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The significance of age distributions of exploited white-tailed deer populations

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THE SIGNIFICANCE OF AGE DISTRIBUTIONS OF EXPLOITED
WHITE-TAILED DEER POPULATIONS

by

Keith DeVere Larson

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

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INTRODUCTION

There has been a transition in the corn belt states from the holding of any-deer seasons to the need for bucks-only regulations--the millstone of the lake states wildlife administrators. This has become necessary in order to rebuild deer populations that suffered excessive exploitation under the liberal any-deer type regulation. The habitats of the corn-belt do not provide sufficient opportunity for deer to escape the hunter and are thus the most vulnerable habitat when compared with almost any other situation in which white-tails live. This situation has evolved until at the present, Iowa and Minnesota, are the sole states in the corn belt which are maintaining good hunting under statewide any-deer regulations.

Populations of white-tails declined drastically and also disappeared from many areas which had the limited cover characteristic of intensively farmed areas. This situation was the case in Ohio, Indiana, and Illinois in particular. The regression to bucks-only seasons was a necessity primarily due to inability to determine exploitation levels with sufficient confidence to use as a basis for the management of the species. Thus, as a result of inadequate management criteria, herds in the corn belt were decimated through excessive hunting pressure. The elusive and largely nocturnal white-tailed deer is impossible to count over extensive range and estimates derived in the several possible ways lack credibility.

Hunting success, which is the usual barometer of the sportsman, holds up fairly well until the population is badly depleted. If it were merely a question of the hunter finding a better population to hunt, which in turn was under-exploited, then the problem of excessive pressure would average out in the habitat. What has happened is that increasing numbers of hunters wish to hunt deer. The demand for necessarily limited permits and licenses forces increased authorizations, due to the progression of the political process, and, thus, over-exploited populations are not permitted to recover.

Hunting success in Iowa's more vulnerable habitats such as the north-central prairie habitats and in the east-central river breaks areas has declined either periodically or progressively due to excessive exploitation, primarily hunting. The lowered success rates are not altogether unacceptable and this situation has masked the significant changes in deer population levels which actually have occurred. Increased numbers of hunters and increasingly efficient hunting methods have created circumstances where some areas with pre-season huntable populations have virtually none following a season. Future populations depend on emigration.

Additional criteria are needed for determining exploitation levels for corn belt deer. Hunting success, population estimates, and various indices to population levels have proven treacherous criteria for management of white-tails in the corn belt.

Definition of the Problem

Age data taken from a sample of the legal harvest represents the primary biological data routinely collected by nearly all of the corn-belt states including Iowa. These data can be assembled by age-class to represent the age distribution of the harvest at a minimum, and depending upon the degree of bias, they may represent a satisfactory estimate of the age structure of the population. If better criteria are to be developed concerning exploitation they most likely will come from such data and other life history features of the species.

The problem

Are there pertinent and valid relationships existing between the components of age distributions or other life history features of deer in Iowa that can provide reliable estimates of exploitation level or rates of population change?

HISTORICAL REVIEW

The mathematical basis for relating the age structure of a population to life history features was established by Lotka (1907a) in his first paper on population analysis. In the same year (1907), Sundbarg reached the conclusion that a human population reveals its condition (tendency to grow or decline) through its age structure. Cole (1957) and Bodenheimer (1938) believe that these important conclusions have not been sufficiently noted by ecologists. When the mortality factors affecting a population are altered, either through natural environmental changes or through human exploitation or attempts at control, there will be a resulting change in the age structure of the population, and this may be observable, says Cole (1957), even before changes in population size or in birth rates provide evidence of the consequences of the changed mortality factors.

Thus, observations of the changes in the age structure of populations may provide valuable evidence of over-exploitation. LeCren and Holdgate (1962), in their introduction to a symposium on the exploitation of natural animal populations, point to the value of data from exploited populations as opposed to stable populations in the study of regulatory mechanisms in natural animal populations. They believe these kinds of data constituted experiments in population dynamics.

The neglect of the analytical methods by biologists is attributed by Cole (1954, 1957), to the tendency of the writers in the field of population theory to concentrate on the analysis of human populations and in part to skepticism about the mathematical methods of analysis. He believes that it will eventually come to the attention of field biologists generally that a great deal of information about the status of a population can be obtained from a study of its age distribution, and that changes in this distribution may be preludes to more dramatic changes in population size.

Existing Theory

Theory of stable age-distributions

Population analysis for all species is of necessity tied to the theory of "stable age-distributions" proposed by Lotka in 1907a. Additional contributions to the theory were presented in succeeding publications throughout his career: 1911, 1922, 1925, 1936, 1939, 1949.

He was able to show mathematically that the distribution of ages in a population in which the birth-rates and death-rates for each age group remain constant and which is increasing in unlimited space would approach a certain distribution which he called "the stable age-distribution" because it would not vary with time. Lotka also proved that as a population approached this stable state its rate of increase also approached a certain constant which he called "the intrinsic

rate of increase".

The rationale for the development of stability in age structures of populations of animals is best presented by Cole (1957): "It is obvious that if a population is always growing, as are the populations in the models used for determining potential population growth, then each age and sex class must ultimately come to grow at the same rate as every other class. If this were not the case, the disproportion between any two classes would come to exceed all bounds. The fastest growing class would continue indefinitely to make up a larger and larger proportion of the total population. It is thus intuitively recognizable that with fixed life history features there must ultimately be a fixed sex ratio and a stable age-distribution."

Allee, et al. (1949), interpreting the works of Sharpe and Lotka (1911), state that when life history features remain constant from generation to generation the population will ultimately settle down to a "fixed" or "stable" age distribution and will exhibit a fixed birth rate. If stability of a population could be shown, one would expect constant or fixed age specific mortality rates, age specific birth rates and a fixed population birth and death rate, according to this theory.

The central characteristic of the theory is that the actual age-distribution varies about the stable type of age-distribution, and tends to return to the stable type if through

any agency disturbed therefrom. Sharpe and Lotka (1911) showed that it will become re-established after temporary displacements. Coale (1968) illustrates the operation of the theory in population analysis of the Swedish people whose experiments in socialism have had population effects, and also in analysis of German populations which were affected by pronouncements of Adolph Hitler and resulting implementation by "der SS".

Previous applications

Lotka's theory has been fully accepted and utilized together with its related mathematical methods by human demographers and their colleagues in actuarial science. Its application in the study of other natural animal populations has been quite restricted. Andrewartha and Birch (1954) and Eberhardt (1960) have held that the requisite assumptions of constant age-schedules of fertility and survival are so rarely met in free-living natural populations that its application thereto is inappropriate. Cole (1954 and 1957) disagrees and is its foremost current advocate for reasons already noted. Eberhardt (1960) considered the theory in connection with the analysis of Michigan white-tailed deer populations but applied the mathematical methods to hypothetical populations rather than directly to real age-distributions.

Population studies that have employed the related techniques have dealt with species of economic importance,

primarily insects (Evans and Smith, 1952; Howe, 1953; Leslie and Park, 1949; Birch, 1948; Leslie and Ranson, 1940).

Mathematical Methods of Analysis

Lotka's intrinsic rate of natural increase

Lotka's pioneer work establishing theoretical relationships also provided the methods for interpreting the relationships between life history features and their population consequences.

Leslie and Ranson (1940), in dealing with laboratory populations of a vole, Microtus agrestis, used the following definition of the "intrinsic rate of natural increase": "It is the relative rate at which a population would ultimately increase or decrease, if the observed mortality and fertility were to remain constant in a stable and unlimited environment." In one sense, they considered it an abstract quantity, since both mortality and fertility would be expected to vary in response to changes in the environment and the increasing density of any naturally growing population. They believed it to be by far the most convenient measure to employ and to be implicit in any system of rates of death and reproduction which is appropriate, for a given population, to the conditions existing at the time of observation.

Chapman (1928) has presented a similar concept concerning rate of increase which he called biotic potential.

This concept considers the potential rate of increase as a fixed species characteristic governed by life history features and suggests that it is seldom realized due to environmental conditions.

Cole (1957) believed that the concept of the intrinsic rate of increase has a wider utility, if, instead of confining it to the measurement of a species characteristic as in the concept of biotic potential of Chapman, it is extended to individual populations. When this is done, the exponential rate becomes a statistic, r , and its value depends upon the prevailing age-schedule of fertility and survival. In this way, r becomes a measure of the difference between two populations of the same species growing under different conditions.

Estimating "r"

Precise calculation Lotka has provided three models in support of his theory and for the precise calculation of "r". Solution of the equations depends on numerical integration or on a choice of one of several methods of approximation (Lotka, 1939). In many practical applications dealing with natural and experimental populations some approximation to the value of "r" may be all that can be justified by the accuracy of the data.

Approximate calculation Andrewartha and Birch (1954) have summarized a convenient method of approximation of "r". The method of "mean length of a generation" is also used by

Leslie and Ranson (1940) and they provide a sample calculation also.

Ratio of population change

The exponential rate of increase or decrease, "r", is a logarithm. For small values of "r" it is sufficiently accurate to be used as a ratio of population change. For larger values of "r", the antilog is referred to as Lambda and represents the ratio of population change in successive time intervals (Cole, 1957).

Life table analysis

Quick (1958) proposed that wildlife biologists place an emphasis on the development of a system of analysis of wildlife populations which did not deal entirely with indices to that population such as changes in numbers of road-kills, or deer pellet counts, but that dealt with the population itself. He called this approach "population analysis", and suggested that it employ the techniques of human demography to understand the dynamics of wildlife populations. The one technique he referred to was "life-table analysis".

The potential for the life-table in animal population analysis was first fully described by Deevey (1947) and illustrated by Murie (1944) when he employed the life table to summarize age distribution data for the Dall Mountain Sheep. In the bio-medical field, this actuarial technique is best

described by Pearl (1940) for use with human populations. The method has been described by Henderson (1915), and Glover (1921) in the earliest analysis of human census data. Pearl and Parker (1924) published the first complete life table for an organism other than man, and Pearl and Miner (1935) have reviewed the early work up to that time.

The use of the life table method had not been extensive for wildlife populations. Quick (1958) applied it to the analysis of data from an extermination of a herd of Danish Roe Deer. This analysis provided invaluable insight to the effects of exploitation at different levels and thus contributed to the understanding of kill curves in common use with natural populations. This work was significant and became an important part of the techniques manual of the Wildlife Society in 1957.

Life tables have been constructed for a variety of game populations. Banfield (1955) prepared one for caribou. Nixon (1968) and Larson (1967d) used life table analysis for white-tailed deer populations; Tabor and Dasman (1957) used it for black-tailed deer populations.

Limitations There is near universal disagreement as to the assumptions and prerequisites to the use of life table analysis. Quick, In Mosby (1963) presents three kinds of life tables; based on a cohort, time-specific populations, and composite populations. He does not clarify the conditions requisite for the use of each type. Original and early

writings on this subject suggest results are applicable under the conditions present when the data were collected. This permitted wide interpretation but little application. The method originated about the same time as the theory of stable age-distributions by Lotka (1907a) and the same assumptions apparently are required. These assumptions concerning mortality and fertility rates seem to be insurmountable to most workers and thus restrict greater applications of a useful technique. Deevey (1947) has made a useful distinction between applications of the method. He has applied the term "ecological life tables" to those prepared from natural populations and "experimental life tables" to those from laboratory populations.

Management Tools in Use

State game departments usually have legal responsibility for maintaining populations of game. This is true in Iowa where the "biological balance law" requires the maintenance of game populations. There is an implication that it would be illegal to so manage or exploit these populations so as to bring about a decline in their breeding populations. Wildlife biologists are charged by these departments with the task of determining safe exploitation levels as can be determined from available biological data and to recommend appropriate hunting recommendations so as to comply with the law.

Several types of data are utilized to interpret the status of populations by state biologists in the corn belt. Personal subjective estimates are usually requested from lay field personnel. These prove of little value for management purposes but frequently are the basis of management plans (Larson, 1967b).

Perhaps the typical rationale for management recommendations, which require a decision as to total number of hunting permits to be issued and also in what area, is tied to the theory of "virtual populations" (Ricker, 1958). The record of numbers of hunters over the previous seasons, their success rates, and the total number of deer killed annually, gives an insight as to the status of the population. Again this is a subjective judgment that assesses past management. The rationale is this: if success rates stay the same, and the number of hunters were increased, the deer population must have been increasing. Thus, if the total kill was not disproportionately larger than last year's, the population was probably not hurt and more permits can be issued next year. It is necessary to consider differences in hunting conditions in these judgments.

Various indices to population levels are also used. One of these is the change in numbers of deer killed by traffic during the year. A relatively constant proportion of these are reported to state personnel and used primarily for this

purpose (Thompson, 1968 and Nixon, 1968). The problem is that changes in traffic patterns are not considered in any statistically significant way.

Estimates of survival rates

Hayne and Eberhardt (1952) have investigated the relationships within age distributions of deer to obtain estimates of survivorship. They based their work on Ricker (1948). They present four ways to estimate survival rates. These all depend on the premise that the rate of decline between age classes of the kill curve or the survivorship curve (lx) would indicate survival rates of the population. They state that the slope of the right limb of the kill curve equals the logarithm of the rate of survival and an estimate of rate of survival may legitimately be made from the trend of the data when: 1. There is equal recruitment to the hunted herd each year; 2. There is equal vulnerability to hunting for the age classes being considered; 3. The survival rate experienced by these age classes is constant with respect to both time and age.

In Eberhardt's treatment of the Michigan data (1960) he used the rate of decline between age-classes as the principal estimate of survival based on age distributions alone in the manner of Hayne and Eberhardt (1952). Because the estimates derived in this way for the several regional populations in Michigan all varied around .70 and did not agree with estimates

from other sources, he concluded that the age distributions alone did not provide the best possible estimate of survivorship. He obtained his estimates of probabilities of survival in this way for use with other life history features. He believed the method depended upon a basic assumption of a constant recruitment rate which is seldom met in practice. Unless the female herd remained absolutely constant, he believed that the ratios used to estimate survival would actually be a composite of survival and reproductive rates, and of uncertain value. For these reasons he agreed with Ricker (1958) and Beverton (1954) that some supplemental data are essential to use the method. He presented correlations with other indices to population and kill levels.

THE APPROACH TO THE PROBLEM

Population analysis, as envisaged by Quick (1958), Leslie and Ranson (1940), Lotka (1939), Deevey (1947), and Cole (1954), became possible for white-tailed deer populations when Severinghaus (1949) developed criteria for determining the age of deer based on replacement time and wear of their teeth.

The ages of deer taken from a sample of the kill in Iowa have been routinely collected since 1953 by the Iowa Conservation Commission. Data for the years 1963 through 1966 were collected under the supervision of the author. Eberhardt (1960) suggests that a minimum of four years data is essential for analysis purposes. In this study, age data from the years 1959 through 1966 have been assembled. This consists of 2,858 female and 3,359 male deer aged over the eight year period.

Collection of Data

Age and sex ratios

Procedures for collection of age and sex data from a sample of the kill during the open season have varied somewhat but in general the differences were designed to obtain a larger sample, make more efficient use of manpower, or improve the identification of the sample data.

A field force of 20 to 40 biologists and assistants visited cold storage locker plants throughout the state during and immediately after each deer season to obtain a sample of

the kill. The sex, age, and county of kill of the deer, and license number of the hunter were recorded every year and additional data on other factors such as health were collected in some years. Biologists were assigned a number of counties in which to visit plants so that nearly all locker plants were visited but there was no attempt to stratify the collection of the sample but merely to obtain the largest sample possible in the time available.

Foetal counts

In late 1965, it became apparent to the author that determination of exploitation levels might hinge in part on natality factors operating in the herd as well as mortality factors. A two year effort was initiated to obtain embryo and foetal counts from road-killed does during the spring and late winter. This period corresponded to the latter part of the 190 to 210 day gestation period of the deer and when significant numbers of female deer were being killed on the highway throughout the state. Data were collected by Conservation Officers on a voluntary basis in order to minimize personal biases from entering the study. They were asked to open the abdominal cavity and count the number of foetuses present. This information was recorded on a postal card form and mailed together with the jawbone from the animal to the author. This study was terminated in 1967.

Road-kill records

The records of numbers of deer killed by vehicles on highways are maintained to serve as an index to population levels among other reasons. These data again were submitted by Conservation Officers for each deer killed on highways in their district throughout the year. They did not become aware of all deer so killed but for those investigated a card form similar to the embryo survey postal card was mailed to the research station and this information was compiled annually.

Hunter-kill and success

Information on legal hunting kill and success by permit holders as used in this study are taken from the compulsory hunter report card sent to the Conservation Commission following the season. These data provide the only way of determining the kill which is satisfactory for management purposes. Success rates are derived from these kill reports as a ratio of deer killed to authorized permit holders who actually hunted.

Organization of age and sex data

The available data concerning age and sex were recorded on computer data cards for analysis with an IBM 360 computer. The column entries were as follows:

<u>Year</u>	<u>License</u>	<u>Sex</u>	<u>Age</u>	<u>County</u>	<u>Checker</u>	<u>Corrected age</u>
1-2	3-7	8	9-10	11-12	13-14	15-16

An analysis plan based on the populations of the many possible management zones with their component counties was prepared in matrix form for programming purposes. Computer programs were developed to perform the calculations and summary analyses of the population parameters. The availability of these computer programs for possible use in the management of other corn-belt deer herds was a secondary objective of this effort.

The various populations of interest

Since 1963, hunters have received permits to hunt in specified areas only, in order to apportion better the hunting effort with deer herds. Until 1967, the state had been divided into two zones with the area of these zones changing each year to adjust the hunting pressure. The two zone plan analyzed in this study was the 1966 zoning plan and is referred to as Analysis Plan #2.

In 1967, the division created six zones. This plan is referred to as Analysis Plan #1. It was considered desirable to analyze the data to interpret the effects of various management plans, in this case, zoning. Therefore, on the basis of zoning with eight years of data, and also looking at statewide data over the eight years of concern, (Analysis Plan #9), there are seventy-two populations of interest.

Mustard (1963) divided the state into four ecological regions for management purposes. Each region held habitats

which varied in type and vulnerability of deer to hunting. Over the eight years, this suggests thirty-two more populations of interest (Analysis Plan #7).

Data have also been collected personally from a deer population which represents the highest in Iowa per unit area. These data were collected during the deer seasons at the Iowa Army Ammunition Plant, near Burlington, Iowa for the years 1964-1966. The data for 1963 for this area were collected by graduate students working under the Iowa Cooperative Wildlife Research unit, at the request of the author. These data add four more populations to the analysis and are processed as Analysis Plan #8 for programming purposes.

These various analysis plans would consider, as outlined above, a total of 108 populations. The data were further organized by treating the sexes separately and combined. In this manner, three hundred and twenty-four populations were treated by the methods outlined in the literature.

Methods of Analysis

Slope of kill curve

Iowa data present a kill curve that is constantly descending from the youngest class to the oldest. Formal methods were used to determine the slope of kill curves and the regression of frequency on age was calculated for the entire distribution (transformed data) and a b value determined together

with confidence limits. The b value would represent the apparent survival rate of Hayne and Eberhardt (1952). Since the whole curve slopes to the right, the data were used beginning with the youngest class. Regression coefficients were computed for all 324 populations. A computation of R^2 was made to determine the proportion of the variance explained by the regression.

