constant from year to year, nor from area to area.

A somewhat different approach is to consider the relationship of estimates of adult doe survival to those for bucks (Figure 33). In this case there seems to be some evidence of consistency within individual Districts. Such consistency might logically be expected and it is demonstrated below that mortality from legal harvest has been only a minor item in losses to the antlerless herd in almost all years considered here (except 1952). The only major identifiable cause of adult buck mortality seems to be legal harvest--so that a correlation between the two sets of survival coefficients suggests a high inseason illegal kill of adult does.

Legal harvest. Legal harvest estimates for the special seasons since 1952 (Table 21) are based on the mail survey questionnaires previously mentioned in this report.

Mortality surveys. Losses from sources other than legal harvest are difficult to measure, and the Michigan data are available only as estimates for very large areas. The principal source here is mortality surveys conducted in the springs of 1955, 1956, and 1959. These surveys

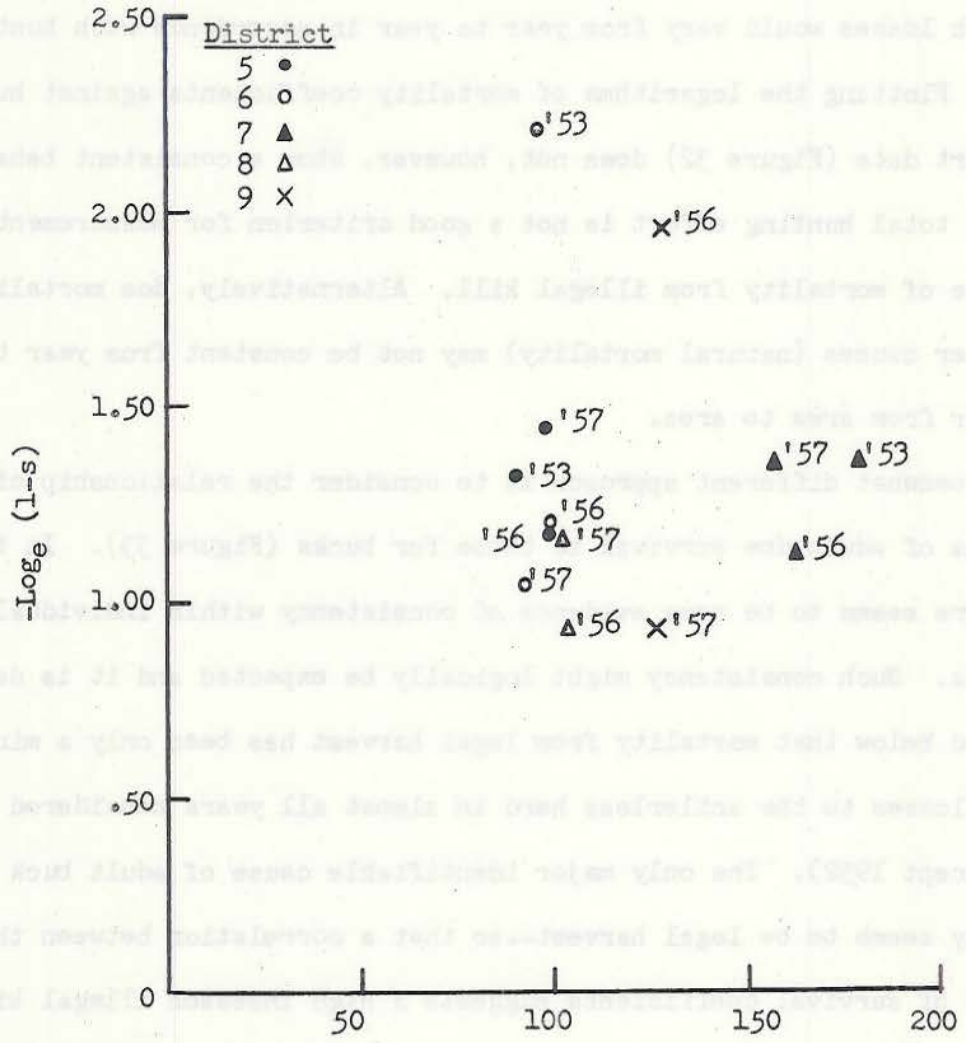


Figure 32. Negative natural logarithms of adult doe mortality estimates compared to levels of hunting effort.

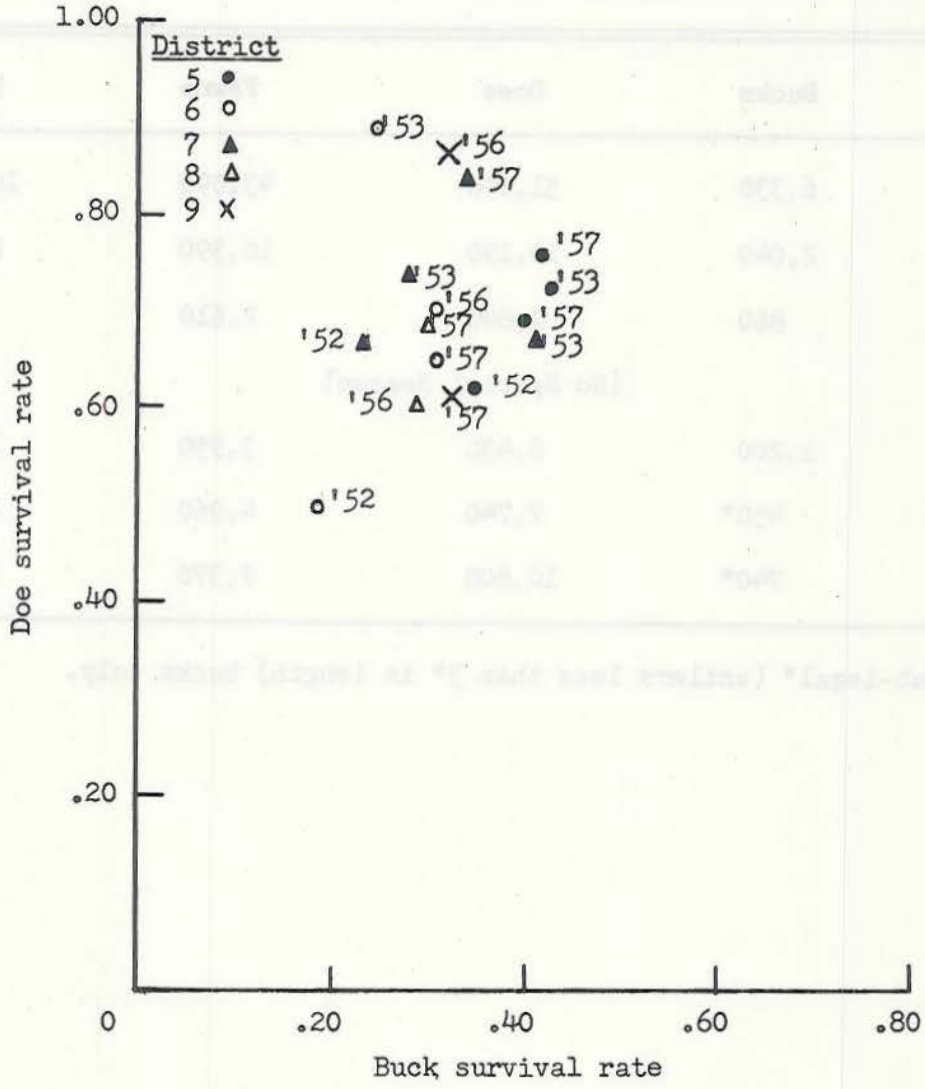


Figure 33. A comparison by sex of estimated survival rates for adult deer.

TABLE 21

DEER KILL IN NORTHERN LOWER PENINSULA SPECIAL SEASONS

Year	Bucks	Does	Fawns	Total
1952	6,330	51,100	43,090	100,520
1953	2,040	14,190	10,390	26,620
1954	880	4,840	2,610	8,330
1955		(No Special Season)		
1956	1,200	6,430	3,950	11,580
1957	450*	7,740	4,960	13,150
1958	740*	10,800	7,370	18,910

*"Sub-legal" (antlers less than 3" in length) bucks only.

were chiefly based on the need for measures of the losses caused by starvation, and are thus probably not typical of the span of years covered by this report.

The methods used in the surveys are described by Whitlock and Eberhardt (1956). The surveys were designed to yield estimates having roughly 25 to 30 per cent confidence limits (two standard errors expressed as a percentage of the estimated total) on overall losses, and thus are not very precise for estimates on sub-areas or components of loss. Furthermore, the cause of death frequently could not be determined accurately, except that a majority of the animals examined could definitely be assigned to starvation or non-starvation categories by inspection of the bone marrow. In many cases, the bone marrow condition was such that death could be presumed to have occurred in the fall or early winter before the stresses of winter conditions and short food supplies reduced fat content of the marrow.

The period covered by the surveys has been defined as from November 15 to the median date of the survey (usually mid-April). In general, carcasses of deer killed before early November will show sufficient signs of decay to be separated from those of deer dying after cold weather begins, but some overlap is inevitable. A number of marked carcasses were placed in a variety of locations throughout the fall months and examination the following spring seemed to confirm the notion that we could separate early fall deaths from "over-winter" losses.

Various details of the surveys and their results are given in the publication mentioned above and in a series of Game Division reports (Eberhardt, 1955, 1956a, 1956b, 1957c, Ryel and Eberhardt, 1959). Due to the relatively small numbers of deer actually examined (usually 100 or less), uncertainties about cause of death, and the rather wide distribution

of the reports to the general public, survey results by sex and age classification have not previously been published. Since comparable information is available from no other source, such a breakdown is presented here (Table 22). The "disease" category is not very meaningful since only very rarely is there sufficient evidence to justify the assumption that a carcass is of a deer killed by disease.

We have not made systematic rechecks in any of the surveys, but there have been instances where carcasses were known to be missed on survey plots. While the men working on these surveys have been almost exclusively Conservation Department employees and conscientious about the job, it is also true that we have had to use large numbers of men (up to 100 in one year) and both interest and ability may tend to fall off after a day or two of wading through the swamps in which many plots fall (due to stratification for the high loss areas of winter deer concentrations). I am inclined to believe that the survey crews may have missed as much as one-third of the carcasses actually on the survey plots. This supposition is almost entirely a guess, however--but it does seem certain that not all of the dead deer on the sample plots were found.

These surveys do not, of course, account for any deer removed from the areas (by poaching) and cover only about half of the year. They do support the assumption that very few adult bucks are lost from causes other than legal hunting. The non-hunting mortality rate used in this report for adult bucks amounts to about 10 per cent of the bucks surviving the hunting season. Assuming (Table 2) an average fall population of about 60,000 bucks in the northern Lower Peninsula and a kill of about 40,000 gives non-harvest losses of about 2,000. Roughly 1,000 of these losses are accounted for by the surveys, leaving about a thousand for losses at other times of the year and for poaching.