Life table analysis

Life tables were constructed for each population after Deevey (1947) and Pearl (1940). A rather long or unabbreviated form of the life table was used since this study was seeking understanding of relationships. The columns used in the table and definition of terms are as follows:

x = age in years, stated as an interval

d'_x = the number dying within the age interval stated in the x column

d_x = d'_x converted to a scale of 1000

l_x = the number surviving at the beginning of the age interval stated in the x column. In another context, when a decimal point is placed three places to the left, the l_x column becomes the probability of survival to the beginning of the age interval stated in the x column

q_x = the number dying in the age interval divided by the number of survivors at the beginning of the interval. The rate of mortality in the life table format.

L_x = the average number living during the age interval

e_x = the mean expectation of life or the mean further expectation of life in years.

Data can be assembled in a life table as described for purposes of summary in several ways. Quick, (In Mosby, 1960), classifies the data organization as time-specific, age-specific (frequently considered as a cohort), and in composite form as in Murie's analysis of the big-horn sheep (1944). The treatment in this study was by both time-specific and by cohort which represents 648 life tables constructed by computer. Composite distributions were assembled during Chi-square analysis to obtain a mean distribution for the years under study.

Slope of the l_x frequency

The regression of l_x frequency on age-class was computed for all populations from transformed data and the b value calculated with confidence limits and R^2 . The b value again represents the slope of the regression line and is another estimate of the rate of survival. The l_x frequency is taken from the l_x column of the life table for each population and the b value computed on a time-specific and a cohort basis.

Ratio programs

Representation of classes Eberhardt (1960) has suggested a way in which the under-representation of the fawn class can be identified. The method is to compute the ratio of fawns to adults in a given year and compare it to the ratio of the same group one year later, that is, the ratio of 1-1/2's to 2-1/2's and older deer. This has been done in this study

and also taken a step further. Ratios have been computed so that the initial ratio of the cohort can be followed throughout the life of the cohort.

The straight right limb method The apparent survival rate can be computed from the right limb of the kill curve when plotted on semi-log graph paper. Hayne and Eberhardt (1952) list this method as one of the ways to determine the apparent survival rate. When so plotted at least the right limb of the curve should be reasonably straight because of the relatively equal vulnerability of the older classes. The method consists of dividing the sum of the numbers in all age classes older than the first class of the straight segment by the same sum plus the number in the first class. Such a ratio is equivalent to the ratio of l_4 to l_3 in the l_x column of the life table. This ratio as well as other ratios representing survivorship to each younger l_x age class of the l_x distribution were calculated on a time specific basis and a cohort basis.

Calculation of lambda and Lotka's "r"

Mean length of a generation The method based on the mean length of a generation is an approximate method of calculation of r . It is adequate for human populations but for some highly fecund lower animals it may not be sufficiently accurate. The geometric increase of a population is given by the equation

$$N_t = N_0 e^{rt},$$

where N_0 is the number of reproducing individuals at time t_0 , N_t is the number of reproducing individuals at time t , and r is the intrinsic rate of natural increase. The number of individuals at the end of a generation will be

$$N_T = N_0 e^{rT} ,$$

where T is the mean length of a generation. Hence,

$$\frac{N_T}{N_0} = e^{rT} .$$

N_T/N_0 is the ratio of total female births in two successive generations, or net reproduction rate and designated R_0 . Thus

$$R_0 = e^{rT}$$

and

$$r = \frac{\log_e R_0}{T} ,$$

and

$$\lambda = e^r .$$

R_0 and T can be estimated from age-schedules of births, m_x , and age-schedules of survival rates, l_x . R_0 is equal to the sum of the cross products (sum of $l_x m_x$ values). T may be approximated according to the following model:

$$T = \frac{\sum l_x m_x}{\sum l_x m_x} .$$

The parameters R_0 , T , r , and λ have been computed from the age schedules of births and the age-schedules of survival rates (probabilities) for the 324 populations of interest in this study.

Precise value of r The precise value of r may be obtained by solving Lotka's equation

$$\int_0^{\infty} e^{-rx} l_x m_x dx = 1$$

In order to determine whether the method of mean length of a generation is accurate enough for deer population analysis a substitution of values obtained was made. An example of the precise calculation of r may be found for human populations in Dublin and Lotka (1925, appendix) or Lotka (1939, p. 68).

The stable age distribution

The stable age distribution may be calculated from the life table and the intrinsic rate of natural increase. If c_x is the proportion of the population of stable age-distribution aged between x and $x + dx$ and b is the instantaneous birth-rate,

$$c_x = b e^{-rx} l_x .$$

Stable age-distributions were calculated for the 108 female populations of interest using Lotka's methods. Chi-square tests of heterogeneity were performed between the actual

age distributions and the calculated stable age distributions. This test serves to verify the existence of a stable state in the actual population and to validate use of the method of calculating r which requires a stable age distribution. Coale (1968) suggests that a population may be considered as essentially stabilized when the ratio of each annual age group to current annual births is a multiple arbitrarily close to one-- say .98 to 1.02-- of the ratio in the stable population. He further states that no more than "w" years (w being the greatest reproductive age attained) after the births are exponential, the age distribution becomes stable.

Coale's ratio was modified to provide a new measure of stability in which the criteria are more appropriate to the variability of the data and also less stringent. A ratio of the net reproductive rate (R_0) in the sample age-distribution to the net reproductive rate (R_0) of the calculated stable age-distribution was considered to be a valid measurement of the differences present in the two distributions. This ratio was calculated for each female population of interest.

Methods of Comparison

It is known that the methods described above have varying degrees of accuracy and may not all be entirely valid. The best method of estimating levels of exploitation in the several populations should require as high a level of accuracy as is possible consistent with the representative nature of the data.

This is so because of the extremely high level of exploitation in Iowa which may very well surpass recruitment in some of these populations. With so little margin for error the best method should have a high degree of accuracy and consistency.

The validity of techniques used together with their level of accuracy were compared with the apparent superior method to determine the most appropriate analysis plan for deer in Iowa or in the corn belt.

Definition of Terms

THE NET REPRODUCTION RATE, R_0 ---This is the multiplication per generation. It is expressed as the ratio of total female births in two successive generations.

THE MEAN LENGTH OF A GENERATION, T ---This is the mean time from birth of parents to birth of offspring.

THE INTRINSIC RATE OF NATURAL INCREASE, Lotka's r ---the constant rate of increase of a population approaching its stable age-distribution.

THE FINITE RATE OF NATURAL INCREASE, λ ---This is the multiplication per female in unit time of a population of stable age-distribution. This is best defined by the equation λ equals e to the r^{th} power.

THE STABLE AGE-DISTRIBUTION---This is the age-distribution which would be approached by a population of stable age-schedule of birth-rate and death-rate (i.e., m_x and l_x constant) when growing in unlimited space.

THE m_x (STATISTIC)---This is the average number of female births for any particular parental age-group of pivotal age x .

THE l_x (STATISTIC)---This is the proportion of individuals alive at the beginning of the age-interval for any particular age-group of pivotal age x . It can also be considered as the probability of living to the beginning of age-interval x . The l_x table gives the age-schedule of survival.

RESULTS OF ANALYSIS OF AGE DISTRIBUTIONS

Test of Aging Variability

A Chi-Square test of heterogeneity of the ages assigned to the collected jawbones of the 1966 season by the field checkers compared with the age assigned by the author revealed a significant difference between checkers (Table 1).

Inspection of the Chi-Square value for the various checkers revealed that the Chi-Square for checker number eight accounted for all of the significance. Examination of the basic data revealed that the excess of error occurred in aging of older animals. Since the assignment of ages to this age category is somewhat arbitrary (Severinghaus, 1949), the data collected by this checker was retained. Further no statistical significance is attached to the Heterogeneity Chi-Square value obtained because the differences occur in the older classes.

These results of the Chi-Square analysis are interpreted to mean that data on age composition of Iowa deer populations may be used in population analysis with some expectation that they are representative of the true ages of the animals represented in the sample. Since the majority of the checkers have had continuous service in field aging of deer, these results are assumed to apply to all data for the years 1959 to 1966, inclusive.

Table 1. Test of significance of errors in aging

Checker number	Sample size	Number correct	Number Incorrect	Chi-Square
6	46	43	3	1.128
8	11	5	6	20.055
11	20	17	3	.241
12	62	55	7	.311
13	83	78	5	2.453
14	23	17	6	4.786
16	17	14	3	.624
17	25	21	4	.492
19	282	24	4	.208
20	20	19	1	.830
21	68	63	5	1.156
23	136	121	15	.290

Combining:

#7, #9, #15,
#18, #22,
and #24

<u>25</u>	<u>22</u>	<u>3</u>	<u>.006</u>
564	499	65	$\chi^2 = 32.580$

Critical value $\chi^2_{.05, 12 \text{ d.f.}} = 21.0$

Sampling and Systematic Bias in Aging Results

Randomness

The necessity of obtaining data at locker plants introduces a factor of bias. It is fairly common in the less prosperous regions for deer to be processed at home. Bias enters because it is expected that the size of the deer bagged influences the decision whether to have it processed at a locker plant or at home. The price of processing climbed to a high of \$15 in 1966 from about \$5-\$8 in 1959. This would tend to further influence a decision concerning processing a fawn deer weighing 60-100 pounds, for example.

There were also observed differences in processing or handling in locker plants. Plants located in good deer habitat would have many customers on the Monday following a weekend opening of the deer season. Because of space limitations, operators were known to quickly dispose of small deer, separate the head portion from the identifiable body portion with the license number on it, or reserve the big old bucks with the big racks for viewing by customers and curious townspeople. It is believed that the best data were not available from the big processors because of these circumstances.

Bias in aging

It is common for deer of 1-1/2 years to be called 2-1/2 years because of the early replacement of the third premolar under conditions of good nutrition. This mistake was fairly

common and upset the age-distributions of the early years of the study. When sample sizes were small there appeared to be even greater irregularity in the distributions than expected to the extent that only when sample sizes reached about 100 females was regularity to be expected.

Incorrect aging of the older classes, 3-1/2 and older, was also a factor which introduced bias. This category represented only a small portion of the deer aged in the study, perhaps about 12%, and did not contribute greatly to the significance of the results.

Differential vulnerability

A kind of systematic bias associated with the differential vulnerability of the several age classes is revealed by Table 2 which traces the increase in this ratio throughout the life of the cohorts born from 1959 until 1966.

The fawn-adult ratio present at fawning time based on fertility rates presented in Table 3 is .810. With this value as a standard, it would appear that there is under-representation of fawns in the samples of this study. It is probable that there is unequal mortality during the first six months of life and thus the data are more a measure of this mortality than under-representation of fawns in the sample.

The change in this ratio between six months and 1-1/2 years may be significant, however. Deer in these two categories have similar survival rates in a stable population. Thus, the

Table 2. These data compare the fawn adult ratio during year one of a cohorts life with the same ratio during succeeding years of life. The fawn-adult ratio at birth in the population should be .810 at the biotic potential of the species in Iowa

Cohort year of birth	Fawn to adult ratio	1-1/2 to 2-1/2 + ratio	2-1/2 to 3-1/2 + ratio	3-1/2 to 4-1/2 + ratio
Females - statewide sample				
1959	.626	.766	1.79	1.79
1960	.629	.679	2.33	1.27
1961	.748	.707	2.39	1.83
1962	.770	.755	2.45	0.70
1963	.787	1.06	2.12	1.55
1964	.760	.811	1.45	--
1965	.750	.928	--	--
1966	.692	--	--	--
\bar{X}	.720	.815	2.09	1.42
Males - statewide sample				
1959	.625	1.010	1.208	2.211
1960	.857	.877	1.213	1.563
1961	.814	.874	1.049	1.500
1962	.675	.863	1.457	2.125
1963	.702	1.017	1.360	1.639
1964	.933	1.441	.909	--
1965	.583	1.103	--	--
1966	.751	--	--	--
\bar{X}	.742	1.026	1.199	1.808
Combined males and females - statewide sample				
1959	.626	.887	1.471	2.029
1960	.750	.777	1.670	1.460
1961	.783	.789	1.496	1.630
1962	.722	.814	1.876	1.333
1963	.740	1.040	1.666	1.560
1964	.845	1.143	1.145	--
1965	.650	1.016	--	--
1966	.723	--	--	--
\bar{X}	.730	.924	1.554	1.602

Table 3. Age schedule of fertility, Iowa deer, 1967

Parturition age	Number with embryos present each class				Total does	Total embryos	Embryos per doe
	0	1	2	3			
Fawns	1	15	7	0	23	29	1.26
Adults	<u>0</u>	<u>6</u>	<u>26</u>	<u>3</u>	<u>35</u>	<u>67</u>	<u>1.914</u>
Totals and Means	1	21	33	3	58	96	1.655

change from .720 females per adult to .815 females and from .742 males per adult to 1.026 one year later reveals a lesser vulnerability of fawns and a consequent under-representation of the fawn class in the samples based on the mean value of these data.

Yearling females alone appear in the approximate proportion born and as would be expected if all classes were equally vulnerable, a ratio of .815 females per adult older than 1-1/2 years.

The sharp increases of these ratios beyond 1-1/2 is attributed to the increased although somewhat equal vulnerability of the 2-1/2 and older age classes. The greater sampling error due to aging and to small numbers of these ages in the sample prevents these ratios from being comparable.

It appears that the data do give a measure of relative vulnerability, as follows; in the order of least vulnerability: female fawns, male fawns, yearling females, yearling males, older females, older males. The older animals seem to have a gradually increasing vulnerability as measured by the gradual increase in mortality rate exhibited by the mean values taken from the eight year composite l_x survivorship curve of Figure 1 for females and the shorter age base of the male population (Appendix B). The greater old male vulnerability is probably the result of greater pressure upon this component of population. This is also exhibited by the 8 year composite l_x survivorship curve for males compared with females (Figure 1).

Survivorship Curves

The l_x column of the life table provides the data for survivorship curves. A comparison of representative curves from southern Michigan, Southern Minnesota, Illinois, Ohio and Iowa is made in Figure 2. These populations are all rather highly exploited and have been for more than a decade. The curve for Iowa demonstrates the steepest slope and thus indicates the highest level of exploitation of the five states' populations.

Survivorship curves from unexploited or lightly exploited populations are presented in Figure 3. All curves in Figures 2 and 3 are composed from time-specific life tables.

Figure 1. Survivorship curves (l_x) of the Iowa statewide female deer populations, 1959-1966, (time-specific basis), compared to the mean composite l_x curves for males and females

The dashed line illustrates the comparison with the calculated stable l_x distribution for the individual years.

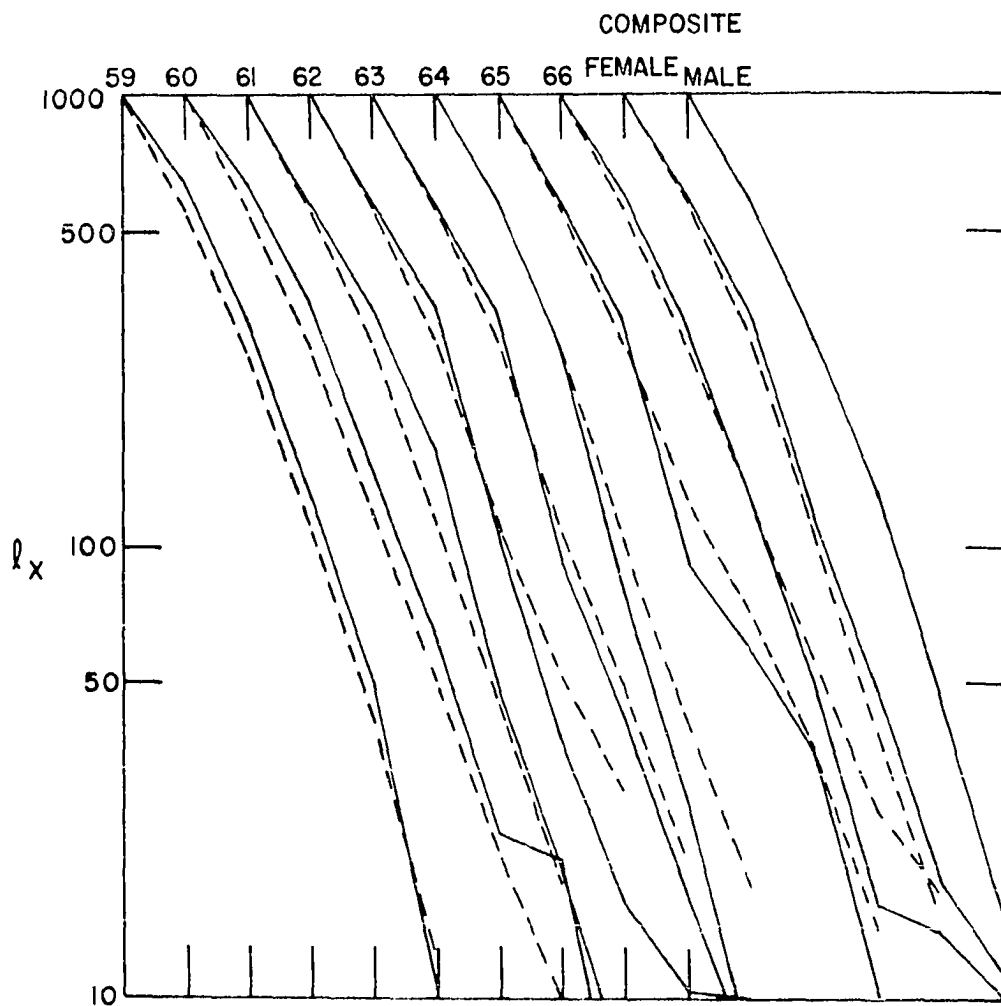


Figure 2. Comparison of survivorship curves (l_x) from mid-western states for white-tailed deer, time-specific basis for l_x

Data taken from Nixon (1968), for data other than Iowa. Iowa curve taken from this study, 1966, statewide population.

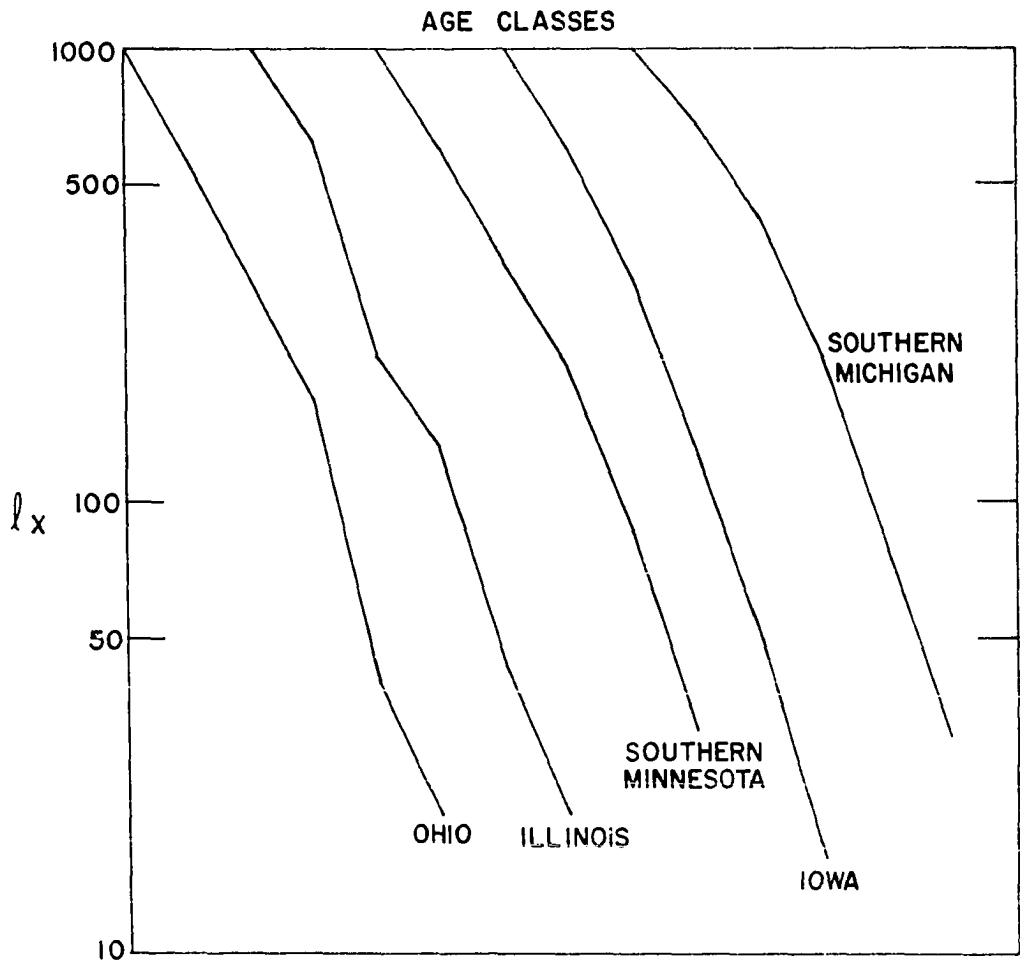
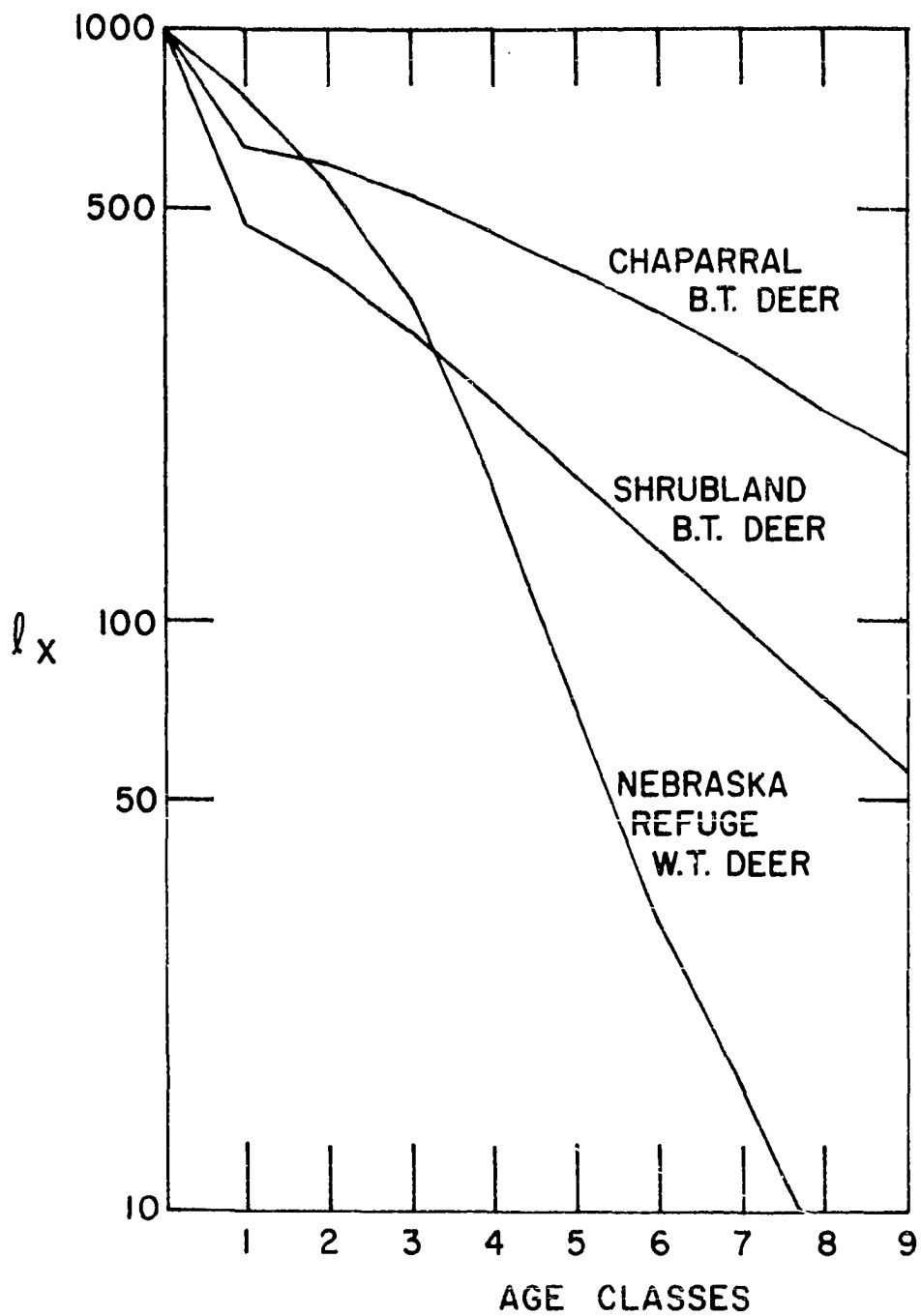


Figure 3. Survivorship curves from relatively unexploited populations of white-tailed deer from a Nebraska closed season area, Havel (1966) and black-tailed deer populations from California habitat types (Tabor and Dasman, 1957)



All authors reviewed are in agreement that exploitation tends to reduce the age base of the kill curve or survivorship curve. This is the central phenomena on which the hypothesis being tested in this study is based, namely; if the shortening age base is a phenomena directly related to exploitation, can the survivorship curve of the age distribution reveal the "level" of exploitation?

Theoretical basis

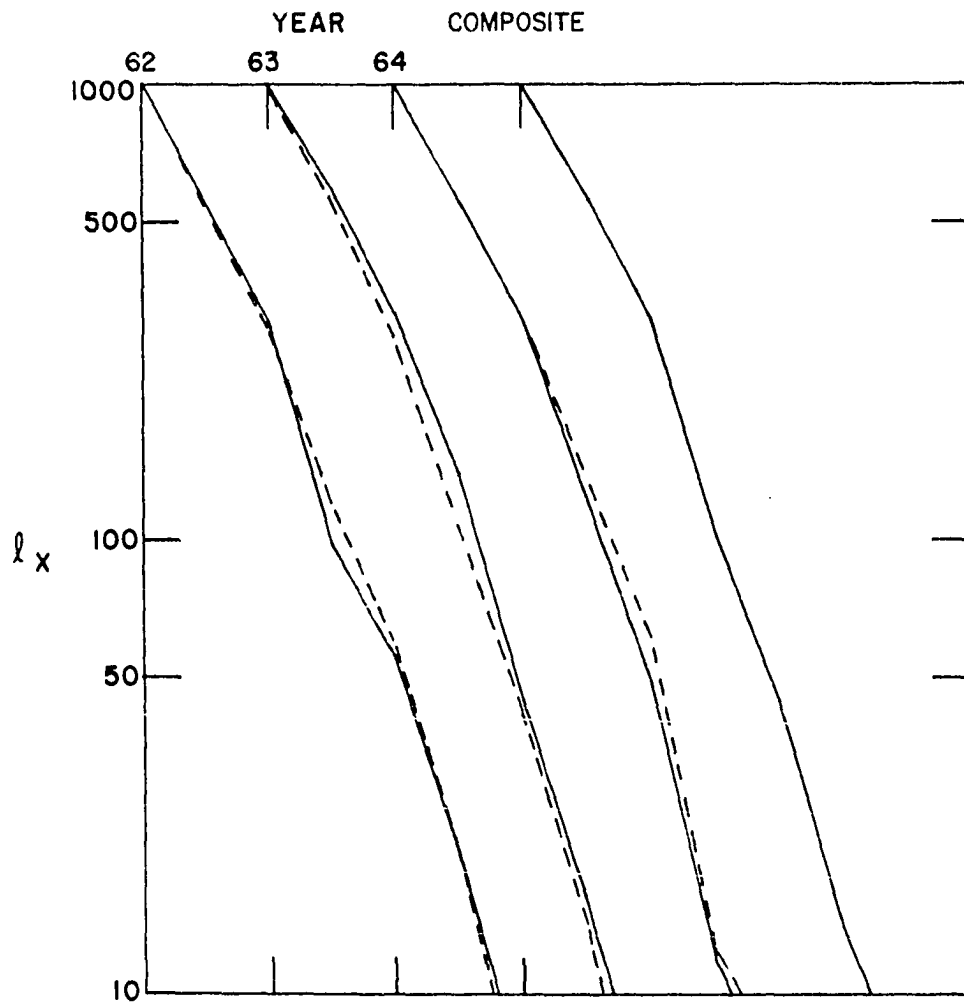
Lotka's theory of stable age-distributions presented earlier must be considered in any test of methods of determining survival rates. This body of theory and methods as developed by Lotka (1907a, b, 1922, 1925, 1939); Sharpe and Lotka (1911), Dublin and Lotka (1925), Dublin, Lotka, and Spiegelman (1949), Andrewartha and Birch (1954), Leslie and Ranson (1940), Leslie (1945, 1948), Cole (1954, 1957), Coale (1957, 1968) has been successfully applied to human population study as well as other species and thus, most probably, criteria applied in this study must conform to its tenets. The results presented herein will be discussed in the light of this theory.

Statewide populations

Survivorship curves for the statewide populations are presented in Figure 1 on a time specific basis and in Figure 4 for the age specific basis. Irregularities in the curves for the older classes are indicative of aging errors as well as

Figure 4. Survivorship curves (l_x) and a dynamic basis for the Iowa statewide deer population compared with an l_x curve constructed on a composite basis for 1961-1964 cohort years of birth

The dashed curve represents an l_x curve from the corresponding calculated stable age-distribution.



small sample error. The aging criteria are not very well developed for older deer.

Time-specific populations In a Chi-Square test of heterogeneity, the 1960, 1962, and 1965 populations were significantly different than a composite population for all eight years of data. Irregularities in the older age classes apparently would account for the differences in these populations. It is quite apparent from an inspection of the plotted curves that there is little difference between these l_x curves for survivorship for the first five categories at least. Actually, the 1966 curve and the composite curve for the years are virtually identical. This is interpreted to mean that the age distribution for the eight years of data is identical for the important areas of the curves, the younger age classes. Approximately ninety-five percent of the deer in these populations are of the first four age-classes. The sampling and aging bias which is frequently apparent in the data of this study for older age classes has little bearing on the value of these data and will be disregarded or corrected for when necessary.

Age-specific populations Similarly, the data plotted as the frequency of survivorship of a cohort for the years 1962-1964, show a striking degree of parallelism (Figure 4).

Chi-Square tests indicate no statistically significant difference between these data and the calculated stable age distribution or with the six year mean or composite age

distribution. Results of Chi-Square analysis are found in Table 4.

Significance of l_x curves

In terms of age base changes, there apparently has been no statistically significant change in the age base of these populations over the years of the study.

In terms of Lotka's theory of stable age distributions, these populations have been stable over these years when viewed through either age specific or time specific analysis (Table 4 and 5).

Age schedule of fertility

Data concerning reproductive rates are presented in Table 3. Rates are established for only two categories of age -- fawn and adult -- due to insufficient sample size. Haugen (1961) has presented preliminary results of a study made from 1957-1959. He found a similarly high rate of production from fawns with nearly all adults producing twins and a small percentage dropping triplets. There were very few barren females in either study. It will be assumed in this study that the rates of Table 3 do not differ significantly from rates prevailing at the beginning of the period for which data are available, 1959, and can be considered constant for these purposes.

Table 4. Statistics derived through application of Lotka's theory of stable age-distributions to distributions of thirty-four age-specific female white-tailed deer populations, 1959-1966, from various management zones in Iowa

Cohort year of birth	Mean length of a generation	Net reproductive rate	Intrinsic rate of natural increase
	T	R_0	r
Analysis Plan #1 - Zone 6			
1959	2.092	.9169	-.04147
1960	1.973	.892	-.05807
1961	2.1156	.970	-.01432
1962	1.700	.712	-.19974
1963	1.8612	.830	-.10005
1964	1.9142	.885	-.06408
Analysis Plan #2 - Zone 1			
1962	1.901	.848	-.08675
1963	1.972	.954	-.02404
1964	1.917	.823	-.10158
Analysis Plan #2 - Zone 2			
1959	1.864	.821	-.10609
1961	1.640	.701	-.21636
1962	1.927	.776	-.13138
1963	1.813	.780	-.013691
1964	1.919	.836	-.09331
Analysis Plan #7 - Zone 1			
1959	2.658	1.043	+.01573
1961	1.989	.842	-.08655

* Significant beyond the .001 level.

Table 4 (Continued)

Ratio of increase (or decrease)	Ratio of R_o to R_o of calculated stable distribution	Tests of stability	
		Chi-Square value (expected from 8 year mean) χ^2	Chi-Square value (expected from calc. stable) χ^2
λ	R_o / R_o		
.959	---	4.4341	10.4094
.944	---	5.3411	17.3982
.985	---	25.8679*	10.7317
.819	0.97	35.4856*	17.2634
.905	---	3.5737	8.4189
.938	---	4.2505	12.4197
.917	---	18.4089	15.8918
.976	---	1.2390	27.0352*
.903	1.02	16.6794	2.8730
.899	1.03	8.8071	31.6545*
.805	1.007	32.6182*	29.5452*
.877	---	19.6470	22.1389*
.872	1.01	6.9265	7.5669
.911	1.05	19.8394	3.3137
1.016	0.99	82.0891*	20.4497
.917	1.001	48.8523*	68.7583*

Table 4 (Continued)

Cohort year of birth	Mean length of a generation	Net reproductive rate	Intrinsic rate of natural increase
	T	R_0	r
Analysis Plan #7 - Zone 2			
1959	1.977	.891	-.05865
1960	1.921	.847	-.08671
1961	1.972	.873	-.06871
1962	1.9488	.784	-.12506
1963	1.940	.893	-.05856
1964	1.936	.841	-.08972
Analysis Plan #7 - Zone 3			
1963	1.478	.574	-.37550
1964	1.868	.853	-.08486
Analysis Plan #7 - Zone 4			
1961	1.755	.735	-.17529
1962	1.811	.748	-.16020
1963	1.917	.888	-.06187
1964	1.911	.873	-.07102
Analysis Plan #9 - Zone 1			
1959	1.914	.864	-.07649
1960	1.918	.887	-.06280
1961	1.694	.742	-.17592
1962	1.922	.803	-.11394
1963	1.873	.843	-.09107
1964	1.919	.832	-.09565

Table 4 (Continued)

Ratio of increase (or decrease)	Ratio of R_o to R_o of calculated stable distribution	Tests of stability	
λ	R_o / R_o	Chi-Square value (expected from 8 year mean) χ^2	Chi-Square value (expected from calc. stable) χ^2
.943	---	12.0872	20.8704*
.917	---	1.1707	9.2859
.934	---	1.9131	9.8665
.882	---	11.6611	11.0061
.943	---	6.6907	9.5576
.914	1.04	2.3796	4.5920
.687	---	83.6633*	17.5693
.919	---	26.8604*	18.0117
.839	0.98	21.1248*	26.9443*
.852	0.96	12.2910	19.7405
.940	---	12.6311	17.2480
.931	---	23.9751*	9.7510
.926	---	5.2197	31.7983*
.939	---	17.6377	39.5374*
.839	1.04	19.2947	16.4211
.892	0.99	11.4238	15.7996
.913	---	4.1982	9.4043
.909	0.97	9.3025	3.2634

Table 5. Statistics derived through application of Lotka's theory of stable age-distributions to distributions of forty-one time-specific female white-tailed deer populations, 1959-1966, from various management zones in Iowa

Year	Mean length of a generation	Net reproductive rate	Intrinsic rate of natural increase
	T	R_0	r
Analysis Plan #1 - Zone 6			
1959	1.839	.841	-.09431
1961	1.902	.828	-.0991
1962	1.687	.707	-.20526
1963	1.993	.869	-.07073
1966	1.985	.7987	-.11323
Analysis Plan #2 - Zone 1			
1959	1.972	.908	-.04912
1961	1.795	.821	-.10968
1962	1.787	.832	-.10297
1963	2.016	.900	-.05206
1964	1.978	.898	-.05443
1965	2.065	.910	-.04566
1966	2.080	.924	-.03819
Analysis Plan #2 - Zone 2			
1959	1.929	.8996	-.05483
1960	2.163	1.014	+0.00634
1961	2.037	.889	-.05794
1962	2.018	.855	-.07785
1963	1.851	.778	-.13534
1965	2.247	.920	-.03703
1966	2.025	.881	-.06252

*Significant beyond the .001 level.