TABLE 22

SUMMARY OF RESULTS OF DEER MORTALITY SURVEYS

Sex and Age Class	Year	Cause of Death								Total Non-starvation Losses
		Shot	Fall or Early Winter	Starved	Dog or Predator	Accident	Disease	Cause Completely Unknown	Totals	
Adult males	1955	1,741	0	0	0	0	0	0	1,741	
	1956	0	394	0	0	0	0	0	394	
	1959	0	0	0	0	707	0	0	707	
Adult females	1955	7,086	1,447	852	0	143	0	0	9,528	8,676
	1956	4,127	6,602	2,512	689	0	0	0	13,930	11,418
	1959	2,478	2,611	1,270	671	1,453	0	0	8,483	7,213
Juveniles	1955	5,451	6,487	4,566	0	594	0	0	17,098	12,532
	1956	1,318	3,807	14,084	2,732	1,083	0	0	23,024	8,940
	1959	4,041	5,364	11,835	0	708	1,153	671	23,772	11,937
Unknown	1955	0	2,374	0	1,776	0	0	0	4,150	
	1956	234	4,064	0	0	0	0	0	4,298	
	1959	0	0	0	0	0	0	944	944	
Total	1955	14,278	10,308	5,418	1,776	737	0	0	32,517	
	1956	5,679	14,867	16,596	3,421	1,083	0	0	41,646	
	1959	6,519	7,975	13,105	671	2,868	1,153	1,615	33,906	

Known vs. unknown losses. Adult doe survival rates estimated here (Tables 17 and 18) average about .70. Using an average northern Lower Peninsula adult doe population of about 150,000 (Table 4) gives an annual mortality of about 45,000 adult does. Direct estimates account for the following losses (as averages of the available data):

November 15 to April 15

Legal harvest	7,000	(plus a few hundred illegal kills salvaged by Conservation Officers)
Overwinter losses	16,000	(assuming one-third missed in the field surveys)
Subtotal	23,000	

April 15 to November 15

Archery kill (October 1 - November 5)	1,000	
Highway mortality	600	(assuming about half of these killed are actually tallied; our records show that half of the total are adult does, and about 60 per cent of total losses occur in this period)
Subtotal	1,600	

Thus a little more than half of the total losses are established as occurring in the over-winter period and some 20,000 losses remain not accounted for. Little evidence exists to show that disease or plant poisoning are important causes of death (Fay, et al., 1956, Youatt, et al., 1959, Fay and Youatt, 1959). Various sorts of accidents do occur, but cannot be major causes of mortality.

Probably the only factor of real importance not covered above is poaching. We have almost no data on such losses, other than the general knowledge that a number of people take deer out of season, some for needed food, others for the sport of "getting away with it." Much of the latter category of poaching seems to occur in the early fall, and the former

removals may be somewhat more prevalent in mid-winter when funds from summer work begin to run short. These unaccounted-for losses seem numerically large, but, when spread over some 16,000 square miles and six or more months of the year, they can scarcely be expected to be very noticeable.

Probably non-hunting mortality is greater from late fall to early spring than during the rest of the year, but I cannot establish this as being definitely true. The supposed concentration of poaching losses in early fall may well mean that late spring and summer losses are the smallest of the year in the adult category.

Illegal kill in the hunting season. The available evidence indicates that the illegal kill of does and fawns during the hunting season under a "bucks-only" regulation is of considerable magnitude. Records of various checks substantiating this supposition in Michigan go back to the 1930's, but for the most part the information is patchy in scope and there is usually little evidence as to the thoroughness of any given check. Hickey (1955) summarized a variety of information, and concluded that the illegal kill under "bucks-only" regulations will usually amount to about half of the legal harvest. Perhaps the only extensive data from sound sampling methods are those already given (Table 22) for the dead deer surveys. The chief difficulty in interpreting the data is that much of the loss could only be classified as "fall or early winter." I believe that only shooting could be responsible for most of these deaths, and the very limited nature of special seasons in these years precludes assigning many of the losses to crippling by permit-holders (there was no special season in 1955, so crippling losses cannot be responsible for any of the antlerless deer found

dead in the survey of the spring of 1956).

It is uncertain whether such losses can be materially reduced. A little encouragement may be drawn from the fact that the lowest estimate of such loss was that of the 1959 survey, after the largest concurrent special season harvest of our limited experience with such seasons. Some further support for the suspicion that illegally killed deer may be salvaged by permit-holders (probably not as much in the sense of actually finding and claiming such a deer, as by "tagging" an antlerless deer accidentally shot by another member of the party) is available from the results of a special study conducted in 1956. Both a field mortality survey and a mailed questionnaire were used to compare two areas, one having a "concurrent" and the other a "subsequent" special season. The data are summarized in Game Division reports (Eberhardt 1957c, 1957d) and are scarcely conclusive, but do suggest some diminution of the illegal losses under concurrent hunting regulations.

Fawn survival. The fawn survival estimates of Table 17 are suspect for reasons previously enumerated in this report. The following is an attempt to make a rough estimate of the actual rates.

Three measurements of female adult:juvenile ratios are available: (1) Embryo counts from accidentally killed adult females (chiefly highway kills: Eberhardt and Fay 1957, 1958, 1959). (2) Fawn:doe ratios in hunting seasons (ratio of fawns to $2\frac{1}{2}$-year-old and older does, since only a small number of yearlings bear fawns in northern Michigan). (3) Ratios of $1\frac{1}{2}$-year-olds to $3\frac{1}{2}$-year-old and older does in the second hunting season following the embryo counts.

The embryo counts are from rather small samples (on the order of 100 or so does annually for the northern Lower Peninsula), and are thus

summarized for two broad areas only (the "Northeast" or critically over-browsed area, and all other northern Lower Peninsula areas). I have consequently used hunting season data from two Districts (6 and 7) as being most comparable to the two areas for which the embryo counts are summarized (Figure 34).

Comparisons (Figure 35) suggest that differences in fawn production, rather than fawn survival, are responsible for variations in reproduction in the two areas as well as from year to year (adult doe survival seems to be about the same over the entire peninsula--Tables 17 to 19). The relationship (Figure 36) between the two kinds of hunting season ratios is rather less consistent, but much of the discrepancy seems connected with the concurrent seasons where, as previously mentioned, fawns are less readily taken by hunters.

Attempts at estimating fawn survival may be made as follows:

(1) Survival for the first six months of life:

Let s_1 = fawn survival for the first six months of life.

s_2 = doe survival for the same period.

F = fawn population at birth (actually as embryos).

D = doe population at the same time.

Then the average ratio of the two sets of fawn:doe ratios (top part of Figure 35) may be expressed as follows:

$$\frac{\frac{s_1 F}{s_2 D}}{\frac{F}{D}} = \frac{s_1}{s_2} = .65$$

The numerical value provided here (.65) is simply that of a line drawn approximately through the plotted points (Figure 35). Fawn survival rates corresponding to various doe survival rates

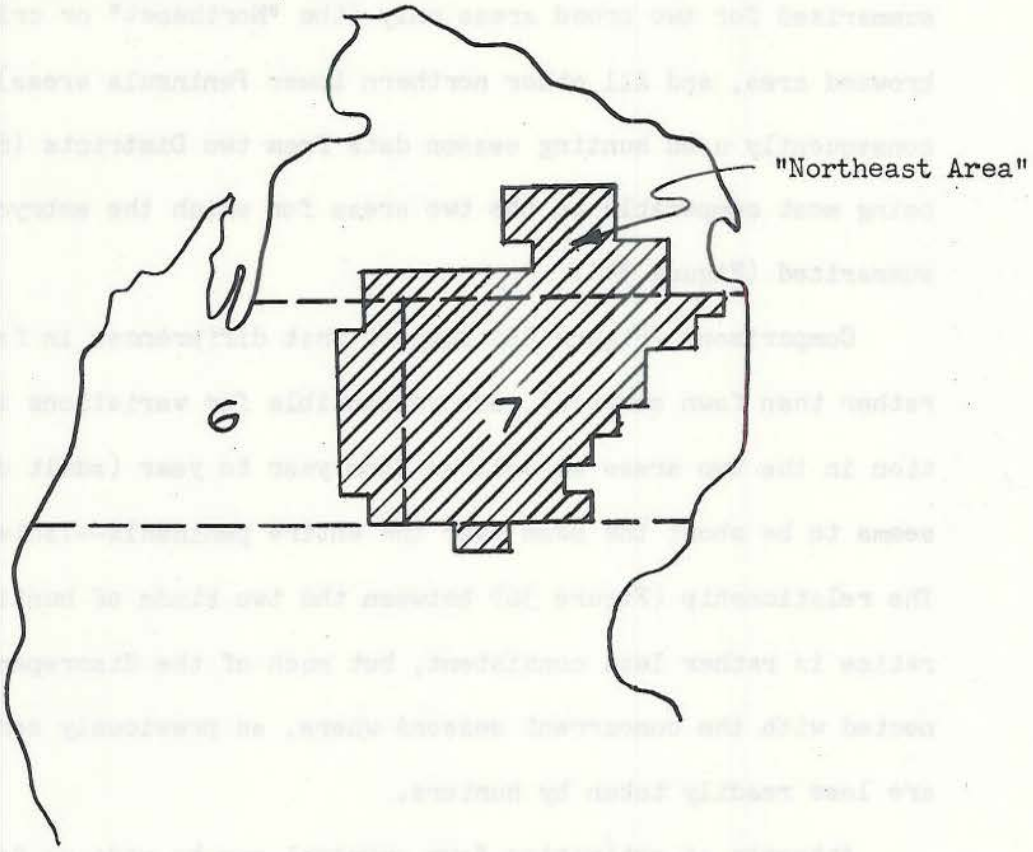


Figure 34. The "Northeast Area" and Game Management Districts 6 and 7.

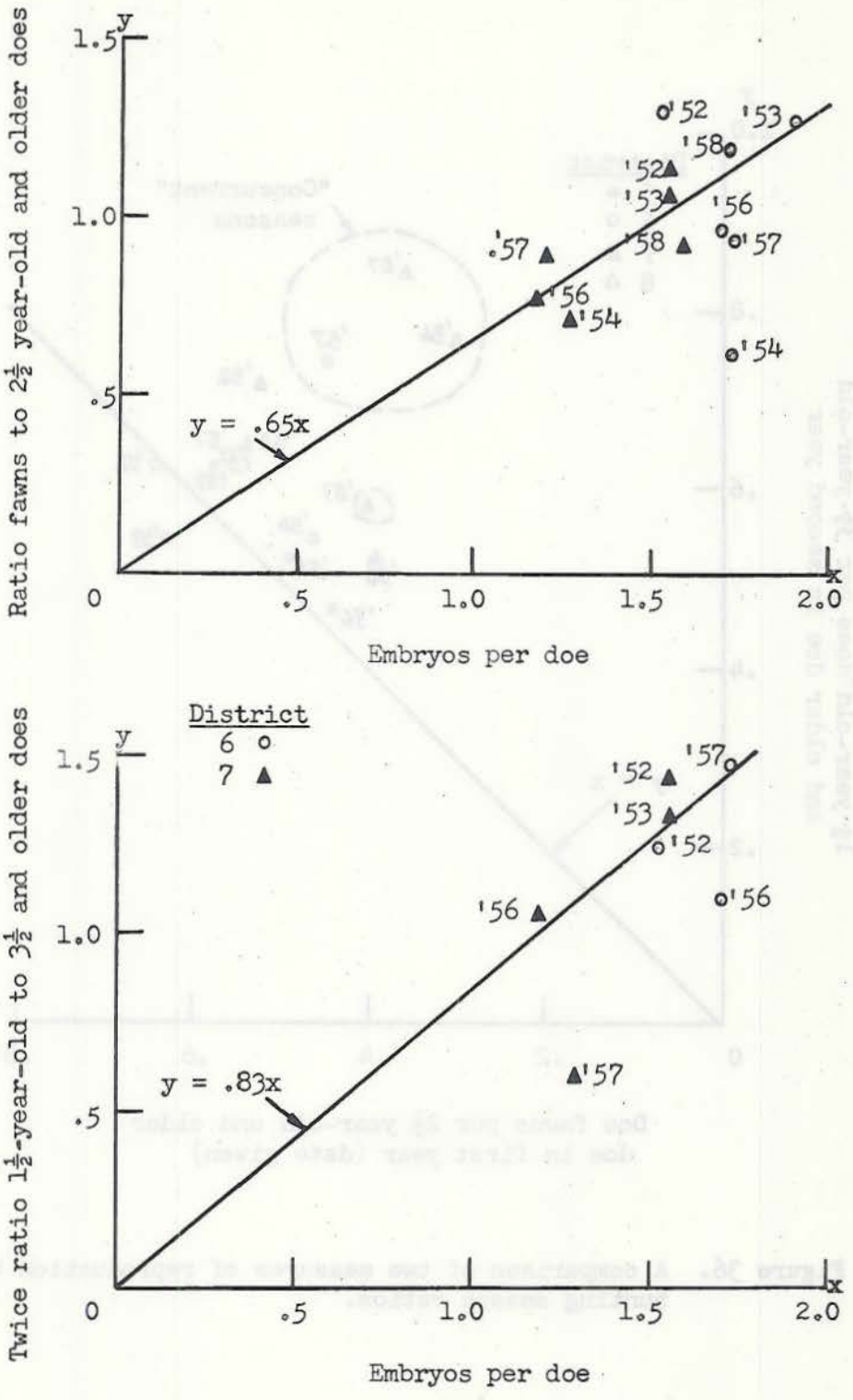


Figure 35. Three measures of fawn production.