Table 5 (Continued)

Ratio of increase (or decrease)	Ratio of R_o to R_o of calculated stable distribution	Tests of stability	
		Chi-Square value (expected from 8 year mean χ^2)	Chi-Square value (expected from calc. stable) χ^2
λ	R_o / R_o		
.910	---	36.0564*	14.7888
.906	1.04	26.5864*	20.5864
.814	0.97	23.4075*	4.3303
.932	1.04	11.1450	4.4006
.893	---	11.4407	16.3645
.952	---	27.4077*	14.1843
.896	---	18.0222	14.3127
.902	---	12.6875	13.8420
.949	---	8.7783	8.6685
.947	---	5.4426	20.8525*
.955	---	25.7693*	24.7820*
.963	---	13.7571	7.2095
.947	---	27.0095*	27.3792*
1.006	---	43.5505*	21.9041*
.944	---	4.9272	15.0994
.925	0.99	14.7412	39.9604*
.873	0.97	23.0195*	36.8599*
.964	0.98	69.4297*	49.9778*
.939	1.04	10.2676	18.8586

Table 5 (Continued)

Year	Mean length of a generation	Net reproductive rate	Intrinsic rate of natural increase
	T	R_0	r
Analysis Plan #7 - Zone 2			
1959	1.929	.902	-.05323
1961	1.943	.864	-.07550
1962	1.792	.731	-.17463
1963	1.801	.754	-.15702
1964	1.848	.799	-.12132
1965	2.076	.889	-.05647
1966	1.963	.889	-.06016
Analysis Plan #7 - Zone 3			
1962	1.861	.828	-.10143
1963	1.978	.851	-.08146
1966	2.439	1.010	+.00421
Analysis Plan #7 - Zone 4			
1961	1.797	.788	-.13255
1962	1.919	.839	-.09133
1964	1.830	.773	-.14107
1966	1.951	.8998	-.05412
Analysis Plan #9 - Zone 1			
1959	1.898	.878	-.06850
1960	2.042	.961	-.01963
1961	1.941	.866	-.07432
1962	1.961	.843	-.08700
1963	1.887	.811	-.11132
1964	1.765	.735	-.17423
1965	2.044	.863	-.07183
1966	2.010	.876	-.06604

Table 5 (Continued)

Ratio of increase (or decrease)	Ratio of R_o to R_o of calculated stable distribution	Tests of stability	
		Chi-Square value (expected from 8 year mean χ^2)	Chi-Square value (expected from calc. stable) χ^2
λ	R_o / R_o		
.948	---	27.8569*	16.1296
.927	---	12.2332	18.0100
.839	0.95	12.7053	4.6270
.855	0.98	14.3320	11.7815
.886	1.03	12.0801	5.3936
.945	1.03	21.8384*	18.1877
.942	---	10.6301	7.8254
.904	1.06	12.2192	27.6716*
.922	1.03	25.5342*	15.5237
1.004	1.04	90.1553*	45.6787*
.876	1.05	51.0879*	59.5657*
.913	1.04	15.2788	44.1401*
.868	0.97	23.4653*	18.8875
.947	---	39.3030*	20.4084
.934	---	18.7046	16.9785
.981	---	13.9604	23.5989*
.928	---	5.1331	19.2251
.917	1.01	8.9946	31.7915*
.895	1.01	7.6538	21.0886*
.840	0.95	16.2766	13.4114
.931	0.999	26.7461*	26.7971*
.936	1.05	8.3977	14.2454

Life table analysis

Life tables constructed by computer are found in Appendix A. Both cohort populations and time specific populations were so treated. It is from these analyses that survivorship is obtained. Survivorship, considered to be survival rates by Eberhardt, 1960, comes from the l_x column of the life-table. It denotes the number surviving from a cohort of 1000 deer based on the frequency of deaths in each interval. As such, it is usually most properly employed for analysis of cohort (dynamic, or age specific) populations. Certain assumptions must be met to use the technique for time-specific or composite populations. Survivorship curves from the populations in this study appear in various places in this section. The life table is a convenient form by which to summarize data. The various parts of the tables will be used in further analysis, such as the mean expectation of life, and the mortality rate per 1000 (e_x and Q_x).

Survival Rate Ratios

Survival rates have been calculated for all populations. They appear in Table 6 and Table 7 for the stable populations selected for study. The three sets of values presented as estimates of survival all depend on an idea most thoroughly presented by Ricker (1948) and adapted for deer population application by Hayne and Eberhardt (1952) and Eberhardt (1960).

Table 6. Statistics derived from age distributions of forty-one time-specific female white-tailed deer populations, 1959-1966, from various management zones in Iowa

Year	\hat{b} value for regression of D_x on age	Coefficient of variance (R^2)	\hat{b} value for regression of l_x on age
Analysis Plan #1 - Zone 6			
1959	.5029	.897	.3952
1961	.4892	.885	.5266
1962	.4443	.896	.3436
1963	.5206	.872	.441
1966	.4560	.953	.4599
Analysis Plan #2 - Zone 6			
1959	.5184	.912	.4450
1961	.5159	.945	.4997
1962	.5144	.896	.3874
1963	.4952	.918	.4597
1964	.4475	.951	.4311
1965	.4668	.965	.4747
1966	.4541	.947	.4358
Analysis Plan #2 - Zone 2			
1959	.4760	.983	.499
1960	.5125	.980	.5091
1961	.4566	.965	.5048
1962	.5293	.957	.4816
1963	.3601	.942	.4359
1965	.4729	.918	.5042
1966	.5056	.954	.4807

Table 6 (Continued)

Coefficient of variance (R^2)	Eberhardt's ratio of survivorship ($2-1/2 +/$ $1-1/2 +$) \hat{s}_1	Mean expectation of further life E_o	Complement of mean of mortality (Q_x) thru 4th age interval \hat{s}_2
.918	.551	1.54	.520
.934	.588	1.61	.510
.947	.488	1.41	.430
.982	.528	1.57	.500
.941	.476	1.48	.465
.951	.529	1.57	.535
.906	.612	1.62	.485
.939	.525	1.54	.480
.987	.546	1.60	.510
.971	.525	1.59	.480
.993	.590	1.63	.495
.943	.536	1.58	.525
.979	.511	1.68	.490
.989	.603	1.79	.560
.996	.586	1.66	.500
.975	.606	1.57	.460
.985	.582	1.51	.425
.973	.519	1.58	.450
.988	.509	1.62	.485

Table 6 (Continued)

Year	\hat{b} value for regression of D_x on age	Coefficient of variance	b value for regression of l_x on age
Analysis Plan #7 - Zone 2			
1959	.4404	.935	.4369
1961	.4549	.913	.5134
1962	.4723	.943	.3853
1963	.4965	.961	.3836
1964	.4424	.942	.4058
1965	.4573	.984	.4762
1966	.4533	.954	.4435
Analysis Plan #7 - Zone 3			
1962	.5347	.867	.4106
1963	.3884	.834	.4422
1966	.5355	.950	.5638
Analysis Plan #7 - Zone 4			
1961	.4880	.973	.3761
1962	.4318	.890	.4458
1964	.5898	.930	.4231
1966	.4777	.932	.4507
Analysis Plan #9 - Zone 1			
1959	.4532	.956	.4727
1960	.4896	.988	.4822
1961	.4380	.937	.5064
1962	.4901	.954	.4581
1963	.4074	.913	.4127
1964	.4131	.946	.3883
1965	.4556	.933	.4763
1966	.4458	.967	.4678

Table 6 (Continued)

Coefficient of variance (R^2)	Eberhardt's ratio of survivorship ($2-1/2 +/$ $1-1/2 +$) \hat{s}_1	Mean expectation of further life E_o	Complement of mean of mortality (Q_x) thru 4th age interval \hat{s}_2
.952	.5135	1.58	.530
.948	.6102	1.63	.515
.965	.5000	1.41	.455
.976	.5538	1.47	.450
.976	.4623	1.47	.455
.994	.5814	1.60	.495
.964	.5500	1.54	.520
.955	.5932	1.53	.430
.988	.5833	1.54	.480
.974	.4928	1.65	.480
.969	.6538	1.49	.420
.971	.6071	1.55	.450
.975	.5000	1.50	.440
.973	.5288	1.62	.505
.975	.5158	1.65	.515
.990	.5661	1.73	.525
.984	.5956	1.64	.500
.976	.5857	1.56	.465
.993	.5696	1.54	.455
.987	.4848	1.47	.435
.993	.5521	1.60	.475
.981	.5186	1.61	.505

Table 7. Statistics derived from age distributions of thirty-four age-specific female white-tailed deer populations, 1959-1966, from various management zones in Iowa

Cohort year of birth	Eberhardt's ratio of survivorship (2-1/2 +/- 1-1/2 +)	Mean expectation of further life	Complement of mean of mortality (Q_x) thru 4th age interval	Sample size
	\hat{s}_1	e_0	\hat{s}_2	n
Analysis Plan #1 - Zone 6				
1959	.500	1.56	.480	72
1960	.567	1.59	.495	79
1961	.532	1.57	.515	106
1962	.511	1.40	.380	118
1963	.481	1.42	.410	133
1964	.409	1.26	.475	103
Analysis Plan #2 - Zone 1				
1962	.527	1.50	.450	142
1963	.530	1.50	.465	170
1964	.411	1.20	.455	146
Analysis Plan #2 - Zone 2				
1959	.549	1.56	.455	174
1961	.570	1.42	.350	244
1962	.525	1.40	.420	293
1963	.476	1.38	.400	276
1964	.410	1.21	.455	247
Analysis Plan #7 - Zone 1				
1959	.608	1.60	.560	38
1961	.590	1.47	.375	62
Analysis Plan #7 - Zone 2				
1959	.505	1.58	.475	88
1960	.554	1.55	.490	89
1961	.538	1.51	.470	113
1962	.522	1.41	.450	116
1963	.495	1.45	.465	119
Analysis Plan #7 - Zone 3				
1963	.360	1.26	.265	111
1964	.336	1.27	.445	75
Analysis Plan #7 - Zone 4				
1961	.574	1.41	.405	120
1962	.532	1.41	.410	146
1963	.532	1.45	.435	150
1964	.398	1.25	.465	137
Analysis Plan #9 - Zone 1				
1959	.546	1.61	.475	274
1960	.589	1.63	.475	333
1961	.562	1.47	.430	372
1962	.530	1.44	.435	435
1963	.497	1.43	.420	446
1964	.414	1.21	.455	393

None of the three methods has merit in estimating survival rates except under very restrictive conditions which render the method unacceptable in analyses of exploited deer populations. The values obtained are either not in agreement with trend data or appear to be proportional to other estimates but have values below that expected and inconsistent with the recruitment rate over the full eight year study period. This obviously would result in a disappearing population which, in the extreme suggested by these data, has not happened.

Two sets of values do have merit as estimators of the degree of fore-shortening of the age base in the populations considered. That is, they are quantitative measures of the slope of the curve and thus are measures of the shortening age base. The question of validity and merit of these values obtained by the three methods will be evaluated in a later section.

Calculation of Lotka Statistics

This method depends on the stability, in Lotka's terms, of the population under study. Although the method was applied to all populations only those which met one of several criteria testing stability were selected for presentation (Table 4 and Table 5).

The Lotka statistics of r , λ , and $c_{t,x}$ were calculated and are presented in Table 5 for time-specific populations and in Table 4 for age-specific populations.

The mean value of "r" for forty-one time-specific populations was $-.0823$. This indicates that on the average these populations were declining. The corresponding value of lambda, the antilog of "r", was $.921$.

The mean value of "r" for thirty-four cohort populations was $-.099$. Again, this represents declining populations. The antilog or lambda was $.9047$.

These values do not represent any specific population but are presented as representative of the values obtained. The status of specific populations will be treated in a separate section.

Prediction of Population Change

Certain statistics of population phenomena appear to be of value because of apparent linear relationship with the statistic lambda. The relationship with "r" is curvilinear due to "r" being a logarithm.

These relationships are illustrated in Figure 5 through 14 where the several estimates of "s" (survival rate), and e_x (mean expectation of life) are plotted against the calculated values of lambda. The populations considered are in four groups: time-specific, age-specific, populations with large sample distributions, and large sample distributions to which smaller sample distributions with stability have been added.

The regressions of the estimates of "s" and " e_x " on lambda have provided prediction equations. Thus, a measure of the age

Figure 5. The b-value of the regression of l_x on age for 21 time-specific female populations compared to estimates of lambda

Prediction equation indicated.

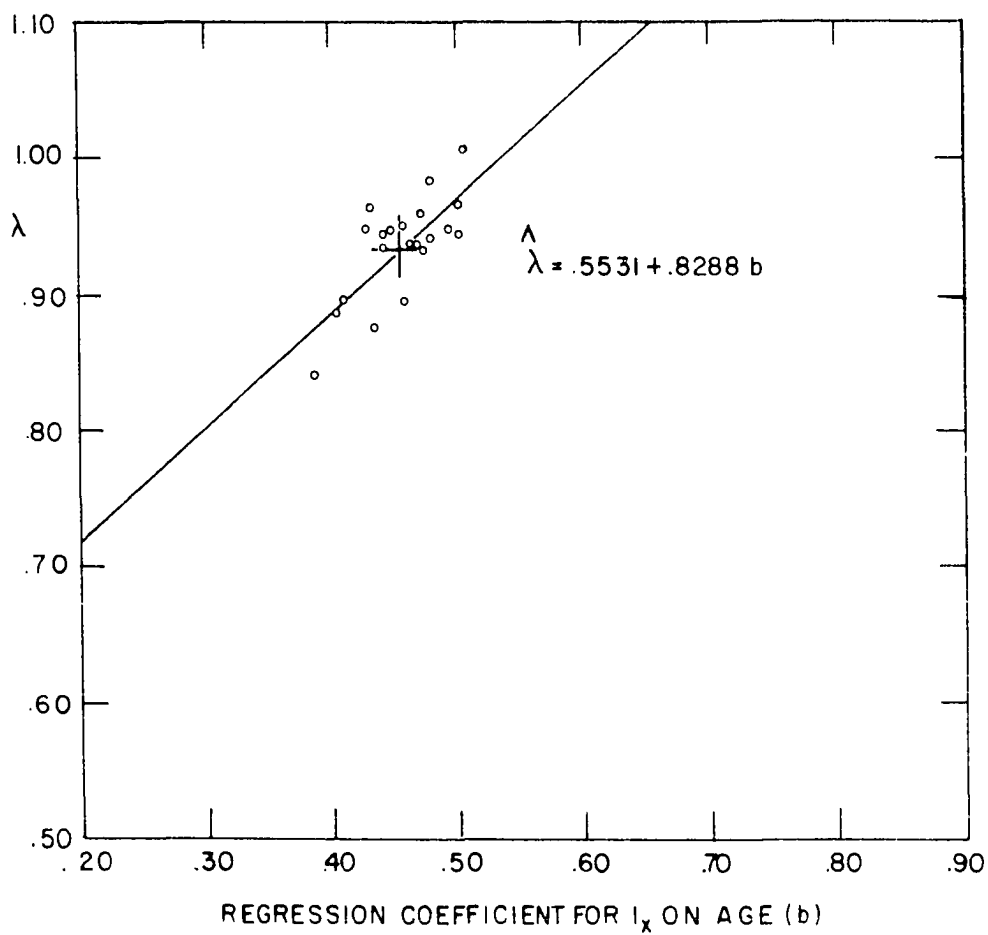


Figure 6. The b-value of the regression of l_x on age for forty-one time-specific female populations compared to estimates of lambda
Prediction equation indicated.

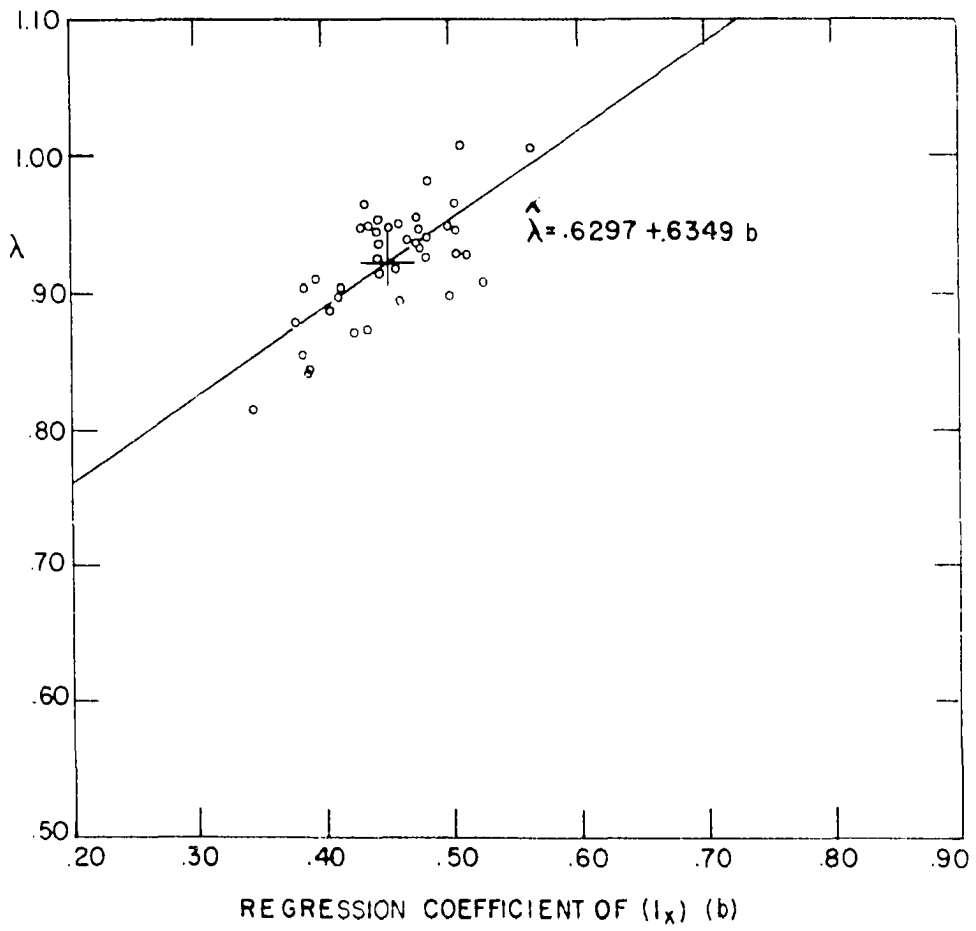


Figure 7. Plot of the regression of lambda on \hat{s} , the survival rate, for twenty-four age-specific populations with prediction equation indicated

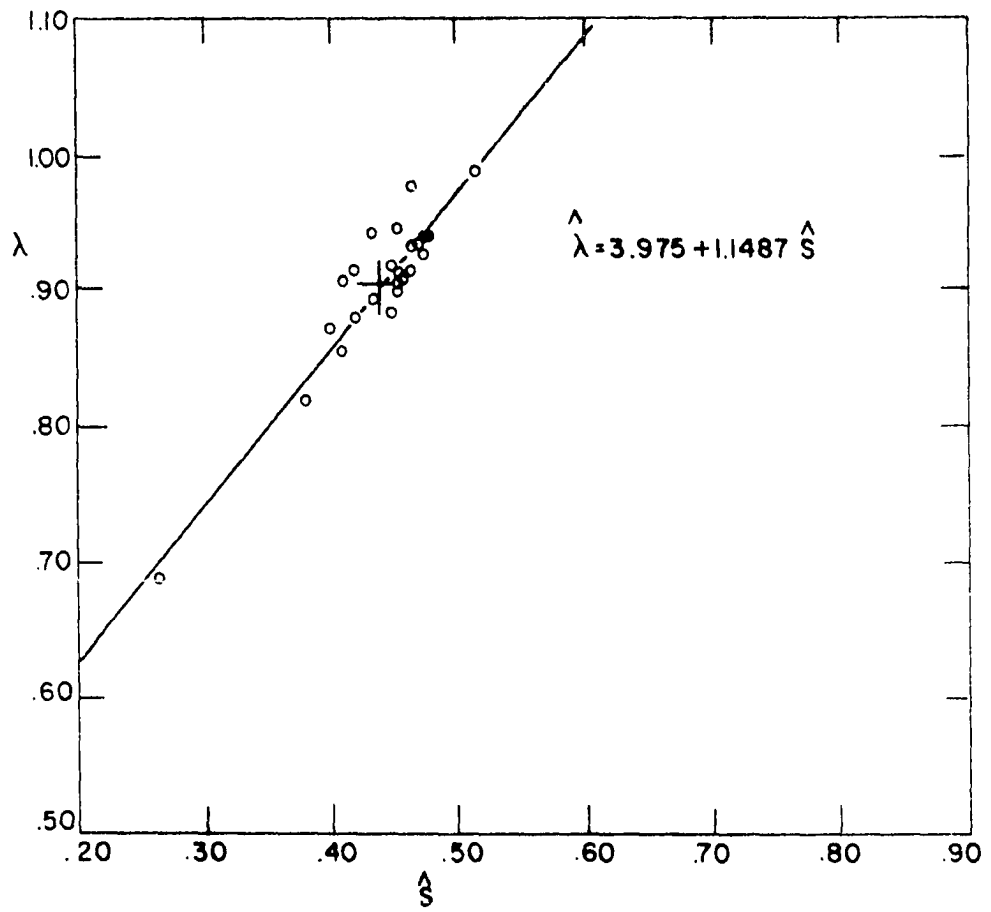


Figure 8. Plot of the regression of lambda on \hat{s} for thirty-four age specific female populations with prediction equation indicated