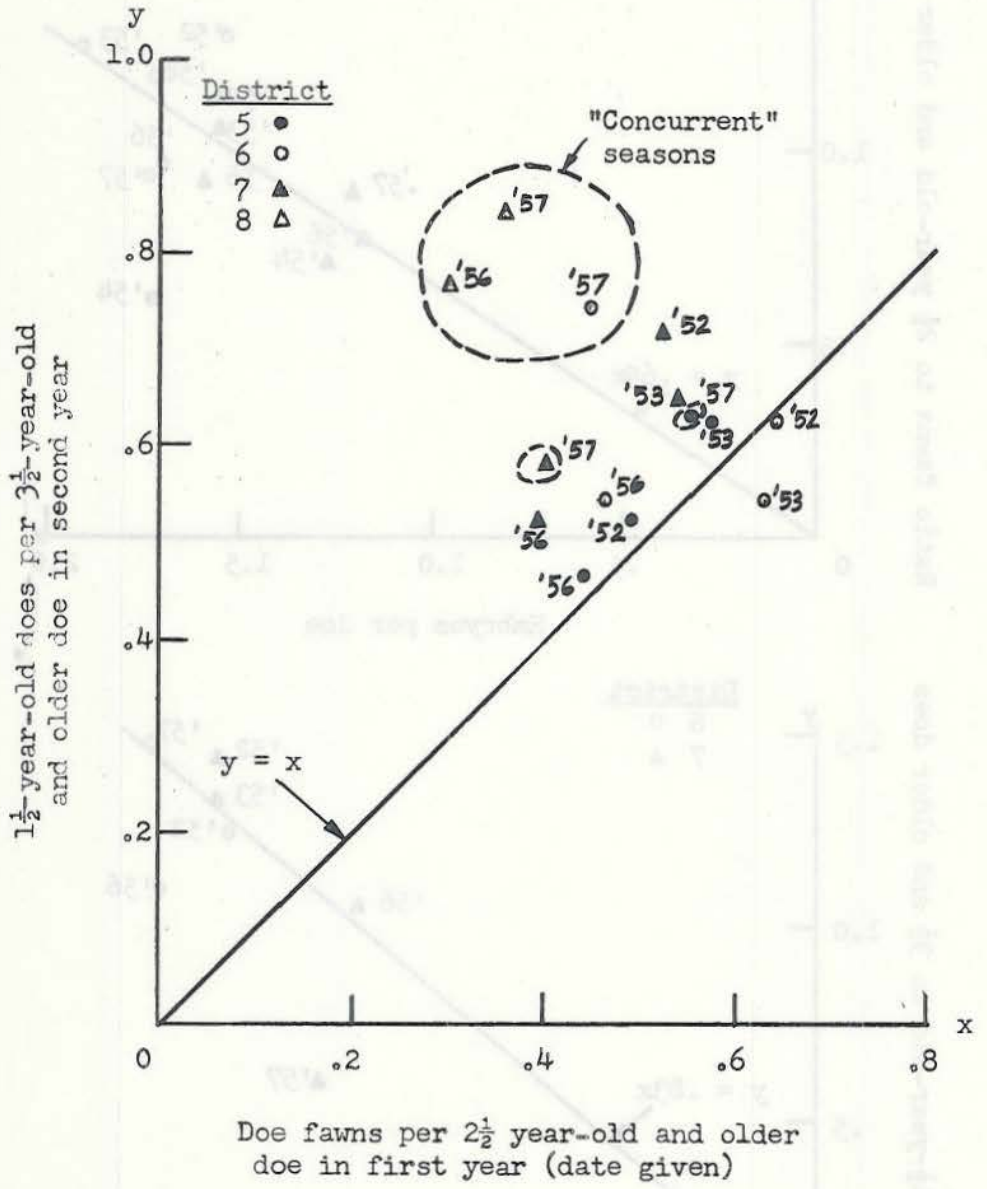


Figure 36. A comparison of two measures of reproduction based on hunting season ratios.

(s_2) are:

Annual doe Survival rate	Corresponding doe survival rate for 6 months (s_2)	Fawn survival rate (s_1)
.65	.806	.524
.70	.837	.544
.75	.866	.563

The same kind of calculations may be carried out for the lower graph of Figure 35, but here I have assumed that the ratio of $1\frac{1}{2}$-year-old does (actually doubled to allow for bucks) to $3\frac{1}{2}$-year-old and older does is the same as that prevailing in June (i.e., the same survival rate for adult does and juveniles beyond one year of age), and have thus computed the rates on the basis of one full year:

(2) Survival for the first year of life:

s_3 = fawn survival for the first year of life.

s_4 = adult doe survival in the same period.

$$\frac{\frac{s_3 F}{s_4 D}}{\frac{F}{D}} = \frac{s_3}{s_4} = .83$$

The numerical value is again that of an "eye-fitted" line, and a computation of fawn survival rates from several values of doe survival gives:

Annual doe survival rate (s_4)	Annual fawn survival rate (s_3)
.65	.540
.70	.581
.75	.622

Contrasting the two sets of fawn survival figures, it seems that the first (to six months of age) requires an overwinter survival rate of over 90 per cent, which does not agree with the results of the mortality surveys (Table 22), where fawn losses at least equal doe mortality (probably the best comparison here is the "non-starvation" column of the table, since the starvation losses are not typical of all years covered here), yet fawn numbers are probably somewhat lower than those of does (including for this purpose, 1½-year-old does).

Evidently consistent estimates of fawn survival for the first six months of life cannot be obtained from the available data, but as an approximation I assume survival beyond six months to be about that of adult does (poaching, not included in the mortality table, may hit does harder in the overwinter period) and use the fawn survival rate for the first year of life (.581) corresponding to the average doe survival of .70 to estimate fawn survival for the first six months as:

$$.581 = .837x$$

$$x = .694 = \text{fawn survival for the first six months of life.}$$

The results of these computations are of uncertain validity, being based on too much deductive reasoning from data which are not consistent throughout. I do not see, however, that we are likely to get much better data, short of possibly extensive deer tagging. Even tagging, an expensive procedure, leaves a great deal to be desired by virtue of the unknowns of tag return rates. Continued study is very likely to turn up some new possibilities, and quite likely the average hunter will soon begin to show less concern about the kind of deer he shoots; if so, the hunting data may thus become truly representative of fawn numbers.

V. POPULATION DYNAMICS

Introduction. Milne (1957) has suggested that "population dynamics," although a very popular term, has not been well-defined. Obviously a great many factors may be considered as affecting the dynamics of a population, and many sorts of inter-relations and interactions are involved. The treatment in this report, however, is limited to short-term trends in population density, and to the influences of reproductive and survival rates. Two general purposes of the analysis are:

(1) A synthesis of the trend in population density derived from reproductive and survival data may yield much valuable information as to why a population behaves as it does. In fact, any scientific approach to "management" of an animal population requires something more than the mere knowledge of trends in population size.

(2) A major portion of this report is devoted to attempts to estimate deer population size, structure, and survival, but it has been frequently indicated herein that our information is subject to a variety of uncertainties, many of which can not be examined simply or directly. I have attempted to contrast different sources of information wherever possible in order to assess possible sources of bias, and this section will serve as a sort of final contrast. Estimates of overall trend in population numbers are compared below with those predicted from survival and reproductive rates and the age structure.

An essential feature in what follows is the notion of the rate of change of a population which is increasing (or decreasing) according to an exponential model:

$$N(t) = N(0)\, e^{rt} \text{ or } N(t) = N(0)\, (1+r)^t$$

where: $N(0)$ = initial population size (at time zero).

$N(t)$ = population at time t (time measured in any appropriate units; here in years).

r = rate of change (per unit of time); r may be positive, negative, or zero.

Two methods of estimating r are used here:

(1) From a series of measurements of population size.

(2) An "expected" value calculated from a particular age distribution and a schedule of age-specific survival and reproductive rates.

The latter value is one of considerable interest to demographers and ecologists. Cole (1957) gives a good general discussion in a survey of the present status of population studies. Lotka (1925) originally derived the concept, which he called the "natural rate of increase" (1925, p. 111) or, in later writings, the "intrinsic rate of natural increase." Lotka's 1939 summary of his demographic work is used as the basis for my analyses.

The two models given above are virtually identical for small values of r (say .01 or less) and the "continuous" model (base e) is ordinarily used because of its mathematical convenience, and because births and deaths are so spread out over the year in many populations as to make the model appropriate. In dealing with deer populations, however, it is important to remember that births occur during a relatively short portion of each year, and that the mortality rate varies considerably through the year. As Skellam (1955) points out, it is nonetheless reasonable to

use an exponential model if population measurements are taken at the same point on an annual cycle each year. Since I use such a scheme here (one measurement at the same time each year), it seems to me preferable to use the "discrete" or "step" model, $N(t) = N(0)\ (1+r)^t$.

Most of the populations dealt with here have not changed very rapidly so I have considered the rates of change to be constant over the periods studied, and have not attempted to deal with the complications of "sigmoid" or "logistic" growth curves.

Rate of population change from density measurements. If the second exponential equation is expressed in terms of logarithms (when natural logarithms are used, the computations may be carried out simultaneously for both models) it appears as:

$$\log_e N(t) = \log_e N(0) + t \log_e (1+r)$$

and is then equivalent to the linear relation $y = a + bx$. By substituting the logarithm of some suitable measure of annual population levels (taken at the same time each year) for y, and letting $x = t = 1, 2, 3$, etc., r may be estimated by linear regression computations.

Estimates for the Study Areas (Figure 1) are shown in Figure 37. I have used the combined index data to estimate r because values are available for each year of the period studied, but have not used the 1952 data because the large special season harvest in that year makes it atypical.

Table 23 and Figures 38 and 39 exhibit the trends of two population indices for the southern Lower Peninsula, and for actual population levels on the George Reserve (data from O'Roke and Hamerstrom, 1948).