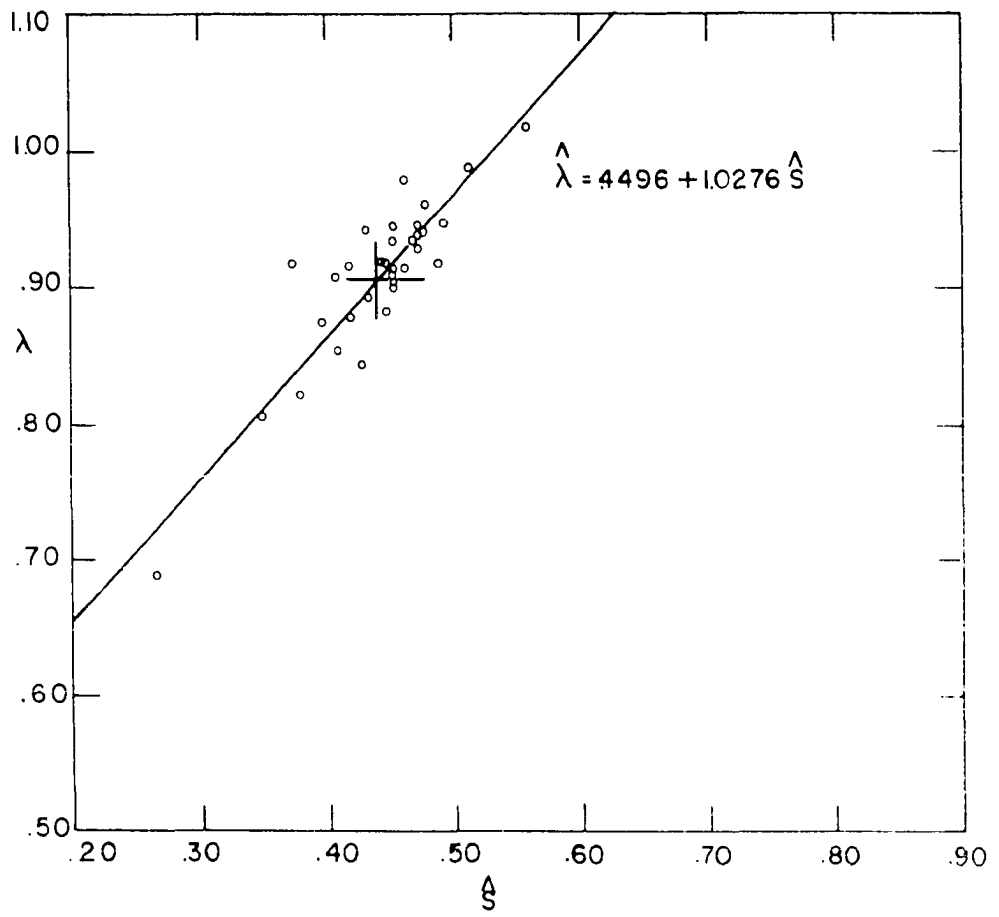


Figure 9. Plot of the regression of lambda on \hat{s} for forty-one time-specific populations with prediction equation indicated

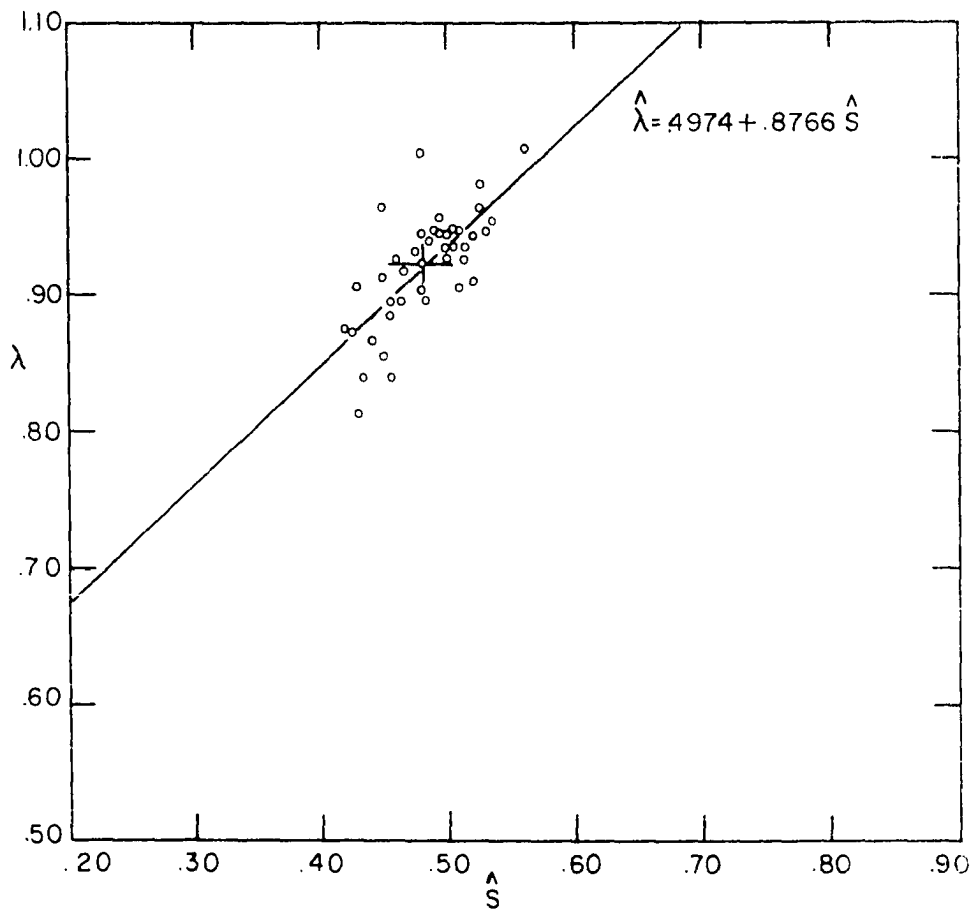


Figure 10. Plot of the regression of lambda on e_x ,
the mean expectation of life for forty-
one time-specific female populations with
prediction equation indicated

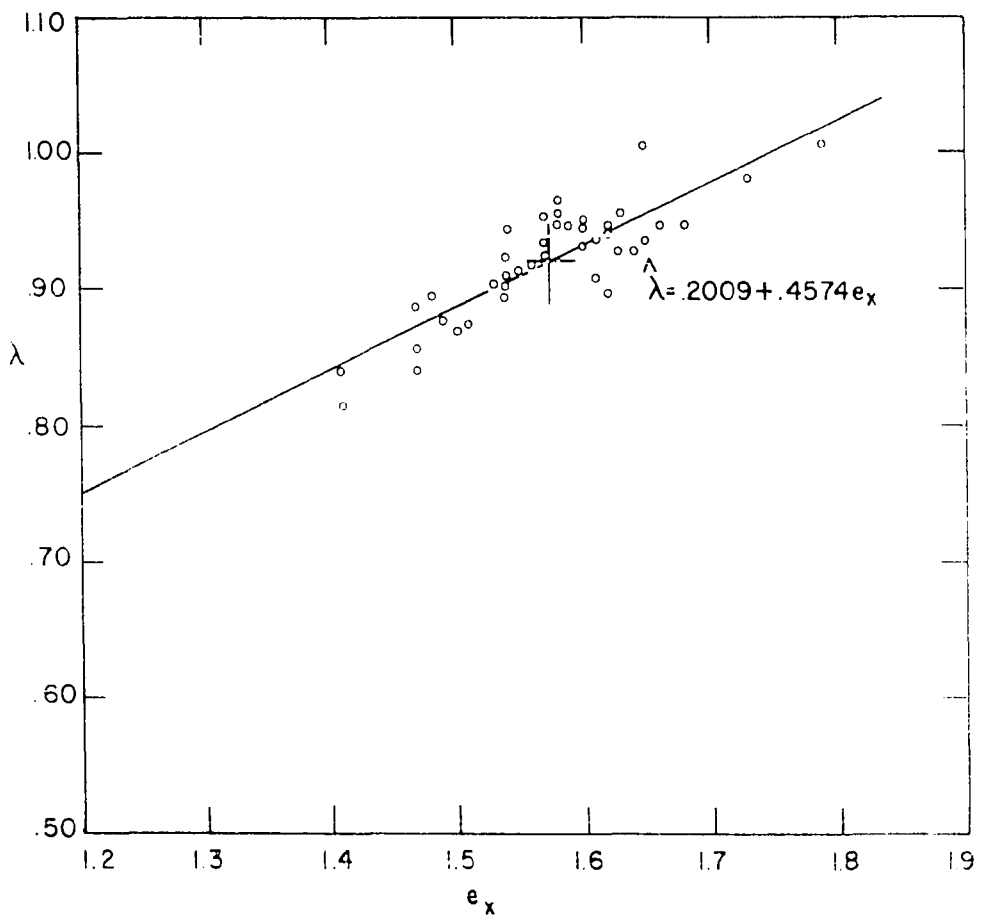


Figure 11. Plot of the regression of e_x , the mean expectation of life, on lambda for thirty-four age-specific populations of females with prediction equation indicated

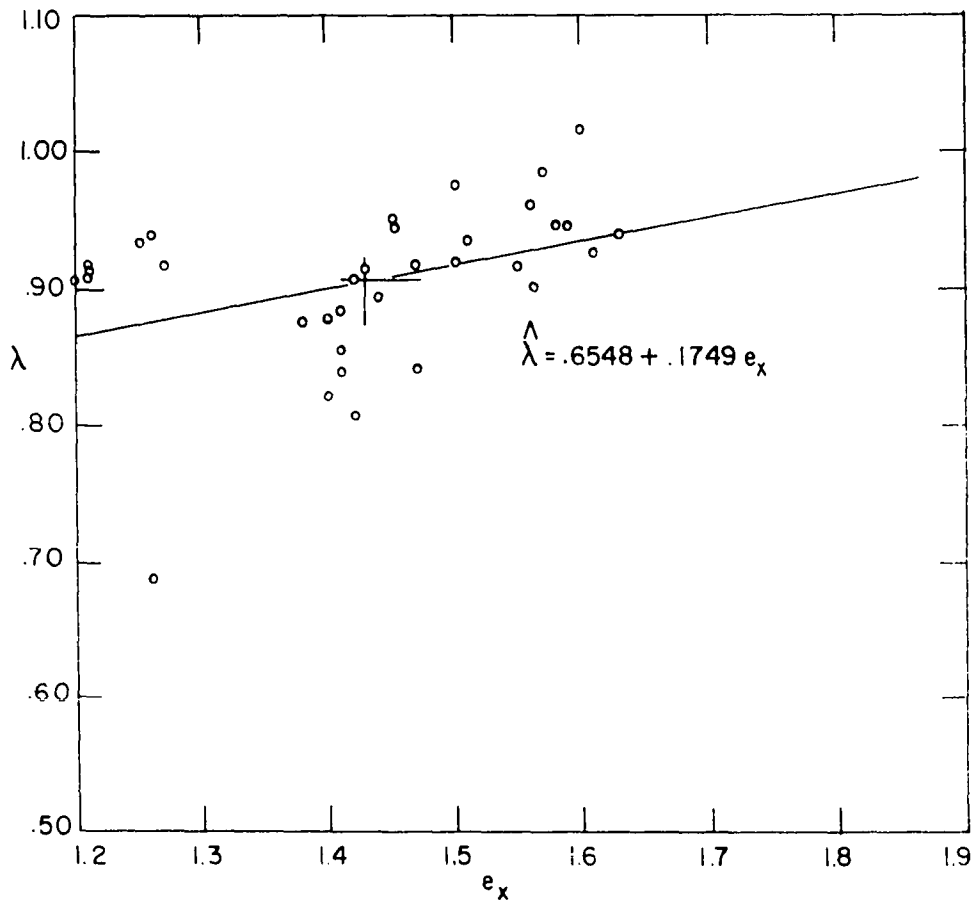


Figure 12. Plot of the regression of e_x , the mean expectation of life, on lambda for twenty-one populations, female and time specific, with prediction equation indicated

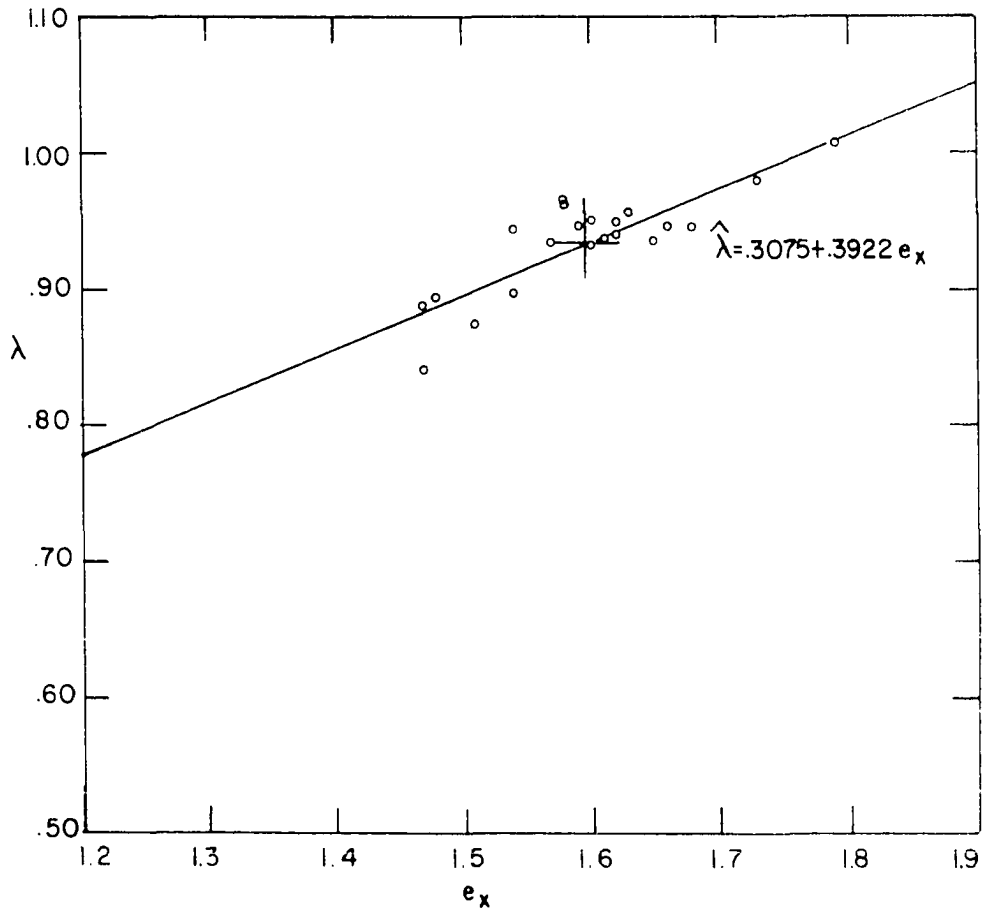


Figure 13. Plot of the regression of \hat{s} on lambda for twenty-one female time-specific populations with prediction equation indicated

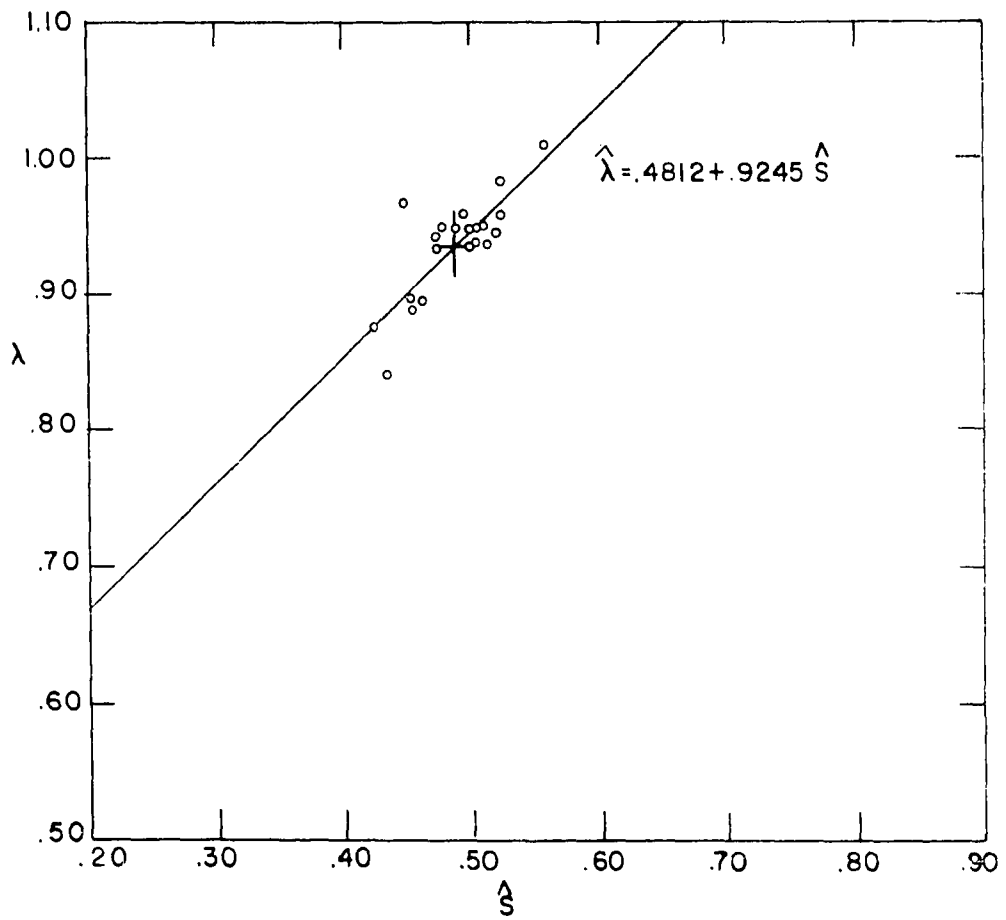
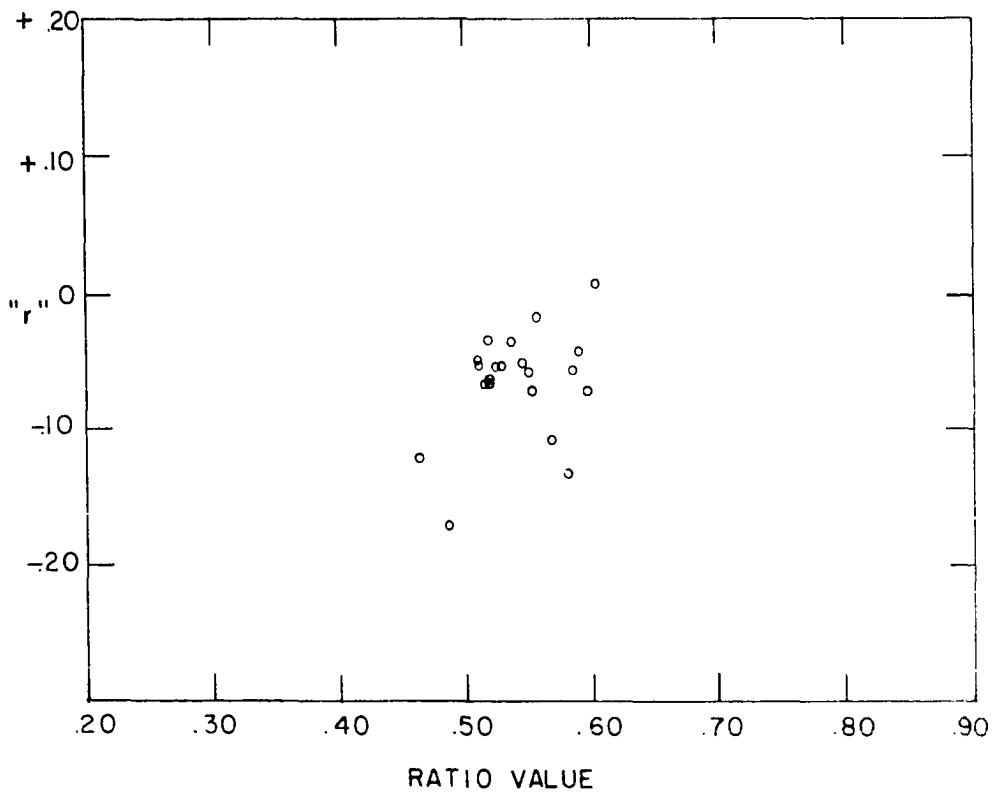


Figure 14. A comparison of Hayne and Eberhardt's survival ratio with lambda for twenty-one time-specific, stable, female populations



distributions obtained by various means and degree of sophistication and difficulty can be used to determine population trends and the status of populations. Table 8 presents expected values of lambda for measures of the several parameters of population change.

Sample calculations of Lotka statistics The basis for use of the approximate method of calculating "r", the mean length of a generation, is in the unity of results obtained by the two methods. A sample calculation is found in Appendix C. A sample calculation of a stable age distribution, $c_{t,x}$, is found in Appendix D.

Table 8. Expected values of lambda from estimates of survivorship, s , and mean expectation of life, e_x , for time-specific stable populations based on prediction equations

Estimates of survivorship, TS				Mean expectation of life		Cohort population	
s_1	λ	s_2	λ	e_x	λ	s_3	λ
.42	.866	.30	.823	1.40	.841	.40	.861
.43	.874	.32	.836	1.42	.850	.42	.881
.44	.883	.34	.849	1.44	.860	.44	.902
.45	.892	.36	.862	1.46	.869	.46	.922
.46	.901	.38	.874	1.48	.878	.48	.943
.47	.909	.40	.887	1.50	.887	.50	.963
.48	.918	.42	.900	1.52	.896	.52	.984
.49	.927	.44	.913	1.54	.905	.53	.994
.50	.936	.46	.926	1.56	.914	.54	1.005
.51	.944	.48	.939	1.58	.924	.55	1.015
.52	.953	.50	.952	1.60	.933	.56	1.025
.53	.962	.52	.965	1.62	.942	.57	1.035
.54	.971	.54	.977	1.64	.951	.58	1.046
.55	.980	.56	.990	1.66	.960	.59	1.056
.56	.988	.58	1.003	1.68	.969	.60	1.066
.57	.997	.60	1.016	1.70	.978	.65	1.118
.58	1.006	.62	1.029	1.75	1.001	.70	1.169

s_1 = mean rate of survival for first four classes of l_x , time-specific basis

s_2 = b value of regression of frequency on age of l_x

Prediction equation for $s_1 = \hat{Y} = .4974 + .8766X$

Prediction equation for $s_2 = \hat{Y} = .6297 + .6439X$

Prediction equation for $e_x = \hat{Y} = .2009 + .4574X$

s_3 mean rate of survival for first four classes of l_x , Cohort basis

Prediction equation for $s_3 = \hat{Y} = .4496 + 1.0276X$

SIGNIFICANCE OF AGE DISTRIBUTIONS

Bias in Basic Data

The values obtained for estimates of population parameters in this study have been imprecise due to the effect of bias. Fertility data have had the greatest influence on results. This factor of bias has been influential in a consistent way and thus the error from this source can be considered a constant. Necessarily then, the specific value of lambda for a population must be considered in a partially subjective way, through a type of calibration by assigning an estimated value for error. The total error also has a component deriving from sampling and from aging errors. Of these, only sampling error contributes significantly to imprecision among the stable populations selected for study. This, too, can be assigned a value, again somewhat subjectively.

Fertility error

The age schedule of fertility should be completely age-specific. The lack of sufficient sample size to obtain values for each age is a major factor of error. The suspected higher rate for 1-1/2 and 2-1/2 year old deer would have a significant effect on lambda. It is not expected that the adult rate would change more than a few hundredths up to perhaps .06. If its effect was felt in the large younger classes it would increase lambda markedly. Cole (1957) has said that the most

significant datum in the current human population explosion is not the number of children per family but the age of the parents at the time of the first born. A similar phenomenon is apparent here.

Although the fertility schedule approaches by a few hundredths the expected true value for each category, it is known that considerable bias entered the study at the time of collection of the data. Embryo counts made from February through June of 1967 increased substantially from very low for the first half of the study to improbably high for the latter half of the study. There appears to be a direct linear relationship between the progression of the gestation period and the foetal counts.

The fawn adult ratio of .810 resulting from these data is not high enough to maintain the population at current levels with the annual mortality rate the herd has sustained during the last decade. There is no evidence that the statewide population has decreased statewide since 1959. Actually, the sustained increased kill would indicate considerable higher population now. A better estimate is needed so that the calculated lambda can be a more unbiased estimate of population change.

Sampling error

The effect of sampling error is to bias the probability of survival estimates. These estimates are tied directly to

the frequency of occurrence of the age-classes in the kill. The first effect on lambda is through the non-occurrence of some of the older age-classes which exist in the population but not in the sample. This technique of analysis demands a large sample size because of its dependency on the length of a generation. If "T", the mean length of a generation, is not based on the complete age-base of the population, an error of several hundredths occurs in lambda.

Aging error

A significant part of the aging error and its effect on lambda derives from the tendency to not assign ages beyond 5-1/2 years. The criteria are not clear-cut enough beyond this age to develop a smooth distribution at this end of the age base (Ryel et al., 1960). It is estimated an error of as much as two to three hundredths is created in lambda due to this aging error.

The populations chosen for stability generally do not exhibit irregularity between the 1-1/2 and 2-1/2 year classes. In some of the unacceptable distributions (non-stable or of small sample size), the 2-1/2 year class is sometimes larger than the 1-1/2 year class. The increased probability of survival that this invalid data produces in the calculation of lambda generates a larger value of lambda which is erroneous. This error can be as high as .10.

Characteristics of Iowa Survivorship Curves

If all the above-mentioned sources of error were corrected, and there are techniques to permit the improvement of these data, there would still remain another source of error. Differential vulnerability between age classes exists in the general population under the management applied. There is strong evidence from the work of Anderson (1953) that the rates change depending upon the portion of the population that is killed by the pressure applied. The level of exploitation thus alters relative vulnerabilities.

In general, for the statewide populations for which survivorship curves have been presented (Figures 1 and 4), there are two distinct limbs to the curve. This reflects the difference between the relative vulnerability of the 2-1/2 and older females and the lesser vulnerability of the fawns, and 1-1/2 year old females. These survival rates average .64 for the younger classes and .41 for the older classes, when calculated on either a cohort or time specific basis.

In the large 1966 sample, where the final ages were assigned by the author, (which in theory produced a distribution free of aging error), the rate of survival declines more smoothly from about 59% to 32% between the fourth and fifth interval. There is still a major change at the beginning of the third interval which produces the distinct right and left limb of the curve. The same indication of a gradually

declining rate of survival between each age class is evident from inspection of the 8-year composite l_x curve (Figure 1). The same major break also occurs there. The range of these data indicates the range of variability in the vulnerabilities of the classes expressed in rates of survival.

This higher rate of mortality in older deer under conditions of a relatively high level of exploitation when compared to natural mortality, is the mechanism which produces the shorter age-base with increased exploitation. In Iowa, this shorter age-base developed after only three hunting seasons. It is postulated that compensatory reproduction occurred (Errington, 1946) and within a few adaptive years the fertility rate had attained the magnitude reported in this study. The age-distributions have not changed markedly since about 1955 (Larson, 1967d). Kline (1969) reports a composite D_x frequency distribution for 1954-1962 which does not differ significantly from 1967 data in the length of the age base or in the frequency of occurrence of the classes. This tends to corroborate the relative stability of the statewide population during the period of this study.

It appears that management efforts to reduce mortality so as not to permit mortality beyond recruitment has its principal effect, when successful, on the survival of fawns and one and a half year olds. The fluctuations in the relatively stable distributions of the last decade have occurred in these classes.

When the D_x frequency drops from a 45-46% range to a 38-42% range, a significant reduction in mortality is believed to have taken place. These changes in frequencies of the first two classes through their effect on probabilities of survival create the range of values for lambda which occur in this study. Survivorship curves which are not statistically different generate a wide range of values of lambda and net reproductive rate. The greater the difference between the slopes for the two limbs of the l_x curve, the greater the value of lambda, at the level of exploitation of these populations. In the year following a year of reduced fawn D_x frequencies the 1-1/2 year class should increase. This fact tends to corroborate the interpretation. Since more than 2/3 of the net reproductive rate derives from these classes it is crucial to monitor survivorship of these classes.

Existing fertility schedules indicate a fawn adult ratio of .4475. When it is assumed that the fawn class is the least vulnerable, it can be held that it should appear in a proportion less than this rate to insure adequate survivorship, i.e. survivorship which assures no population change as a minimum management objective.

Successful management designed to reduce mortality will have the effect of elevating the left limb of the survivorship curve. In subsequent years at the same rates of mortality, these changes will alter the right limb of the curve. The small changes in management usually applied should not have

much immediate effect on the extremely vulnerable older classes. Management plans should take these phenomena into account. Drastic changes in management would be required to alter the nearly 60% mortality rate of the older classes in order to achieve a satisfactory change in net reproductive rate.

It is believed that the phenomena reported by Anderson (1953), that the older classes occur at a somewhat higher rate in the natural population than in the sample, is quite probably true in the Iowa population. This probability adds one more source of error in the calculation of lambda if only the unaltered sample frequencies are used. Total error is reduced and acceptable accuracy is obtained if the sample frequencies are extended arbitrarily to give a longer age base which declines at the same rate as the right limb of the survivorship curve of the population. This technique adjusts for two types of sampling error: error in "T" and error in probabilities of survival of the older classes.

Theory of Stable Age Distributions

Interpretations

Past interpretations of age-distributions of Iowa deer populations have been very sketchy. The conformity of the curves was interpreted to mean no significant change. The actual thought was that the population must be "stationary", that is, no change in numbers of deer was taking place from

year to year. As the thought and discussion considered the fact that the herd was sustaining increased mortality due to significant increases in authorized exploitation, the unchanging distributions became a disturbing inconsistency. It could not be that the populations were stationary. The seeming paradox prompted this study of the significance of age-distributions.

Lotka's theory states, in part, that a population having a stable age-distribution will have a constant rate of increase (or decrease). This means that there is a specific rate which applies to specific age-distributions provided they are approaching a stable condition, and provided reproductive rates are constant, as is assumed in this study. The theory further provides that populations will become stable at some future time when they exhibit constant age-schedules of birth-rates and death rates. In this instance, then, the statewide populations over the period of study must have experienced a specific birth-rate, a specific death rate, and a relatively constant rate of increase or decrease, because the populations demonstrated a stable condition by one or more tests of stability.

Because the eight years covered by the study are more than a generation, more than 99% of the 1959 population had been replaced by 1966. Therefore, the rate of increase for the state as a whole must have been very nearly zero ($r = 0$) at a minimum but could have been as high as ten percent per annum

under the near uniform mortality conditions prevailing. The factor of rate of increase, thus, depends upon unbiased age-schedules of fertility and unbiased probabilities of survival exhibited by these populations.

Estimates of lambda

Only three populations had calculated estimates of lambda which were above 1.0, a stationary population. Approximately half or more of the populations should be above 1.0, if the statewide populations were to have no change as a minimum necessity to be compatible with the evidence that statewide populations have been stationary or increasing over the period of the study. For half of the estimates of lambda to be above 1.0, an adjustment of .10 would be necessary. The suitability of this adjustment factor for lambda will be discussed further under "Adjustment of lambda".

Theoretical validity of calculations of "s", survival rate

It is apparent that calculations of "s" based on any ratio between components of age-distributions are in conflict with Lotka's theory under most circumstances.

A completely stable age distribution would have a value for "s" which would not change from year to year since the population has reached a stable age distribution. With identical values of "s" from year to year, the population could be increasing, decreasing or stationary. If a different value for "s" was obtained following a period of stability, it could

reflect a changing birth rate (age-schedule of fertility), a changing mortality rate (a changing age schedule of survival) or a combination of both. The "s" value obtained would most likely reflect mostly a changing age-schedule of survival since most ratios between components in the distribution do not adequately reflect changes in the birth sequence.

If reproductive rates changed or were variable from year to year due to environmental factors, and survival probabilities would thus be irregular, ratios between components of the distribution would be very erratic and reflect the changes in the birth sequence as well as survival deriving from mortality schedules. These conditions would preclude calculation of "r", because of a lack of a stable condition and a calculation of "s" would be similarly unreliable for the same reasons. There is a lack of theoretical validity for use of estimates of "s", taken as ratios between components of age distributions, for estimates of the proportion of a population surviving, the survival rate. An example of an invalid relationship is found in Figure 14.

If it can be safely assumed that birth rates are a constant factor, certain ratio techniques would have a certain validity. This is currently the case in Iowa as evidenced by the stable populations of Figure 1 and 4 and the age schedule of fertility, Table 3.

Validity of "s"

The complement of the average value of Q_x , mortality rate of the life table, for the first four age classes, is an estimate of survival rate for that portion of the population or approximately 85% of the population. Sampling and aging error is minimized in this group and such a measure reflects the fortunes of this group in terms of survivors. It is also the younger components of exploited populations that determines the capacity of a population to increase, decrease or just maintain its numbers. The value obtained is not a precise estimate of the proportion of a herd surviving, however, it is a sensitive index to survival when reproductive rates are constant. It needs to be calibrated to recruitment values to become a precise estimate of survival. It is equal to the complement of the fawn D_x frequency when that frequency is a good estimate of that component of population and when $r = 0$. Through use of a prediction table, such as Table 8, this estimate of survival rate can be a quick method of determining lambda for populations such as have been studied here. Simply determine the l_x frequency for the population; plot the fourth value on the fourth ordinate of semi-log paper; draw a line from this point to the 1000 value on the first ordinate; and the point of intersection with the second ordinate is the estimate of "s", the slope of the line. This short cut method precludes completing a life table for Q_x values.

Values for survival based on formal regression methods of the total age distribution have a similar validity as "s", and assumptions prerequisite for their use identical for those of "s", just described. They have value as quantitative measures of the slope of the l_x curve but are not precise estimates of a proportion of a population surviving. Because of aging and sampling errors attendant with the older classes, the regression of l_x frequency on age of the first four or five classes only should be calculated. A value nearly identical to "s" above should be obtained. For that reason the calculation of slope by regression methods should be done by computer or the above short-cut method of obtaining slope should be used.

If a proof is attempted by substitution in Lotka's formula, the results would show that such a ratio estimate of "s" would only be valid when $r = 0$. Some evidence would be needed that the population was stationary to validate such an estimate. With such evidence at hand, no estimate of "s" would be needed as it would have to be equal to the complement of the fawn D_x frequency. This would be a known value.

Ratios between components of age distribution have two useful functions: one, to determine relative vulnerabilities, and two, they do represent a quantitative measure of a slope, the l_x survivorship curve.

Under the conditions of this study, where an assumption of a constant fertility rate is made, based on some evidence, the rate of increase, Lotka's "r", is a function of the changing slopes between age-classes of the survivorship curve. There is a curvi-linear relationship between the slope and "r", and a linear relationship between the slope and lambda.

It is believed that no one estimate such as a single ratio can describe the survivorship phenomena exhibited by an l_x survivorship curve and thus, a single quantity denoting "a" survival rate, "s", is inappropriate. For the purpose of determining exploitation levels and the capacity of a herd to maintain itself, the survivorship curve can only be interpreted as a series of age-specific probabilities of survival in relation to the age-specific production, which is precisely what the Lotka calculations do.

Conflicting theoretical views

The application of Lotka theory to deer population analysis has been utilized by Eberhardt (1960) with Michigan data. No other reference has been found in the literature although Cole (1957) has recommended its use in wildlife population analysis.