The two southern Lower Peninsula indices (Figure 38) suggest a very rapid deer population growth, but these measures may also reflect an increasing interest in "farmland" deer, both on the part of hunters and by

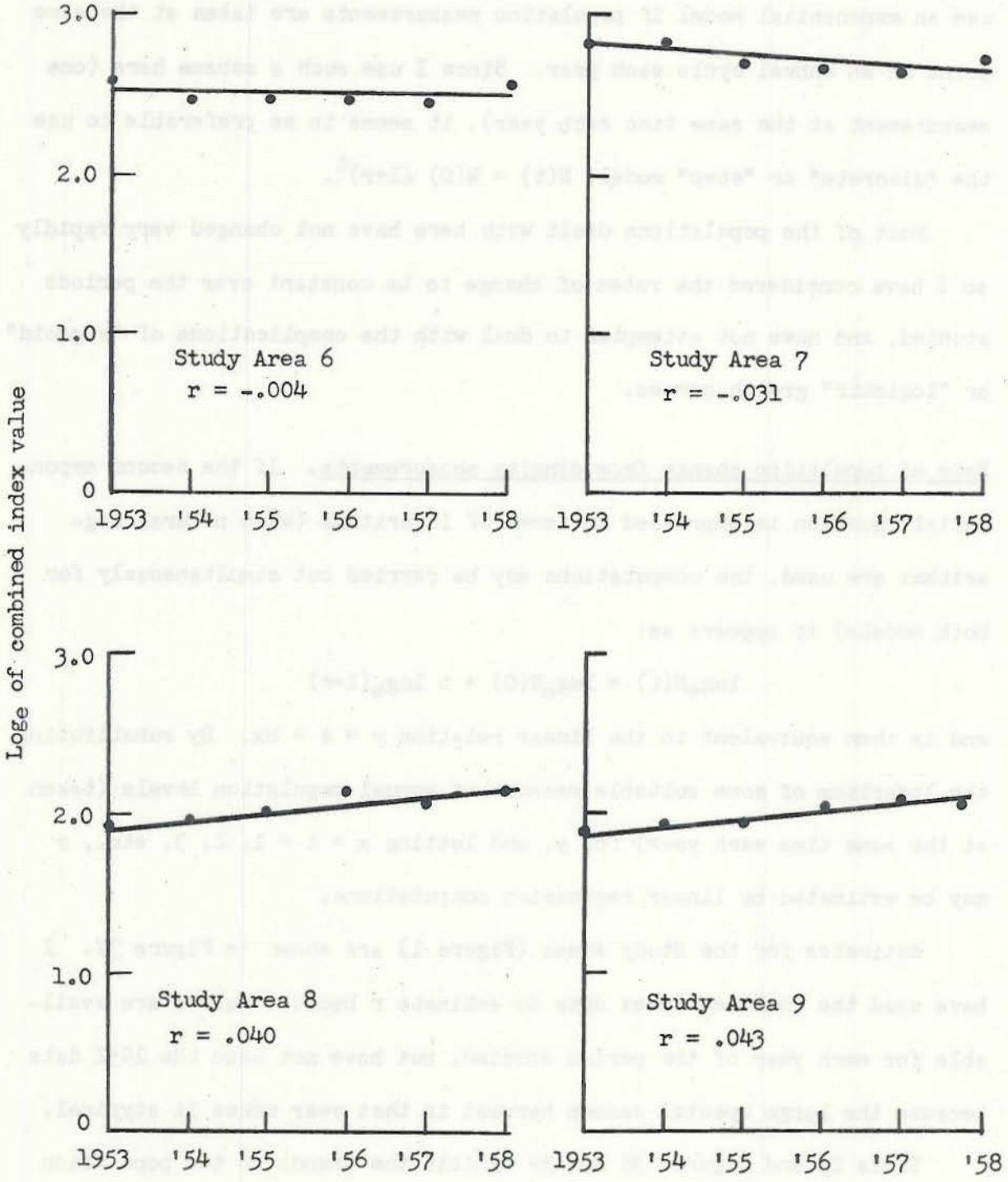


Figure 37. Population trends on Study Areas (See text, p. 155.)

TABLE 23

ESTIMATES OF RATE OF POPULATION CHANGE (r)
FROM TREND IN DEER POPULATION LEVELS

Indices of Southern Lower Peninsula Populations

Year	x	$\log_e$ of Buck Kill	$\log_e$ of Deer Seen per 100 Hours
1952	1	7.025	.262
1953	2	7.370	.588
1954	3	7.433	.262
1955	4	7.836	.470
1956	5	7.815	.955
1957	6	7.863	.693
1958	7	8.149	1.131
Regression slope		.169	.125
Estimate of r		.184	.133

Populations on the George Reserve

Year	x	Early Winter Population	$\log_e$ of Population	Proportion of Population Removed
1933	1	160	5.075	.062
1934	2	210	5.374	.457
1935	3	128	4.852	.148
1936	4	192	5.258	.214
1937	5	169	5.130	.592
1938	6	118	4.771	.305
1939	7	112	4.718	.330
1940	8	119	4.779	.386
1941	9	100	4.605	.510
1942	10	100	4.605	.430
1943	11	89	4.489	.371
1944	12	81	4.394	.370
1945	13	77	4.344	.286
1946	14	74	4.304	--
Averages		124		.343
Regression slope			-.074	
Estimate of r			-.071	

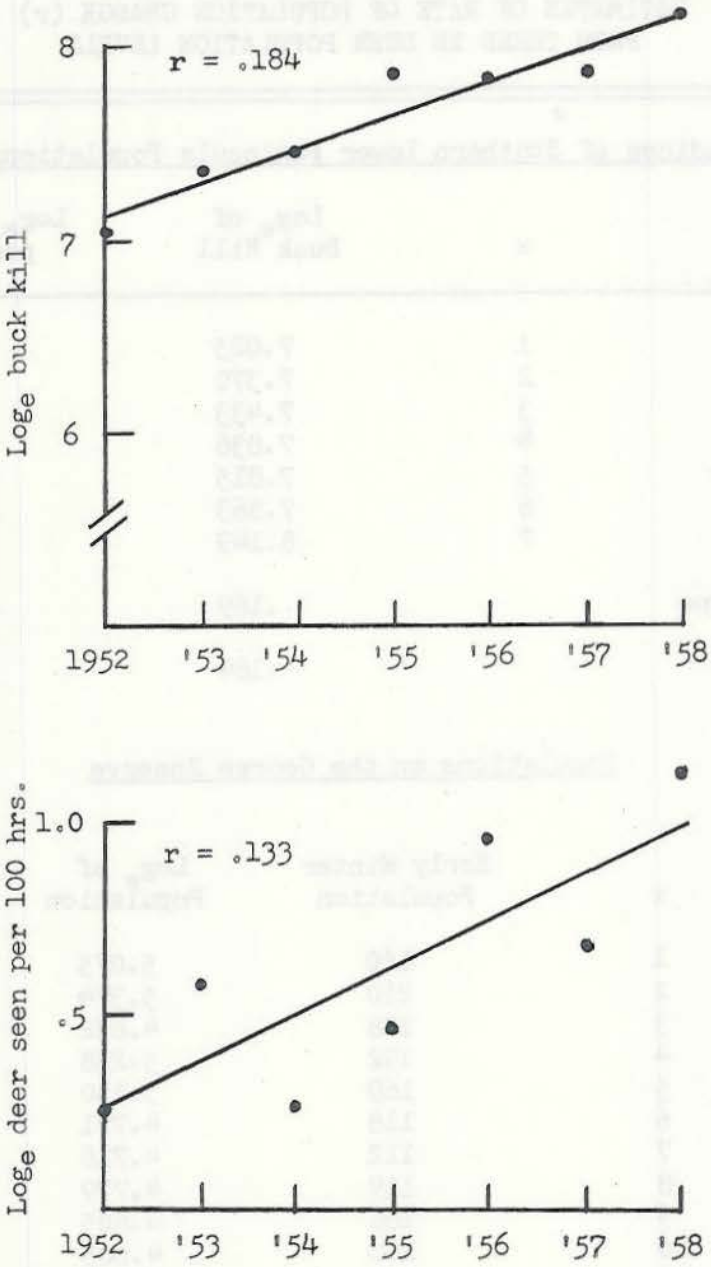


Figure 38. Trend of two deer population indices for southern Lower Peninsula.

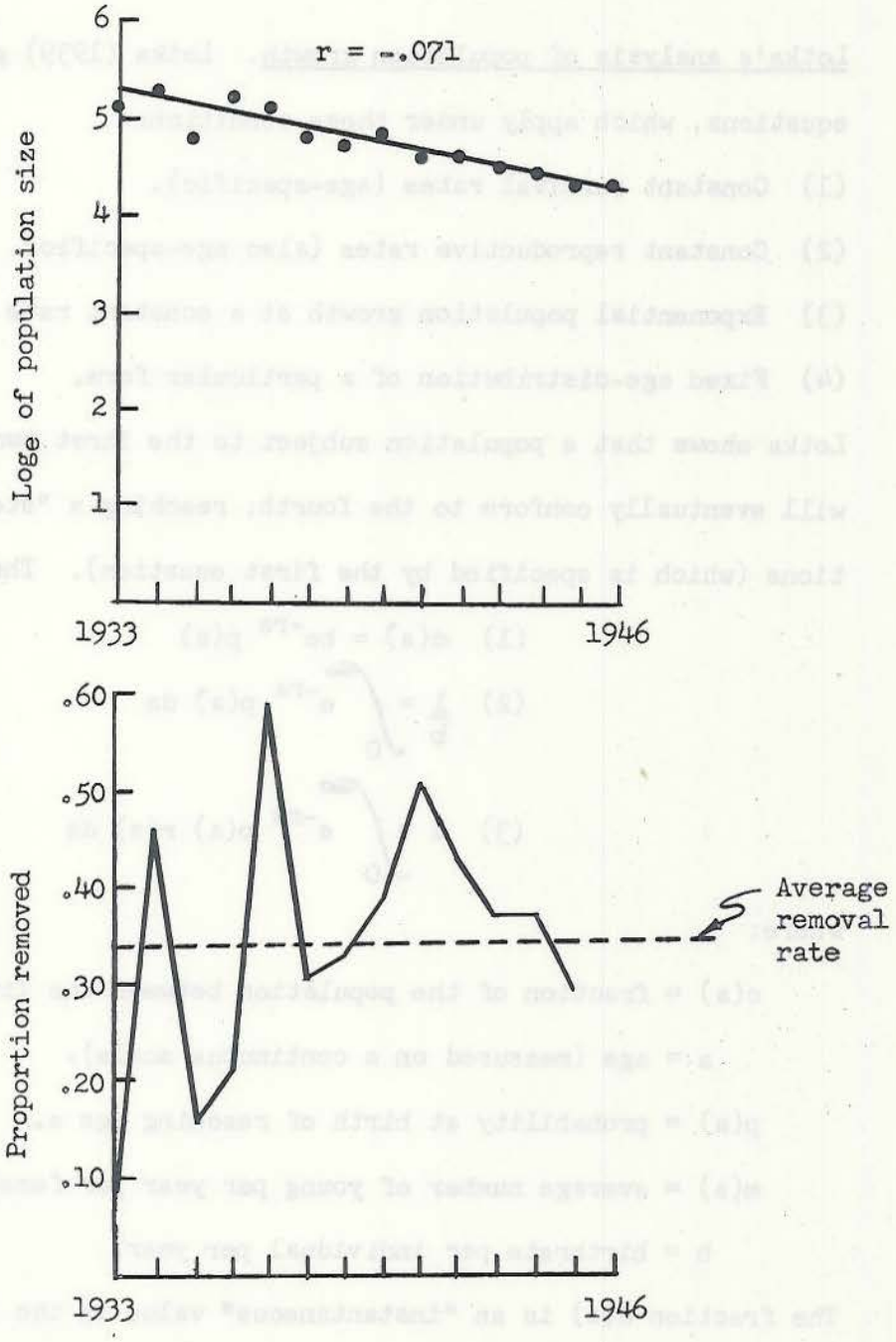


Figure 39. Deer population size and removal rates for The Edwin S. George Reserve of the University of Michigan.

the Conservation Department personnel who tally "deer seen per 100 hours."

Lotka's analysis of population growth. Lotka (1939) gives three basic equations, which apply under these conditions:

(1) Constant survival rates (age-specific).

(2) Constant reproductive rates (also age-specific).

(3) Exponential population growth at a constant rate (r).

(4) Fixed age-distribution of a particular form.