Eberhardt's application of theory contains conflicts with the theoretical interpretations of this study. He determined survival rate by using Hayne and Eberhardt's (1952) ratio of 1-1/2's and older to 2-1/2's and older. This is simply the

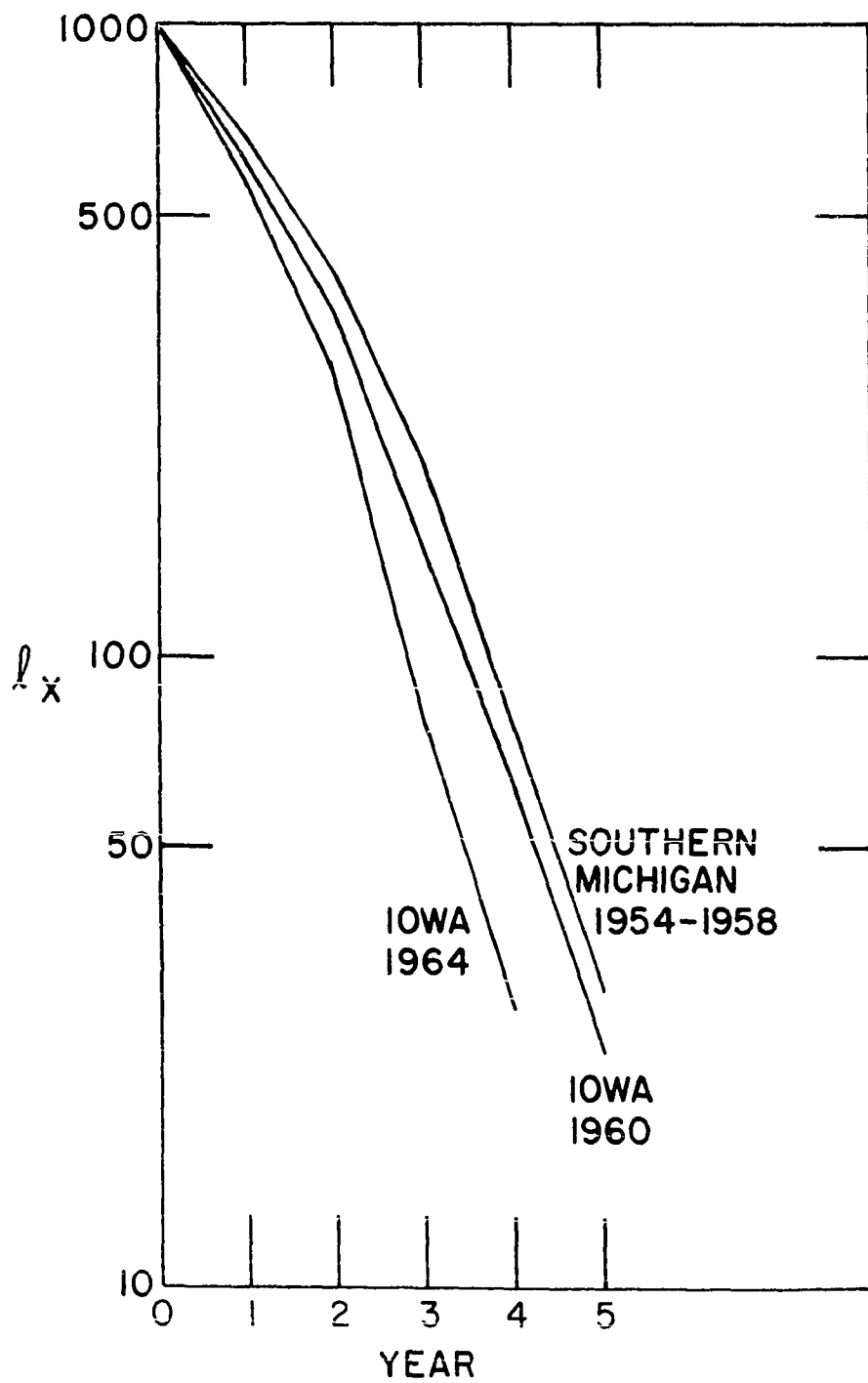
ratio of l_4 to l_3 of the survivorship curve. He then discarded the real age-distribution and calculated an l_x distribution based on a uniform decline in numbers for each age interval based on this estimate of "s". From this hypothetical survivorship distribution he calculated c_a , (the c_x of this study), the stable age-distribution of the hypothetical probabilities of survival based on "s". The calculated "r" resulting from this is variously attributed to the hypothetical probabilities of survival (Table 24, p. 165, Eberhardt, 1960), and the calculated stable age-distribution (Table 25, p. 167 and Figure 41, p. 166, Eberhardt, 1960). These three distributions will give widely varying values of "r" with the two calculated distributions having no valid relationship to the real distribution (Figure 15).

Besides the failure to use real data, there is further confusion resulting from his assumptions for application of the l_x distribution. On the subject of stable age distributions, (p. 166, his study), and on the subject of survivorship curves (p. 175 and p. 177), he demonstrates a view of stationary populations, and life-table assumptions that is inconsistent with theory on these subjects. He states:

"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 the survival and age-specific reproductive rates hold constant."

Figure 15. Comparison of range of survival rates, l_x distribution, for females in Iowa, and for southern Michigan

The Iowa 1964 curve represents a population declining by 5% per year and the 1964 population is one increasing by 10% per year. The "r" for southern Michigan is estimated at +.141 or an increase of 15% per annum.



Evidence that a population is relatively stationary, such as was determined by Tabor and Dasman (1957) for blacktails, is evidence also that the population has a stable age-distribution. In that relatively rare case, the two situations occurred only because there was no more space for expansion of the population and socio-physiological factors prevented further growth of the population. This is also a special case where the Lotka calculations are said to be inapplicable (Andrewartha and Birch, 1954) because an assumption of expansion in unlimited space is required. This requirement could be open for question but is not an issue here and is not dealt with in any detail in this study.

The interpretation in this study is that any l_x frequency for cohort populations is proper in the life table form regardless of the rate of growth of the population or its relative stability. To apply Lotka statistics to this population, only evidence that the distribution is essentially unchanged or would be unchanging for a length of a generation is required. This is evidence of a stable age distribution. Again, zero is only one of the many possible values of "r" found in the stable condition. With high levels of mortality, stability is evident within 3 or 4 years. Recent evidence (Coale, 1968) indicates a more rapid adjustment under these conditions and a generation is therefore not required under Iowa conditions. Stability is the product of the birth sequence and death rates.

When both factors are high, as well as constant, irregularities are rapidly smoothed out and stability is the result in less than a generation for deer populations.

Appropriate time-specific life tables can be constructed when the population is stable as is required for correct application of Lotka statistics.

The second sentence of the Eberhardt quotation is likewise inconsistent with theory. Nearly identical age structures will develop within one generation or less if survival and age-specific reproductive rates hold constant. If only one of the rates changes, a different age structure will result. If both change, a still different age structure will result. The perpetuation of an age structure is the result of stability created by constant birth and death rates. When stability is reached, its form is maintained through the birth and death sequence (Coale, 1968); constant factors in this condition.

Eberhardt may have meant that reproductive rate changes in one population will change the age structure of that population to a new and different stable form which will be perpetuated. To speak in terms of identical survival rates is misleading in this instance. Survival rates are expressed in the form of the l_x frequencies. If these are identical it may mean that birth and death rates are identical and the curves for these two populations would be the same and not different. A practical example of the situation to which he possibly refers would be when two populations, having identical stable age structures,

continue to have identical mortality rates but develop different birth rates. In this instance new, different stable age structures would develop for each population within less than a generation.

Violation of assumptions

The Lotka theory has not had wide application in wildlife population ecology. Besides the requirement that the population under analysis be increasing in unlimited space, the requirements that it be stable with a constant birth and death rate suggests to the wildlife biologist that such conditions rarely exist in natural populations whether exploited or not.

Actually, these requirements refer to the validity of a calculation for the intrinsic rate of natural increase, "r", of a stable population. For purposes of population analysis, it is believed that these requirements and assumptions can be modified or violated to provide a useful technique applicable under widely varying conditions. In this study, it is believed that the results are no more variable than the original data would be under the best of conditions.

The requirement of the theory that the population have a stable-age distribution has apparently led Eberhardt to substitute the calculated "r" of the stable distribution for the "r" of the real distribution. The lack of suitable and available data prompted the construction of hypothetical survivorship curves. It seems evident that this distribution

is twice removed from reality. It reflects only a distribution that would eventually result if differential vulnerability did not exist, fertility rates held constant, and all classes continued to survive at the same rate.

Stable age-distributions have been plotted along with real distributions in Figures 1 and 4, of this study. Since many of the calculated values of "r" were negative quantities, the plot of the stable distributions fall mostly below the real distribution. The value of calculating the stable age-distribution lies primarily in forecasting what existing birth rates and death rates will do with the population. For example, if a stable distribution lies below the real distribution and the r is negative for the real distribution already, and birth rates are relatively constant, the interpretation should be this: the population will decline until the new stable distribution is reached, the "r" will change in the negative range and when the new stable distribution is reached, the "r" will remain constant at a negative value while the population continues to disappear. This is believed to be the mechanism of the declining populations observed in Iowa.

Status of Populations

The state has been divided in the past by several management plans. Prior to 1963, there were no zones for management. From 1963 until 1966, management plans included two zones which

differed each year. In 1967, six zones were created (Figure 16). Mustard (1963) divided the state into four ecologically dissimilar regions (Figure 17).

Only zones in which stable populations have been demonstrated during some of the years of study will be discussed in terms of population change. Data have been generally inadequate for sample size for the smaller subdivisions.

Prior to this time, the status of populations was determined largely from kill data as demonstrated in Figures 18 through 23, inclusive.

Regional divisions

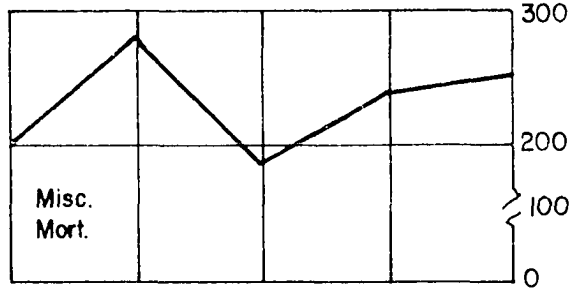
Region one--northeastern Data are really inadequate to assess this population. Only two stable distributions can be illustrated in Figure 24a. Figure 24b traces the trend in lambda. This population probably possesses the highest rate of increase in the state. A noticeably greater supply of older deer is evident. It is possible that this area could have a lower fertility rate. The true lambda (rate of population change) would be lower than the calculated one in that event. If the suggested adjustment of $.10 \pm .02$ were made in lambda a rate of increase would result which could not be justified by field observations. Better data on survival and fertility are essential to manage this population.

Figure 16. Iowa deer management zones, 1967

Figure 17. Primary deer regions of Iowa, ecological basis

Figure 18. Data from deer management zone 1, 1960-66

The kill (bottom line) is contrasted with the number of hunters (top line) and the miscellaneous non-hunting mortality.



HUNTER SUCCESS RATE

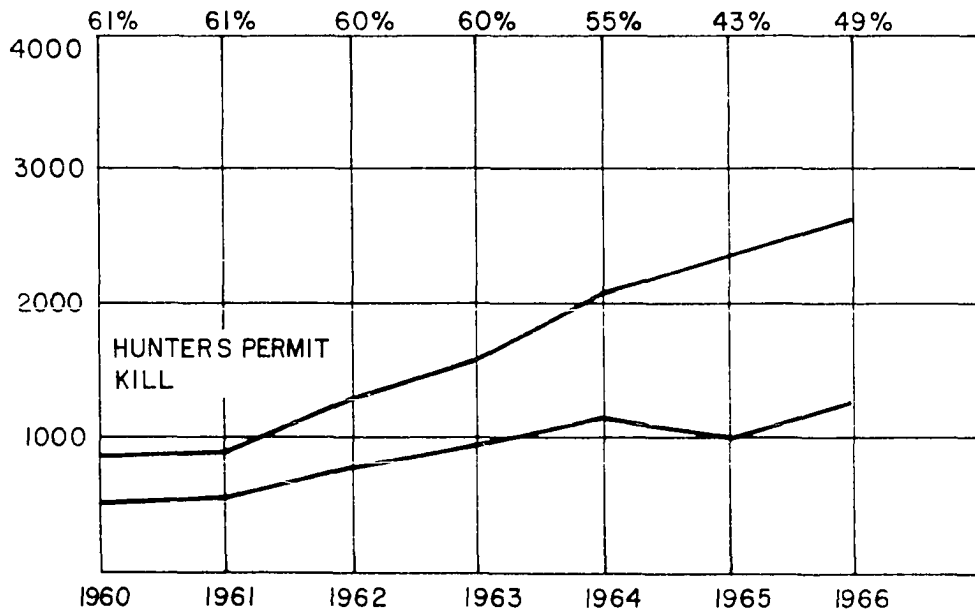
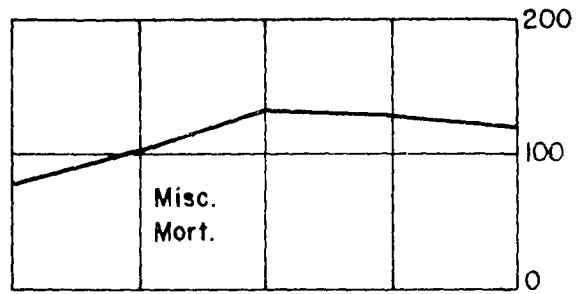


Figure 19. Data from deer management zone 2, 1960-65

The kill (bottom line) is contrasted with the number of hunters (top line) and the miscellaneous non-hunting mortality.



HUNTER SUCCESS RATE

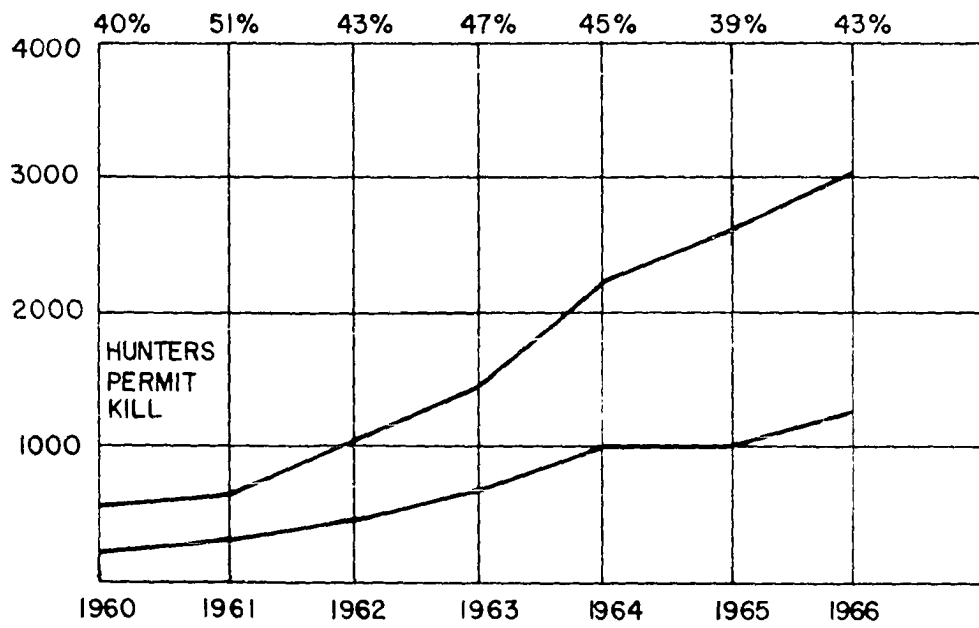


Figure 20. Data from deer management zone 3, 1960-66

The kill (bottom line) is contrasted with the number of hunters (top line) and the miscellaneous non-hunting mortality.

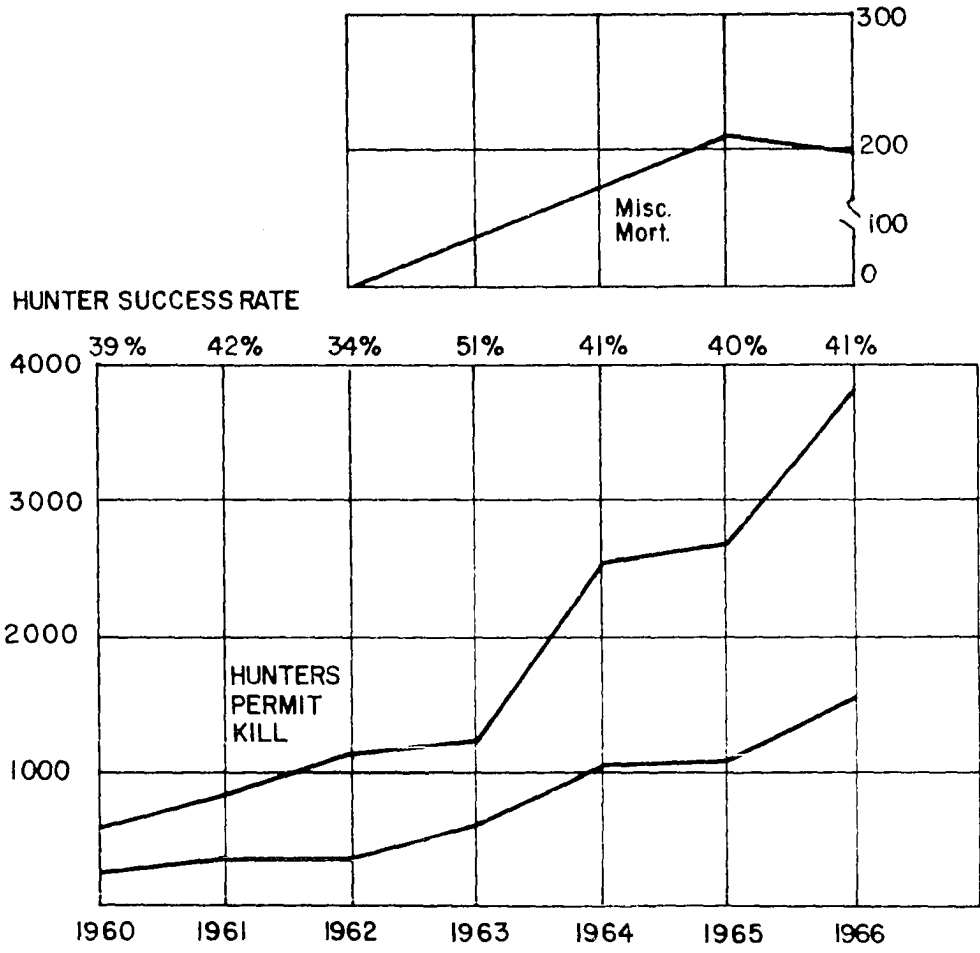
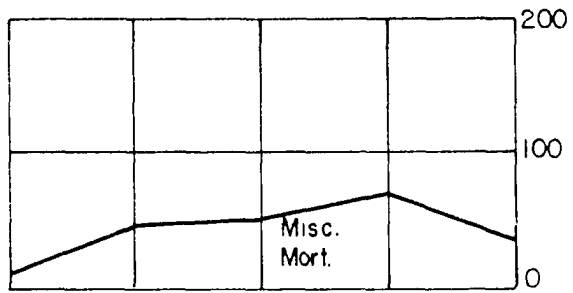


Figure 21. Data from deer management zone 4, 1960-66

The kill (bottom line) is contrasted with the number of hunters (top line) and the miscellaneous non-hunting mortality.



HUNTER SUCCESS RATE

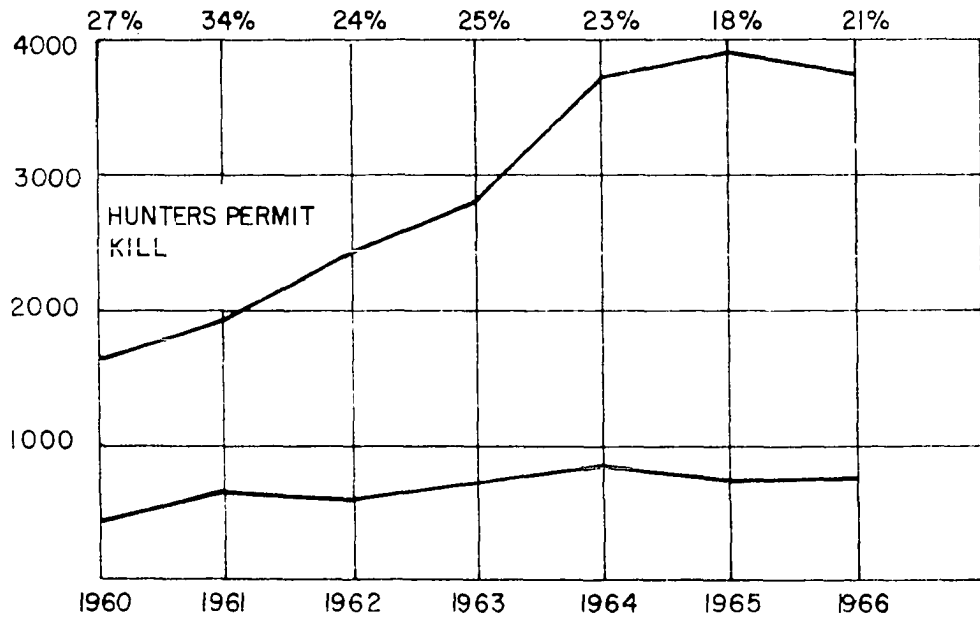
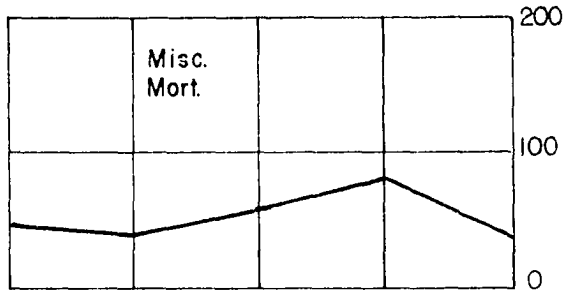


Figure 22. Data from deer management zone 5, 1960-66

The kill (bottom line) is contrasted with the number of hunters (top line) and the miscellaneous non-hunting mortality.