Lotka shows that a population subject to the first two of these conditions will eventually conform to the fourth; reaching a "stable" age distributions (which is specified by the first equation). The equations are:

$$(1)\quad c(a) = be^{-ra}\, p(a)$$

$$(2)\quad \frac{1}{b} = \int_0^{\infty} e^{-ra}\, p(a)\, da$$

$$(3)\quad 1 = \int_0^{\infty} e^{-ra}\, p(a)\, m(a)\, da$$

where:

c(a) = fraction of the population between the limits a and da.

a = age (measured on a continuous scale).

p(a) = probability at birth of reaching age a.

m(a) = average number of young per year per female of age a.

b = birthrate per individual per year.

The fraction c(a) is an "instantaneous" value in the sense that the age distribution is regarded as a continuous function, so that c(a) represents the proportion of the population at age a, where a is taken as some very precise definition of an age (i.e., expressed in units of, say, a hundred-thousandth of the total life span of the species). Equation (1) thus defines the age structure of the population, and the integral

of c(a) from zero to the maximum possible age (expressed as infinity) is therefore necessarily unity, and consequently yields equation (2).

The above equations, as ordinarily used, apply only to the female segment of the population. If male mortality rates remain constant, or nearly so, values of r obtained from the equations will also apply to the total population. I have not attempted to consider the length of time required for a deer population to reach the stable age distribution, and so depend in this report on comparisons of age distributions calculated from equation (1) with those actually observed in the herd as a basis for appraising the applicability of the equations. In the herds here considered, mortality and reproductive rates evidently vary from year to year, so that the theoretical computations can serve only as an approximation to reality.

Methods of solving Lotka's equations. Unless the functions p(a) and m(a) are given some mathematical expression ("explicit" functions of a) the integrals above cannot be solved directly. Ordinarily, values are supplied in tabular form for specific ages or age-groups and solution of the equations depends on numerical integration or one of several approximations. Lotka (1939) gives methods having varying degrees of precision, and Andrewartha and Birch (1954) have a convenient summary of the simpler methods. One method depends on the computation of the "mean length of a generation," and Leslie and Ranson (1940) give a worked-out example for laboratory populations of the vole, Microtus agrestis. An alternate method of solution is to replace the integrals with summations and compute values of r by iteritive (trial and error) methods as in the work done by Birch (1948) and Leslie and Park (1949).

The analyses of the present report are principally concerned with

the deer population at the time of fawning, so that the variable, a, takes integral values only (0, 1, 2, etc.). As a consequence, it seems appropriate to replace the term e^{-ra} with $(1+r)^a$ and the integrals with summations, thus changing the continuous model to represent the discrete situation where the population is considered only at one point in the course of each year. Lotka's (1939) development of equations (1) to (3) appears to hold equally well with these definitions, and solutions are easily obtained for the values of interest here. I have therefore computed estimates of the several quantities on this basis, but also give in the tables comparable values of r calculated by the method of "mean length of generation."

Reproductive and survival data. I have not attempted to compute age-specific survival estimates beyond the first year of life because of our uncertainty about the accuracy of aging methods (Ryel et al., 1960), and I use here a value of .58 for survival from late embryonic life to one year of age, and, for females, .70 per year thereafter (see Part IV of this report). Since, as far as we can tell now, shooting plays a major part in mortality of adult deer, the assumption of a constant rate may not be as questionable as one might at first assume.

Perhaps the most objectionable feature of the assumption of a constant adult survival rate is in its application beyond, say, 10 years of age. Alternate procedures may be either to assume a steadily decreasing rate beyond 10 years, or to arbitrarily truncate the age distribution at some point. I have not done so, however, because nearly three-fourths of the "old" (over 10 years) does examined in Michigan have been carrying embryos (Eberhardt and Fay, 1959). I do not believe that one can safely assume these animals to be senile. Also, as is shown below, less than

five per cent of the female deer population survives beyond ten years, so it does not seem to be a matter of great consequence if a constant survival rate is used throughout.

Reproductive rates used here are those given by Eberhardt and Fay (1959), with the exception that the values used in the calculations have been converted to female births by multiplying by .47 (47 per cent of embryos examined for sex have been females). The "productivity" data are obtained by autopsy of does shot or accidentally killed in the spring of the year, so these are really embryonic-rates rather than birth-rates. Due to the rather limited reproductive data available, calculations are here restricted to four broad areas; the entire Upper Peninsula, two subdivisions of the northern Lower Peninsula (the "Northeast" area, and the remainder of the northern Lower Peninsula--Figure 34), and the southern Lower Peninsula. Also, I have used the entire available span of reproductive records (from 1951 to 1959) to compute age-specific reproductive rates.

Most noticeable features of the age-specific reproductive data (Figure 40) are the relatively high reproductive rate of one-year-olds in the southern Lower Peninsula, and the steady increase of the rate to six years of age in the northern areas (only a very few deer beyond four years of age have been examined in the southern Lower Peninsula).

Estimates of r from Lotka's equations. Estimates of r obtained from the "discrete" analogue to equation (3) are given in Table 24 along with the reproductive and mortality data. An estimate for the southern Lower Peninsula has been included (using a constant survival rate of .70 for all classes) for comparative purposes, but can be regarded only as speculative due to the lack of survival data. A summary of the estimates of r is:

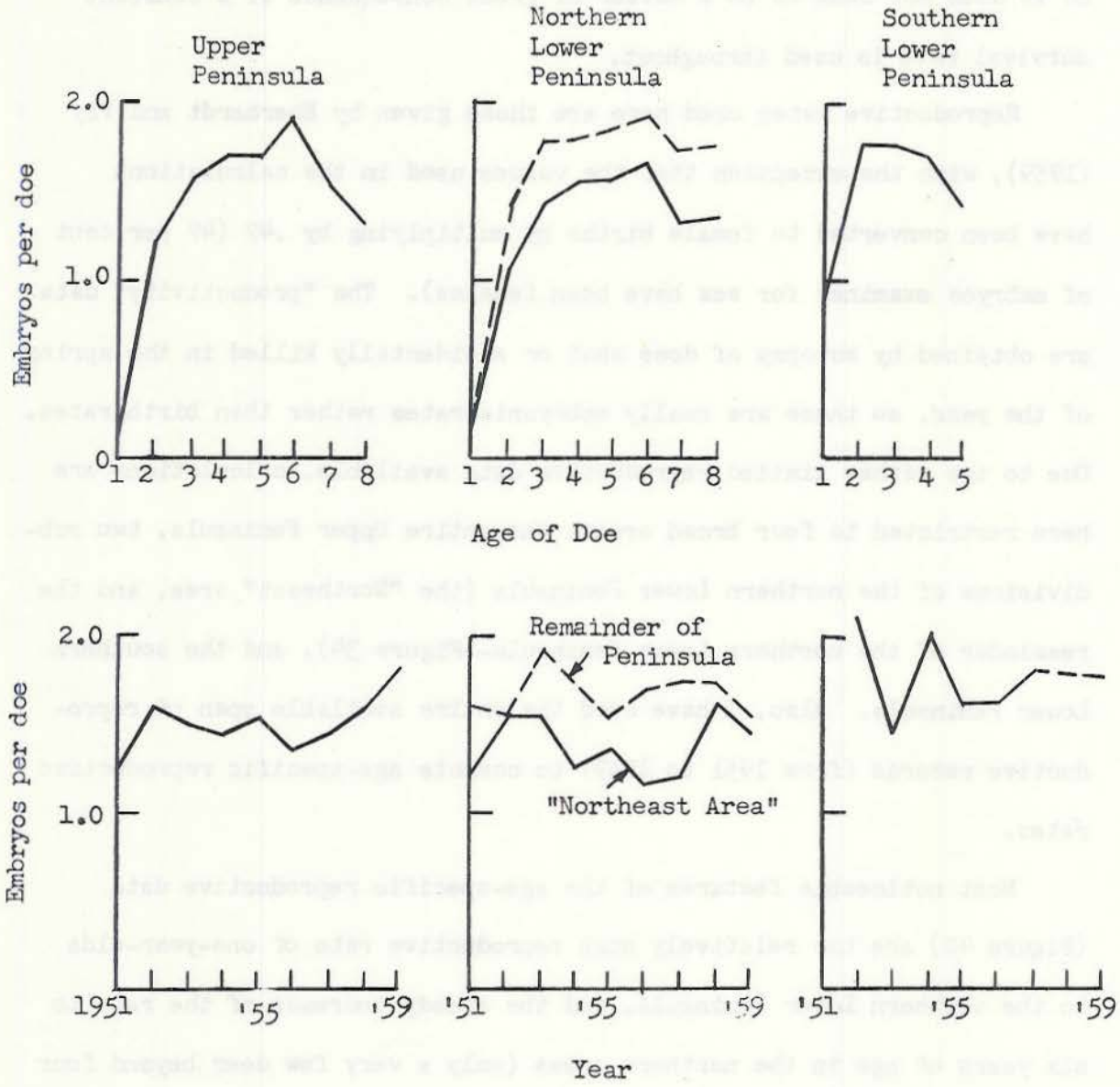


Figure 40. Embryo production rates as determined from autopsy of accidentally killed deer. Reproductive rates by age of doe (upper figure) are based on averages of records from 1951 to 1959. Lower figures are annual averages of records from two-year-old and older does.

TABLE 24

ESTIMATES OF RATE OF POPULATION CHANGE (r)
FROM REPRODUCTIVE AND MORTALITY DATA

		Northeast Area	Remainder of Peninsula	Southern Lower Peninsula		
Age a	Survival to Given Age p(a)	Reproductive Rate m(a)	m(a)	a	p(a)	m(a)
0	1.0000	0	0	0	1.000	
1	.5800	.047	.085	1	.700	.390
2	.4060	.503	.658	2	.490	.832
3	.2842	.663	.832	3	.343	.832
4	.1989	.733	.846	4	.240	.799
5	.1392	.743	.870	over 4	$.70^x$	.799
6	.0974	.771	.898			
Over 6	$.58(.70^x)$	.644	.827			
Estimates of r						
Analogue of Eq.(3)		-.035	+.023			+.141
Method of "mean length of generation"		-.026	+.026			+.127

Notes:

(1) Constant reproductive and mortality rates are assumed beyond those shown (sum of products computed from geometric series $m(a).70^x$).

(2) Lower Peninsula value of m(a) has been used as .799 beyond 4 years of age due to lack of sufficient records.

Source	Northeast Area	Remainder of Peninsula	Southern Lower Peninsula
Analogue to equation (3)	-.035	+.023	+.141
Method of "mean length of generation"	-.026	+.026	+.127
Estimates from combined index data			
Area 7	-.031		
Area 8		+.040	
Area 9		+.043	
Southern Lower Peninsula			+.133;+.184

Stable age distributions. Evaluation of the two different sets of estimates of r set forth above requires consideration of age distributions, since Lotka's methods yield values of r based on a specific age distribution (the stable age distribution) which may or may not exist in a given population, depending on its recent survival and reproductive history. Stable age distributions calculated (Table 25) from equation (1) are shown in Figure 41 in the form of the "survivorship" or "l_x" curve of the usual life table. A logarithmic scale is used, with the "zero" class computed as 1,000 animals in each case. A curve for a stationary (r=0) population is included for comparison, and, of course, only the stationary population is appropriately shown in the life-table form. However, the point here is that rather different age structures may develop from the same survival rates and be perpetuated as long as survival and age-specific reproductive rates hold constant.

Ages of "shot and accidentally killed" female deer. The only available age data corresponding directly to the theoretical stable age distributions are those obtained from the does examined for reproductive data.

TABLE 25

STABLE AGE DISTRIBUTIONS AS COMPUTED FROM REPRODUCTIVE AND SURVIVAL DATA

a	p(a)	Northeast Area c(a)	Remainder of Peninsula c(a)	a	Southern Lower Peninsula p(a)	c(a)
0	1.0000	.3136	.3577	0	1.0000	.3865
1	.5800	.1885	.2028	1	.7000	.2371
2	.4060	.1367	.1388	2	.4900	.1455
3	.2842	.0992	.0950	3	.3430	.0892
4	.1989	.0719	.0650	4	.2401	.0548
5	.1392	.0522	.0444	5	.1681	.0336
6	.0974	.0378	.0304	6	.1176	.0206
7	.0682	.0274	.0208	7	.0824	.0126
8	.0478	.0199	.0142	8	.0576	.0077
9	.0334	.0144	.0097	9	.0404	.0048
10+	$.58(.70^x)$	.0382	.0211	10+	$.70^x$	.0076
		.9998	.9999			1.0000
r		-.035	+.023			+.141

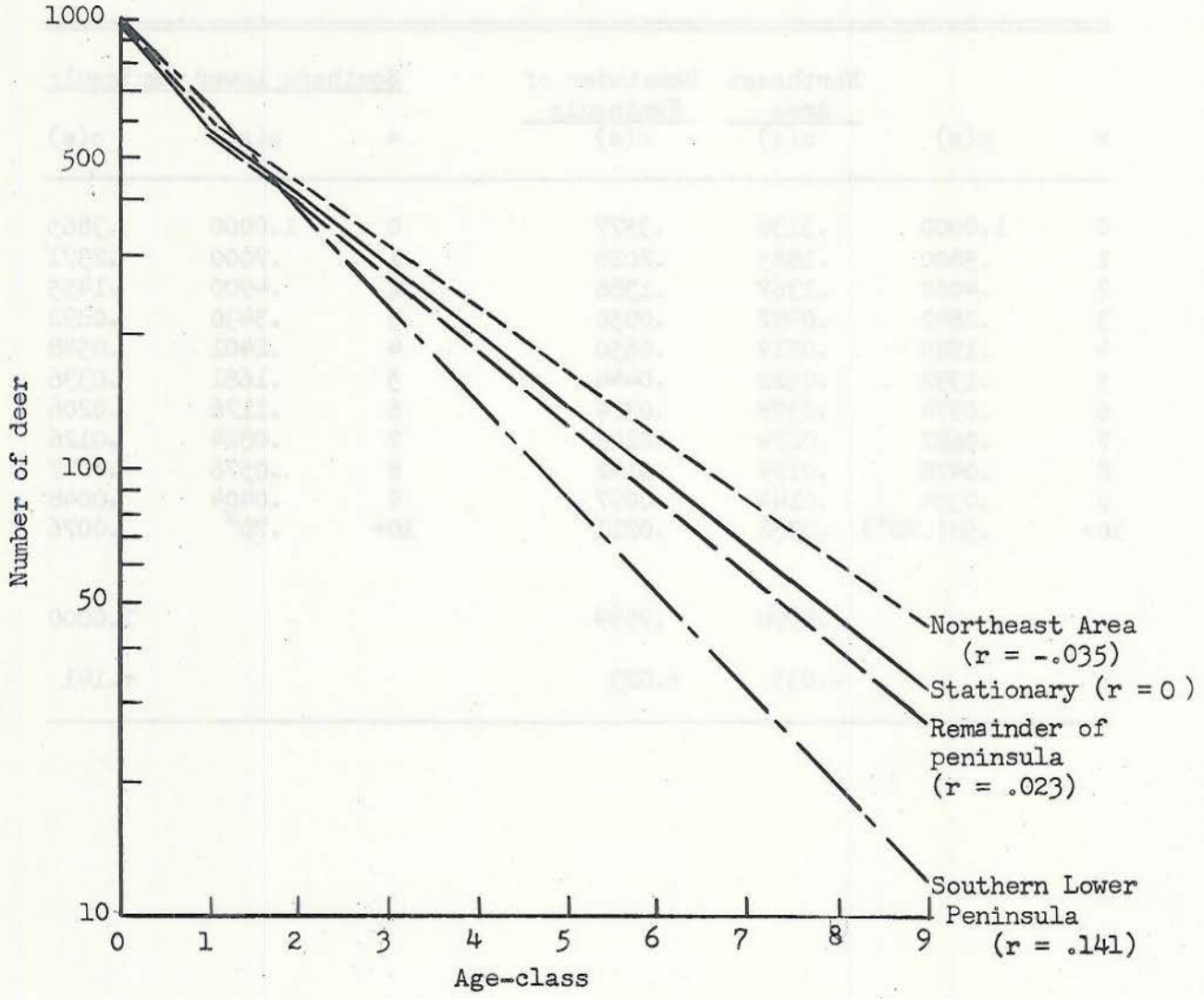


Figure 41. Some stable age distributions as calculated in this report.

Since records of one-year-olds were not properly maintained until 1954, only data from the period 1954 to 1958 are used here (Table 26). In each case (Table 26), an "expected" distribution has been calculated from the stable age distributions (Table 25). In the following comparison of grouped data, the zero class in the "observed" column is based on female embryos:

	Northeast Area		Remainder of Peninsula			Southern Lower Peninsula	
Ages	Exp.	Obs'd.	Exp.	Obs'd.	Ages	Exp.	Obs'd.
0	150	155	252	268	0	134	116
1-5	262	268	385	391	1-4	183	223
Over 5	66	56	68	45	Over 4	31	9

The comparison above indicates that the average Northeast area age distribution very closely approximates that expected from a stable situation, and thus substantiates the close agreement in the estimates of r by the two methods. In the remainder of the northern Lower Peninsula, there seems to be a higher fraction of younger deer than that predicted from the stable age distribution, which is the situation to be expected if the true rate of increase is greater than that used for computation of the stable age distribution. However, there is also a fundamental difference in the direction of population change. The long-term trend (going back into the middle or late 1940's) in northern Lower Peninsula deer populations has been downward, and the special season harvest of 1952 does not seem to have taken as large a proportion of the population in the Northeast area as in the remainder of the Peninsula. Therefore, a rather consistent, long-term downward trend in populations may be postulated for the Northeast area, and this trend would permit the establishment of a stable age distribution. The past situation in the less

TABLE 26

AGES OF "SHOT OR ACCIDENTALLY KILLED" FEMALE DEER

	Northeast Area		Remainder of Peninsula		Southern Lower Peninsula		
Age	Observed	Expected*	Observed	Expected*	Age	Observed	Expected*
0	155	151	268	251	0	116	134
1	83	90	110	143	1	90	82
2	63	65	114	98	2	73	51
3	64	48	98	67	3	43	31
4	33	34	43	46	4	17	19
5	25	25	26	31	4+	9	31
6	14	18	21	21			
7	10	13	12	15			
8	13	10	6	10		348	348
9	4	7	0	7			
10+	15	18	6	15			
	479	479	704	704			

*Based on a stable age distribution.

heavily populated remainder of the Peninsula is uncertain, but there was definitely a drop in the population level in 1952, and the subsequent trend has been upwards, so this reversal in trend may well have prevented the establishment of a stable age distribution. Putting it another way, the effect of a heavy harvest in 1952 was necessarily to concentrate the recent population in the younger age classes, and the disparity in values of r computed by the two methods thus seems likely to be due to a lapse of time insufficient to reach a stable age distribution. The true present rate of increase outside of the Northeast area is probably best taken as that obtained from the combined index data (or a comparable rate might be computed on the basis of the existing, rather than the theoretical, stable age-distribution).

The lack of survival estimates and the marked difference between expected and observed age distributions in the southern Lower Peninsula leaves the situation there in considerable doubt. Possibly, survival is actually higher than the values used here, or, the population may not be growing at the rapid rate computed here.

Ages of female deer found dead. The extensive mortality surveys described earlier in this report (Part IV) provide some data on ages at death, which presumably may be used as a check on the assumed mortality rates. There are, however, two difficulties. One is that the surveys are usually conducted only when we believe important starvation losses have occurred. The other problem is that the surveys are set up on the basis of stratified random sampling, with allocation of plots to strata dependent on magnitude of expected mean losses and estimated variances. In other words, we sample most intensively in areas where losses are expected to be greatest. The different sampling rates are properly weighted

in estimation of total losses, but, since relatively few deer are found in any one survey, we cannot produce useful estimates of overall age structure in the same manner. In general, then, the data on ages of deer found dead will be heavily weighted to starvation losses. Table 27 shows the records of female deer found dead in these mortality surveys (without adjustments for sampling rates), and an expected distribution derived from the stable age distribution calculated for the Northeast area (since the bulk of starvation losses occur there). The expected distribution was obtained by applying the annual mortality rates (.42 for fawns, .30 for adults) to the stable age distribution. These results are about what one would expect under starvation conditions; higher mortality observed in the fawn and older age classes. However, since these data are so heavily weighted to starvation losses, and since the overall evidence does not show starvation losses to be the major mortality factor, about all I can do here is to suggest that possibly a small adjustment should be made in the mortality rates used above. On the other hand, the good agreement between the stable age distribution and that actually observed in the "shot and accidentally killed" sample argues that the present mortality schedule may be very close to correct.

Ages of female deer in legal harvests. Age distributions for adult female deer are shown in Figure 42 for the two broad northern Lower Peninsula areas used in calculation of rates of population change from reproductive and mortality data. Each line on the graph represents the sample obtained in one hunting season, with the ages on each line arranged in sequence from left to right ($1\frac{1}{2}$ to $4\frac{1}{2}$-year-old classes are shown). The dates given are those of the year-class, i.e., the points plotted at, say, 1955 represent the does born in that year, but examined

TABLE 27

AGES OF FEMALE DEER FOUND DEAD IN EXTENSIVE MORTALITY SURVEYS

Age	Observed	Expected*
0-1	106	77
1-2	18	33
2-3	14	24
3-4	18	17
4-5	9	13
5-6	5	9
6-7	6	7
7-8	8	5
8-9	4	3
9-10	2	3
10+	8	7
	198	198

*Based on a stable age distribution.

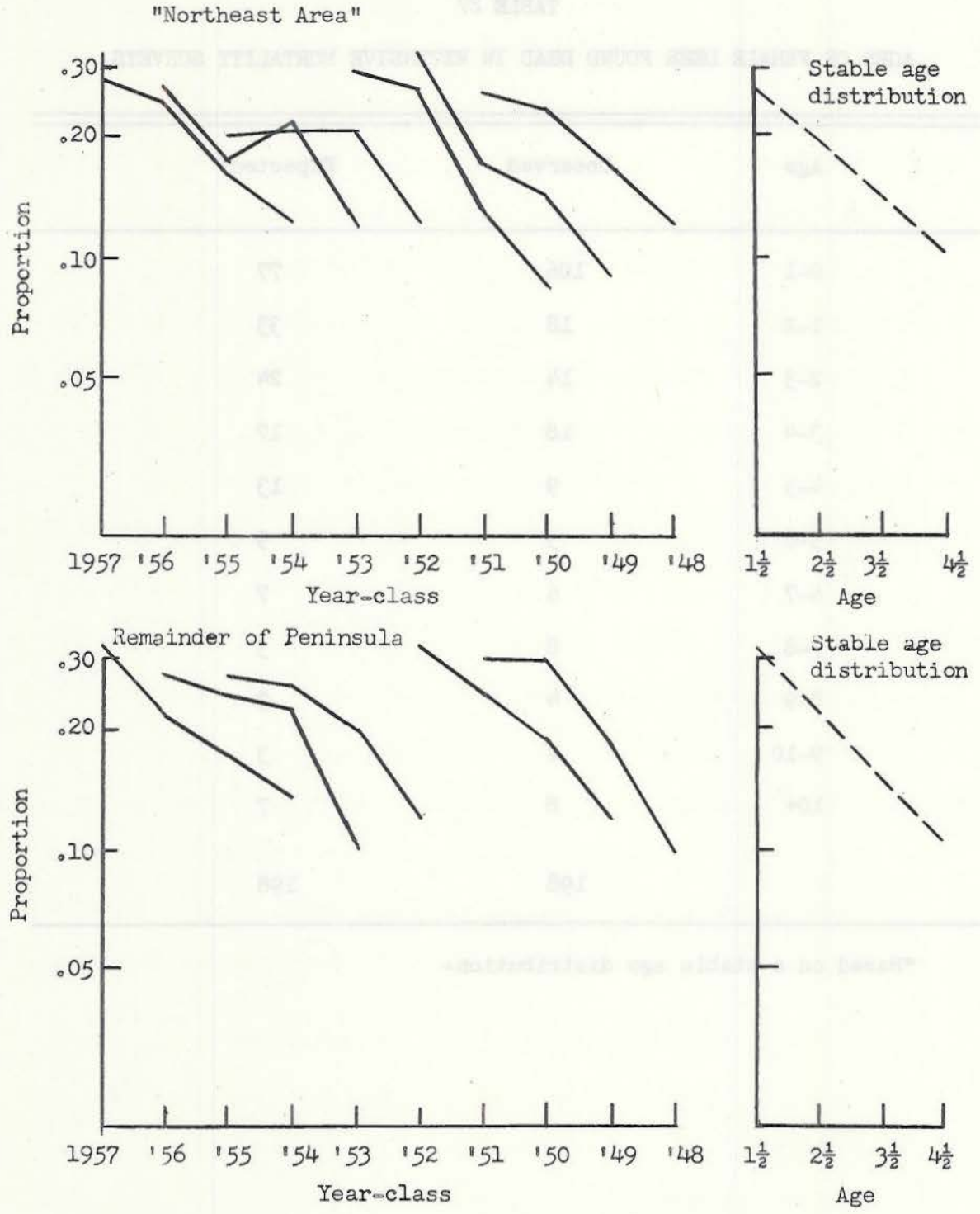


Figure 42. Adult doe age distributions as determined from deer examined during hunting seasons

as $1\frac{1}{2}$-, $2\frac{1}{2}$-, and $3\frac{1}{2}$-year-olds in the hunting seasons of 1956, 1957, and 1958. Since there was no special season in 1955, data from that year are lacking here, and not enough animals were examined outside of the Northeast area in 1954 to justify plotting the results. The corresponding stable age distribution is shown on the right side of each graph.

Changes in the age distributions for the Northeast area seem to follow the fawn production data (Figure 40) rather closely, with lowered reproductive rates reflected by decreasing proportions of $1\frac{1}{2}$-year-old deer. The remainder of the Peninsula shows a trend similar to that of the Northeast area, but with much less pronounced fluctuations.

The age data indicate that the assumption of a stable age distribution is not strictly correct inasmuch as reduced fawn production has resulted in convex age-curves, which do, however, seem to have straightened out in the last year of record. One attribute of the convexity is that the adult doe population is concentrated in the higher-producing classes, demonstrating one of the mechanisms responsible for the resiliency of a deer herd--a temporary reduction in reproduction results in a lower population density, reducing competition for food, and the population contains a high proportion of the older, more fecund individuals.

"Survivorship" curves. The deer populations dealt with in this study have evidently not been stationary during the period investigated, and the usual life table will not be strictly applicable here. For comparative purposes, however, the difference in age structure between a stationary population and one gradually increasing or decreasing (Figure 41) will probably not be of major importance. The survival curve used in this study may therefore be contrasted (Figure 43) with curves given by Taber and Dasmann (1957) for three populations believed to be stationary.

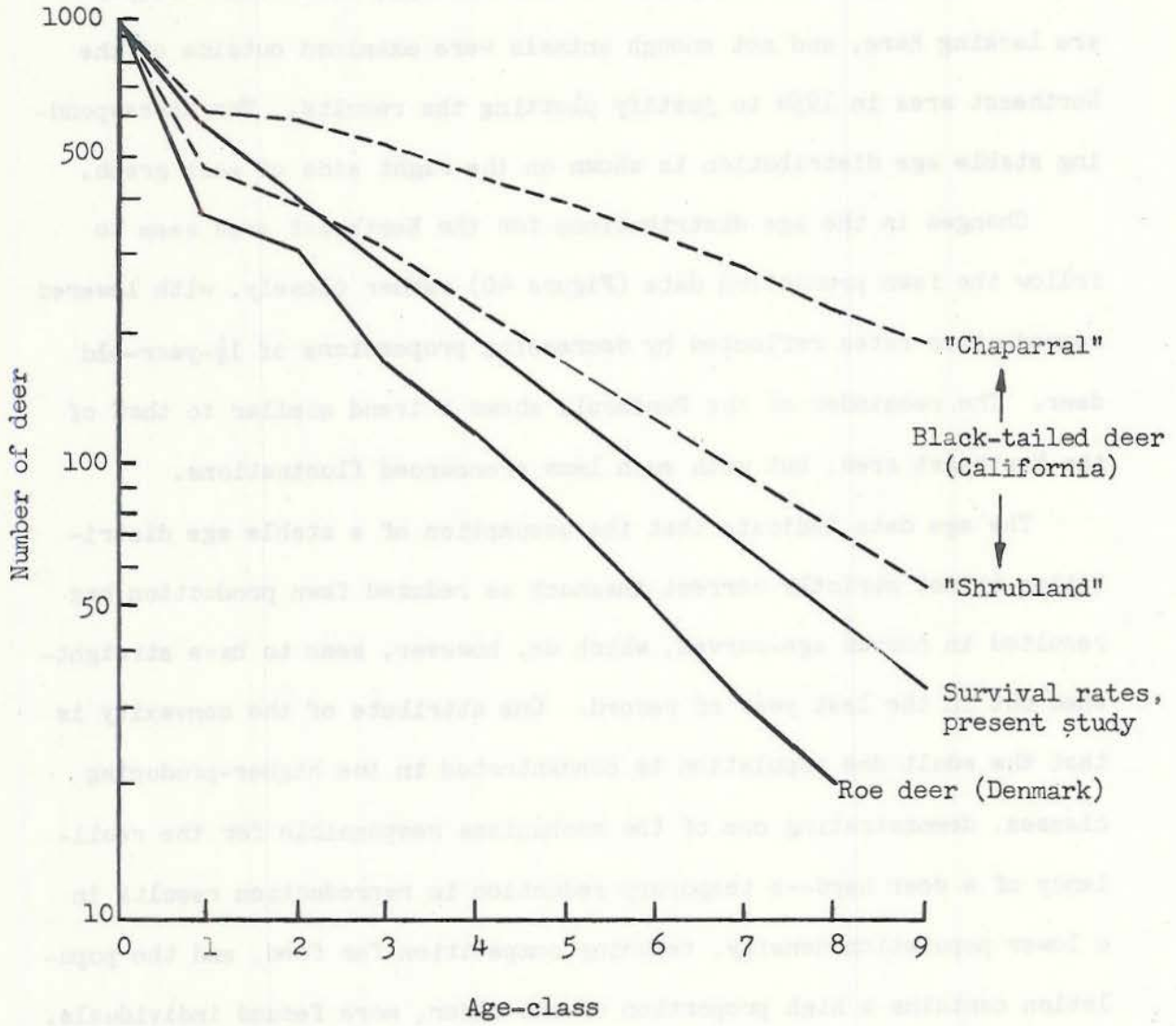


Figure 43. Survival rates from present study compared to three "survivorship" curves reported by Taber and Dasmann (1957).

Reproduction and population density. Reproductive rates (Figure 40) both by age-class and as yearly averages, demonstrate significant differences between the two broad areas of the northern Lower Peninsula, and seem to be the principal cause of the opposite population trends in the two areas. Quite possibly the marked increase in reproductive rate in the Northeast area in 1958 and 1959 has resulted in an increase in population levels in this important area.

The age-specific reproductive rates for major subdivisions of the state (compared in Figure 44) have been used to compute approximate adult doe survival rates required for stationary (constant) populations in these areas (Table 28). Stable age distributions have been assumed, and an arbitrary choice of fawn survival rates is necessary. Inspection of equation (3) shows that, if r is to equal zero, the sum of the products p(a)m(a) must be unity, and so the computations (Table 28) amount simply to varying adult doe survival values until the sum of the p(a)m(a) becomes unity.

The complement of these survival rates may be compared (Figure 45 and Table 28) to approximate population densities for the several areas. The extreme right hand value in the figure is for the George Reserve, and is based on the average rate of decrease and average removal rate (Figure 39)--reducing the removal rate to about .31 or .32 would presumably stabilize the population under the exponential model here assumed to apply.

No doubt several factors other than population density also affect reproduction in the various parts of Michigan, but there does seem to be an indication here (Figure 45) of the inverse relationship usually postulated between reproduction and density. Evidently the southern and

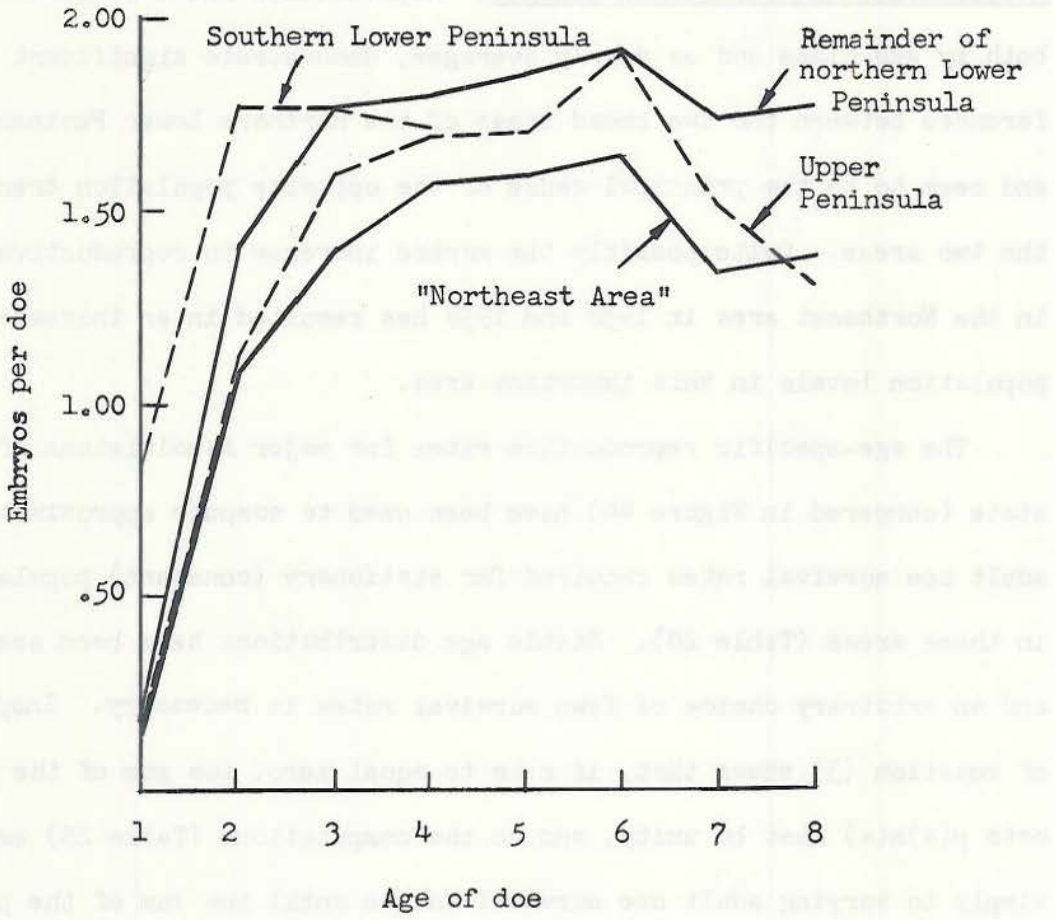


Figure 44. A comparison of age-specific reproductive rates for four areas of Michigan.

TABLE 28

ESTIMATES OF ADULT FEMALE SURVIVAL RATES FOR STATIONARY POPULATIONS AT GIVEN FAWN SURVIVAL RATE AND AVERAGE OBSERVED REPRODUCTIVE RATES

	Southern Lower Peninsula		Northeast Area		Remainder of N. Lower Peninsula		Upper Peninsula	
Age of Doe (a)	Average Reproductive Rate m(a)	Survival Rate for Stationary Population p(a)	m(a)	p(a)	m(a)	p(a)	m(a)	p(a)
1	.390	.600	.047	.580	.085	.580	.056	.580
2	.832	.366	.503	.423	.658	.394	.569	.412
3	.832	.223	.663	.309	.832	.268	.747	.292
4	.757	⋮	.733	.226	.846	.182	.799	.208
5	.757	.61[x]	.743	.165	.870	.124	.799	.147
6	.757		.771	.120	.898	.084	.893	.105
7+	.757		.644	.73[x]	.827	.68[x]	.649	.71[x]
Assumed fawn survival rate		.60		.58		.58		.58
Doe survival rate for stable population		.61		.73		.68		.71
Maximum removal rate for adult does		.39		.27		.32		.29
Approximate population level (deer per square mile)		5		30		15		20

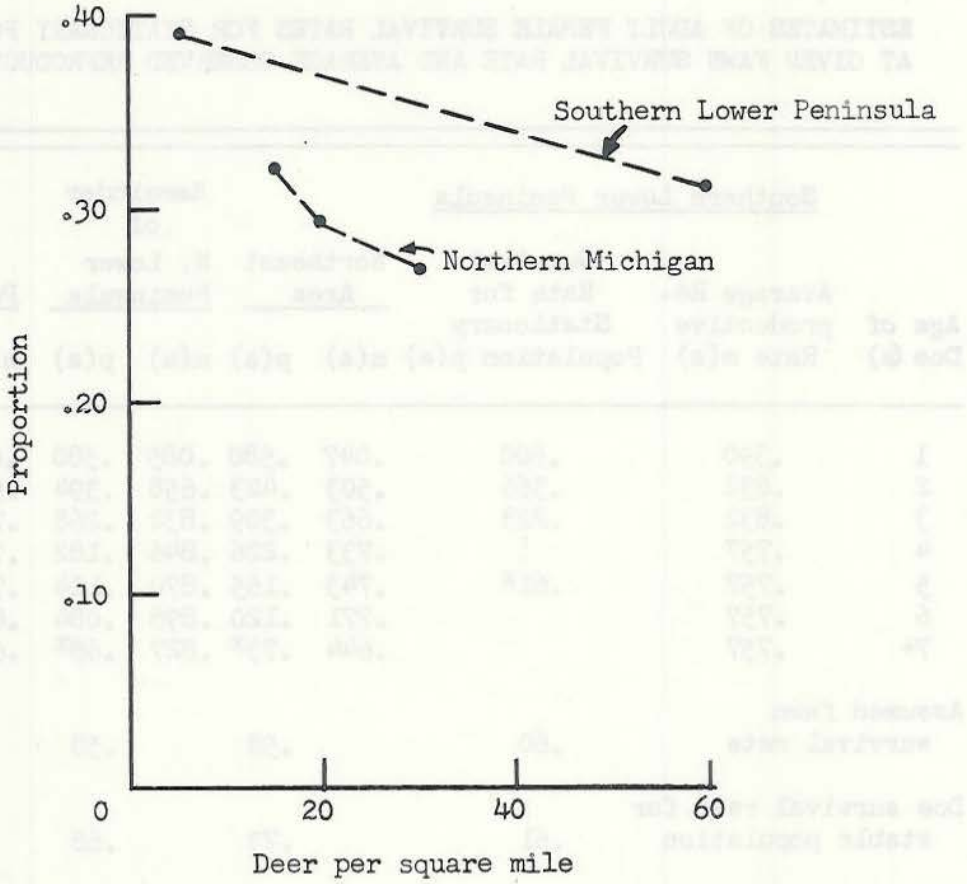


Figure 45. Calculated mortality rates for stationary populations (Table 28).

northern regions of the state are considerably different, and that difference seems quite surely to be a consequence of the high fawn production of young does in southern Michigan (Figure 44). In the north, the Upper Peninsula, with its intermediate population densities, has a fawn production rate between those of the two Lower Peninsula areas as one would expect if a density-reproductive mechanism controls population levels. Probably the light snow cover and intensive agriculture of the southern Lower Peninsula contribute considerably to differences in reproductive rates, and it seems certain that a deer population in the southern part of the state can be harvested a good deal more intensively than can one in the north.

While the evidence here supports the concept of higher reproduction at lower population densities, the observed differences are not sufficiently great to indicate that reductions of the size of deer populations in northern Michigan would be wholly compensated for by increased reproduction. In other words, the denser populations of northern Michigan do have lower reproductive rates, but their yield in numbers of deer still exceeds that of the less dense populations which have the higher reproductive rates.

SUMMARY

This study was conducted to analyze certain methods of estimating the relative abundance and vital characteristics of the white-tailed deer (Odocoileus virginianus) in Michigan. The study covers the years 1952 to 1958, with major emphasis on northern Lower Peninsula deer herds.

Deer population estimates from the pellet-group count method were used in the study, but analysis of the method was limited to a summary of previous investigations in Michigan. Extensive field experience with the method, as well as tests on areas of known deer populations, however, show that it cannot as yet be accepted as a wholly reliable standard by which to judge other methods of estimating deer population size.

Population estimates based on sex, age, and kill data from the hunting harvest were found to be feasible on the assumption of a low rate of non-hunting mortality in adult male deer. Precise population estimates could be made only for the earlier years of the study (1952 and 1953). The assumption of an exponential kill-effort relationship was necessary to compute estimates for subsequent years. The possibility of differential harvest rates was considered, and an under-representation of fawns in samples of the kill was found to be the most important effect in Michigan.

Evaluation of adult buck population estimates derived from data on

legal kill and hunting effort demonstrated that vulnerability to hunting is not constant. Positive identification of the underlying causes could not be established from the available data, but the evidence suggested two major aspects: a sharp decline in vulnerability during the first week of the hunting season, and an inverse relationship between number of hunters per unit area and hunter-efficiency. Estimation of the proportion of the deer population taken per unit of effort (hunter-day) was further complicated by the necessity of using a biased method of estimation, and by a marked decline in hunting effort during the season. Results of the study show that kill-effort data probably cannot be used to produce direct and trustworthy estimates of deer population densities until more information is available on the behavior of deer and of hunters.

A method was demonstrated for combining different indices of deer population levels through linear transformations. Several possible criteria for evaluating indices were investigated. It was shown that the lack of absolute measures of deer population levels precludes a completely objective choice of methods for weighting different indices in combining them into a single measure. The chief disadvantage of a combined index was considered to lie in its not providing direct estimates of numbers of deer, while the major advantages were found to be ease in maintaining a continuity of records and low cost of basic data.

Comparisons were made of three independent methods of estimating deer population levels, pellet-group counts, the sex-age-kill method, and the combined index. A high degree of correlation among the methods was demonstrated.

Useful estimates of deer survival rates were shown to require a knowledge of the age and sex structure of the herd as well as of the

population level in at least two successive years. Rates estimated from the age structure alone were found to be unsatisfactory under Michigan conditions except possibly as representing an average survival value over a span of years. Under-representation of fawns in samples obtained during the hunting season caused considerable difficulty in estimating survival rates for this class. Results of sample surveys for over-winter herd losses were appraised. Illegal kill was considered to be a major mortality factor for antlerless deer.

The dynamics of Michigan deer populations were studied by comparing rates of change calculated directly from annual measures of population level with rates synthesized from data on reproductive and survival rates. Close agreement was noted in an area where the deer population had apparently reached a stable age distribution. Reproductive rates were shown to vary inversely with deer population densities. A maximum possible sustained annual mortality rate for adult female deer in northern Michigan was estimated to be about .30, while the much higher reproductive rates observed in the two youngest adult female age-classes in southern Michigan apparently would sustain a mortality coefficient approaching .40.

APPENDIX

PROPOSED ALTERNATE DERIVATION OF A KILL-EFFORT RELATIONSHIP

DeLury (1947) gives the following equation for the relation of kill per unit effort, C(t), to cumulative kill, K(t).

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

(For definition of terms and a discussion, see page 43 of this report.)

In the situation considered by DeLury, one unit of effort may take a variable number of elements of the population (e.g., commercial fish-netting operations). The unit of effort used in the present report is defined as the hunter-day, and a hunter cannot legally take more than one deer each year in Michigan. Consequently, k (defined as the proportion of the population taken by one unit of effort) might be more appropriately replaced by the probability of bagging a deer.

A possibility for an alternate derivation is proposed in the following steps:

(1) Assuming sightings of deer (by a hunter) follow the Poisson distribution:

Probability of seeing n deer in one "hunt" = $\frac{e^{-M} M^n}{n!}$

(2) If the probability of bagging a deer at each sighting is p, then in repeated trials ("Bernoulli" trials), the waiting time to the first success is (Feller, 1957):

Probability that the r^{th} sighting results in a kill = pq^r ($r = 0$ denotes the first trial; i.e., $pq^0 = p$) and presumably

hunting stops at the first success.

(3) Probability of killing a deer in n trials = $\sum_{r=0}^{r=n-1} pq^r$

(4) Probability of killing a deer = $\sum_{n=1}^{\infty} \frac{e^{-M}M^n}{n!}\left\{\sum_{r=0}^{n-1} pq^r\right\}$

$$= \sum_{n=1}^{\infty} \frac{e^{-M}M^n}{n!}(1-q^n)$$

$$= \sum_{n=1}^{\infty} \frac{e^{-M}M^n}{n!} - e^{-M}\sum_{n=1}^{\infty} \frac{(qM)^n}{n!}$$

$$= 1 - e^{-M} - e^{-M}(e^{qM} - 1)$$

$$= 1 - e^{-Mp}$$

(5) The meaning of the constant M used above needs definition. Clearly it depends on the number of deer per unit area, and somehow on hunter (and deer) activity. A crude approximation may be drawn from an analogy with plot sampling, where M is the mean density of the items of interest (randomly distributed) per unit area. One might thus identify M as:

$$M = \frac{N}{A}$$

where N = deer population on an area of size A, with A measured in units of "hunter-coverage." A closer definition will require both time and spatial coordinates, or consideration of relative velocities of deer and hunter, in the manner of Skellam's (1958) sophisticated treatment of a similar situation.

(6) For present purposes, the above leads to:

Probability of killing a deer at time t of the season = $1-e^{-\frac{P}{A}[N(0)-K(t)]}$

where N(0) is the initial population and K(t) the cumulative kill up to time t, in DeLury's notation.

(7) The empirical measure corresponding to the probability of killing a deer is the mean kill per unit of effort, C(t), but, as discussed in the kill-effort section of this report, there is the problem that this is usually measured as an average, rather than an instantaneous value.

(8) In most deer-hunting situations, C(t) will be small (less than .10), and the quantity in (6) may be approximated by:

$$C(t) = \frac{P}{A}\left[N(0)-K(t)\right]$$

which is DeLury's equation, with $\frac{P}{A} = k$.

(9) The constant term ($\frac{P}{A}$ or k), thus appears to depend on the vulnerability per encounter and a poorly defined measure of a "probability" of encountering a particular deer. At any rate, the notion of area seems implicit in the constant.

(10) The derivation above suggests an approach to the problem of changing vulnerability (see kill-effort section) wherein one would evaluate the frequency of encounters with deer (sightings) and the proportion of encounters resulting in a kill as separate items.

(11) An opportunity for field study of the above model exists in the controlled hunts in a fenced square-mile area (Van Etten, 1957). The unpublished data now available from this area indicate that the notion of a Poisson frequency of encounters, and constant probability of kill per encounter, may be realistic. However, too few deer are killed in any one season to give much information on changes in vulnerability.

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