HUNTER SUCCESS RATE

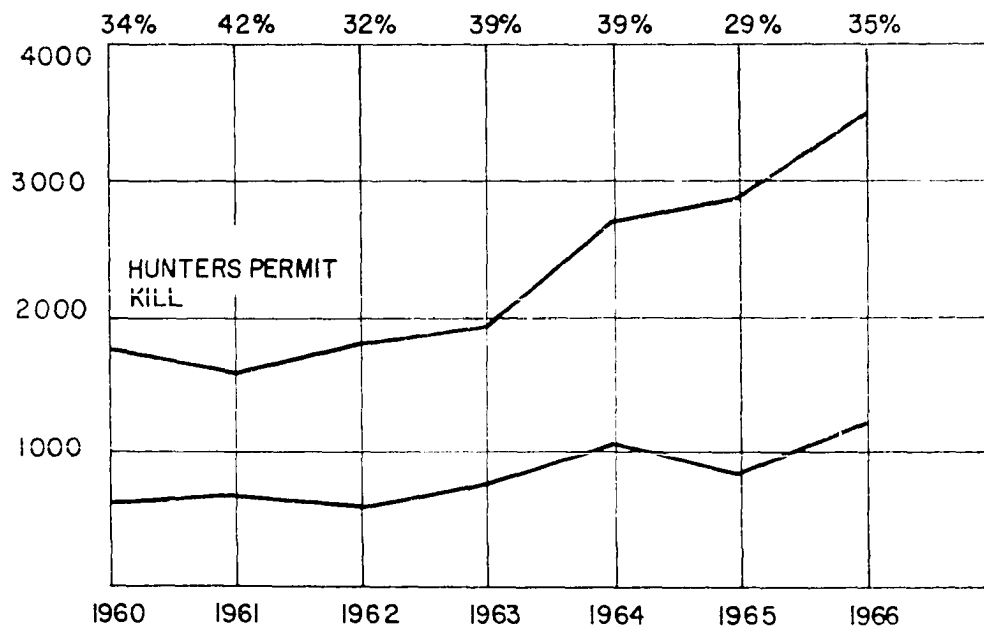
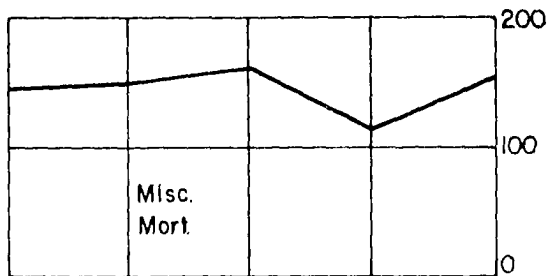


Figure 23. Data from deer management zone 6, 1960-66

The kill (bottom line) is contrasted with the number of hunters (top line) and the miscellaneous non-hunting mortality.



HUNTER SUCCESS RATE

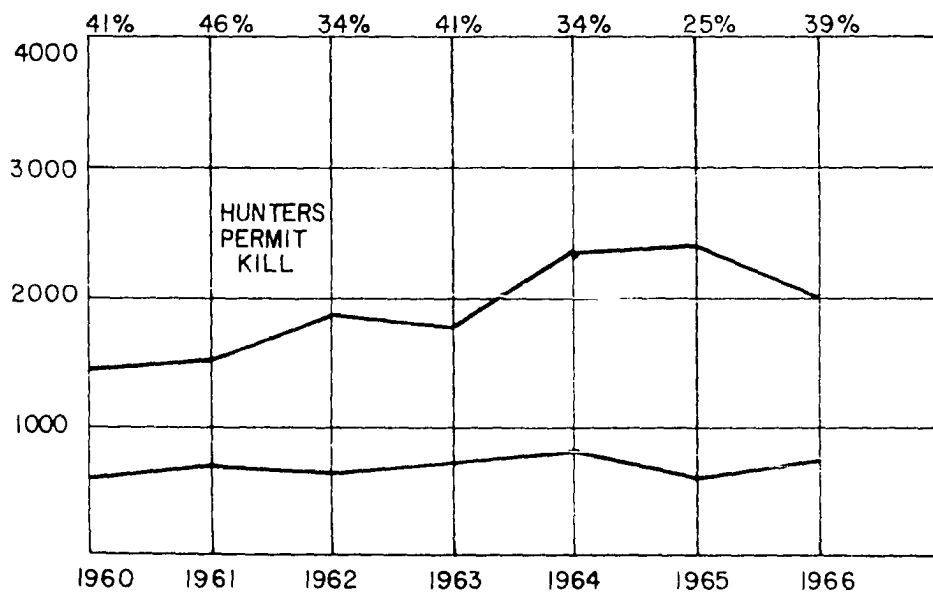


Figure 24a. Survivorship (l_x) curves for stable, time-specific populations of region one with associated estimates of lambda compared with a slope for no population change and the unablized 1966 population

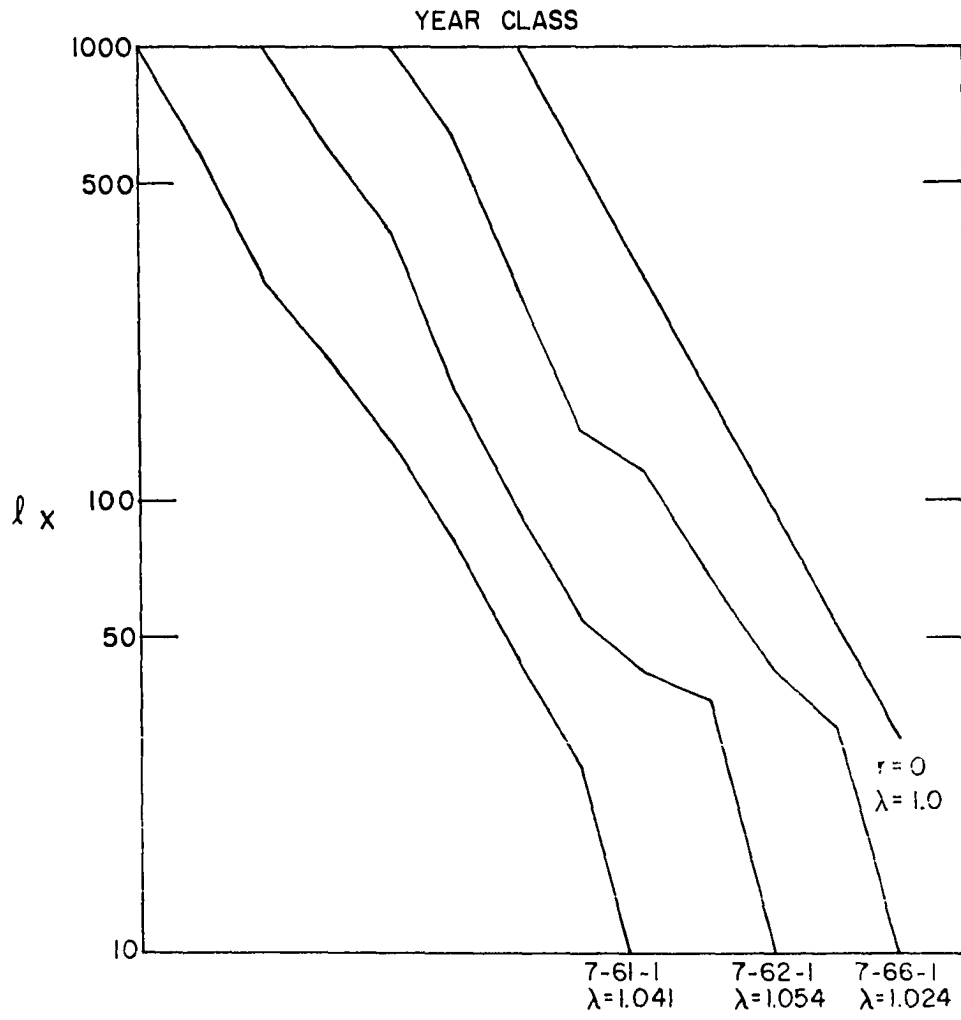
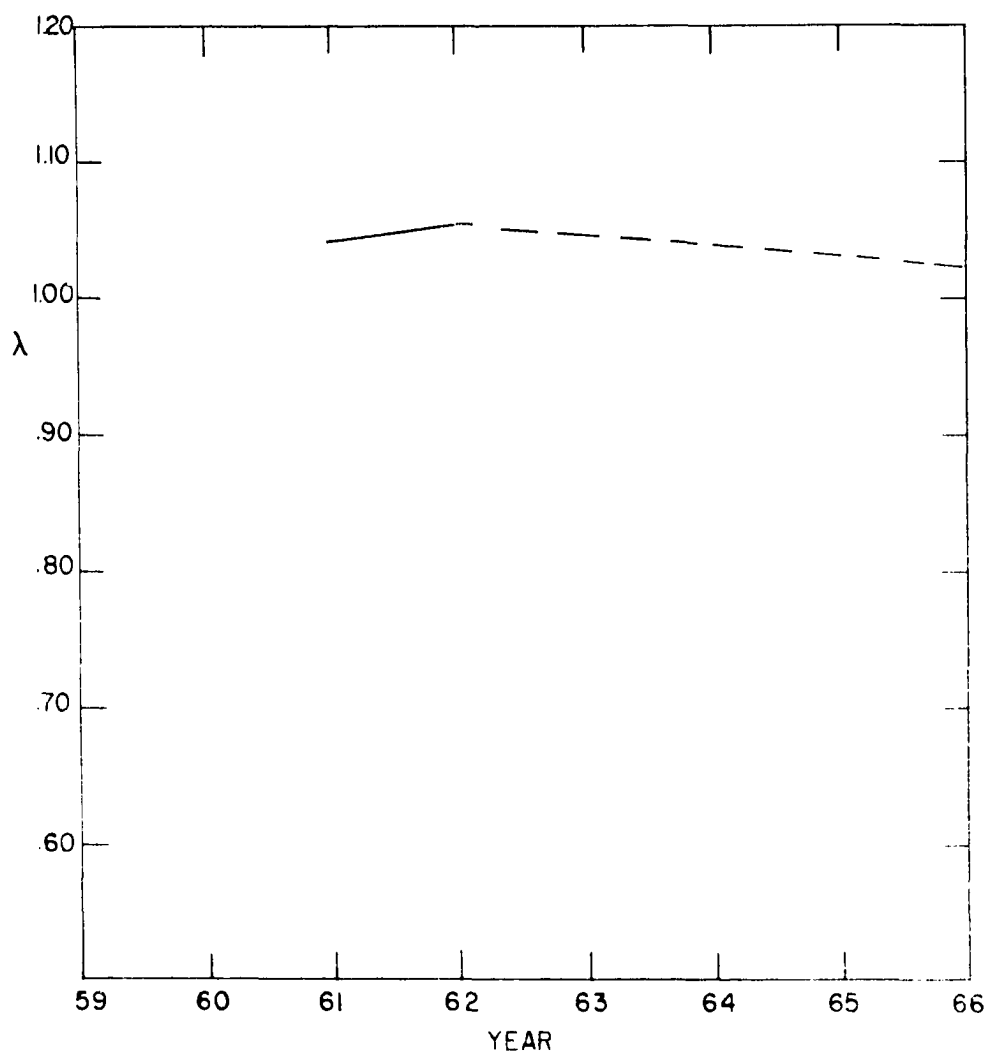


Figure 24b. Trends in population change for region one,
north-eastern Iowa, as expressed by
estimates of lambda



Region two--northern prairie This population probably declined from 1962 until 1964 and then increased about 5% per year in 1965 and 1966. All the curves in Figure 25a represent stable populations with only the 1960 data inadequate. Figure 25b illustrates the changes in lambda during the decline and reestablishment. The adjustment of $.10 \pm .02$ is considered appropriate here.

Region three--western hills Only two populations were found to be stable (Figure 26a) although five are presented. This is an illustration of aging and sampling error making stability impossible to assess. This relatively under-exploited population has probably always been increasing. The adjustment factor is also appropriate here. Although irregularity exists the lambda's (Figure 26b) are nearly proportional.

Region four--southern The 1966 data indicate that this population has increased in numbers with an increase of 5-7%. Only the 1962 data indicates an increase as well (Figure 27a and b). The comparison of these curves illustrates the necessity for the collection of jawbones for accurate data and to be used with Lotka statistics. The 1966 curve is smooth, as expected, from accurate aging and large sample size.

Figure 25a. Survivorship (l_x) curves for stable, time-specific populations of region two with associated estimates of lambda

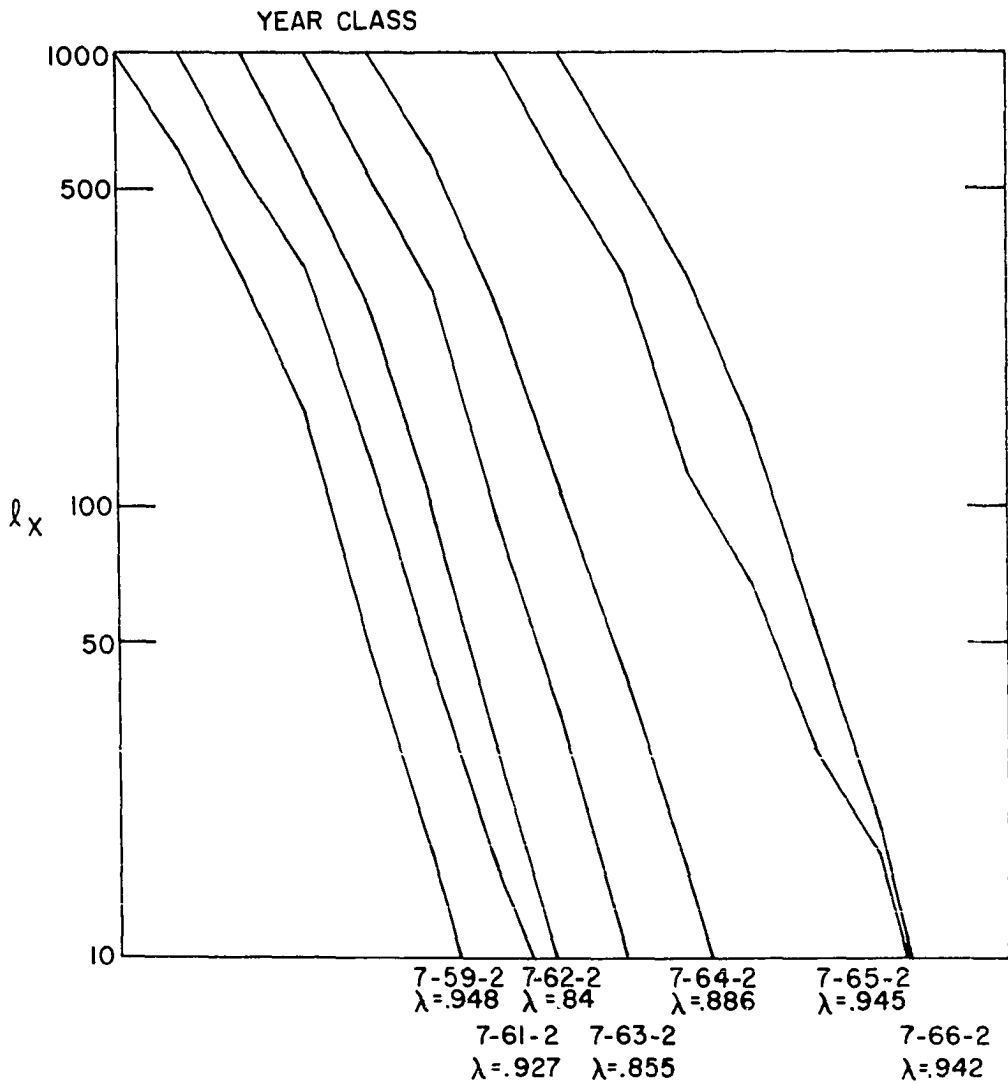


Figure 25b. Trends in population change for region two,
northern prairie, as expressed by estimates
of lambda

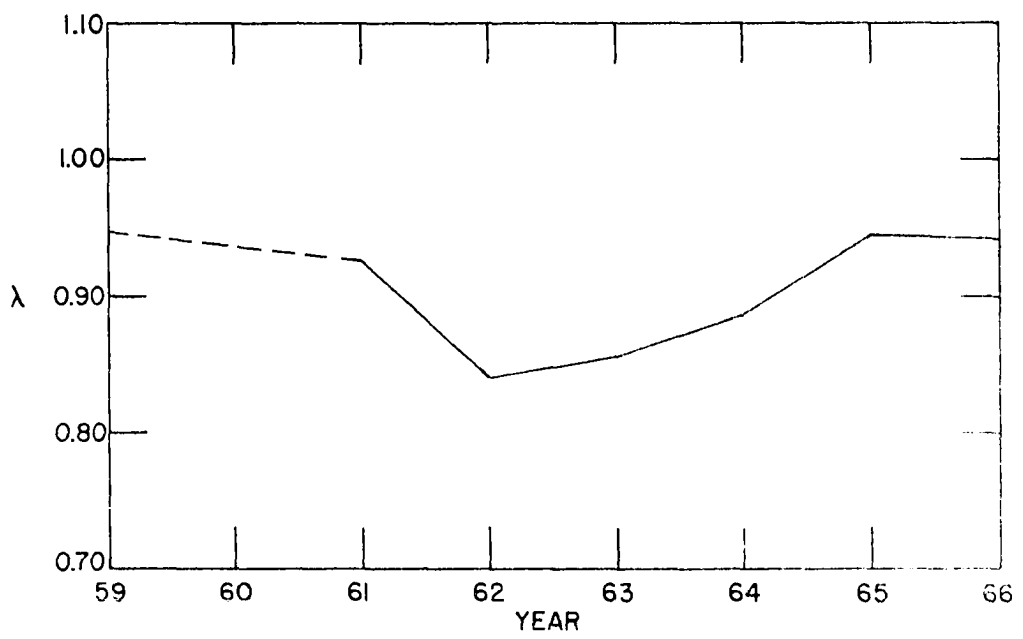


Figure 26a. Survivorship (l_x) curves for time-specific populations of region three for 1963 and 1966 with stability compared with unstable populations

Estimates for lambda are indicated.

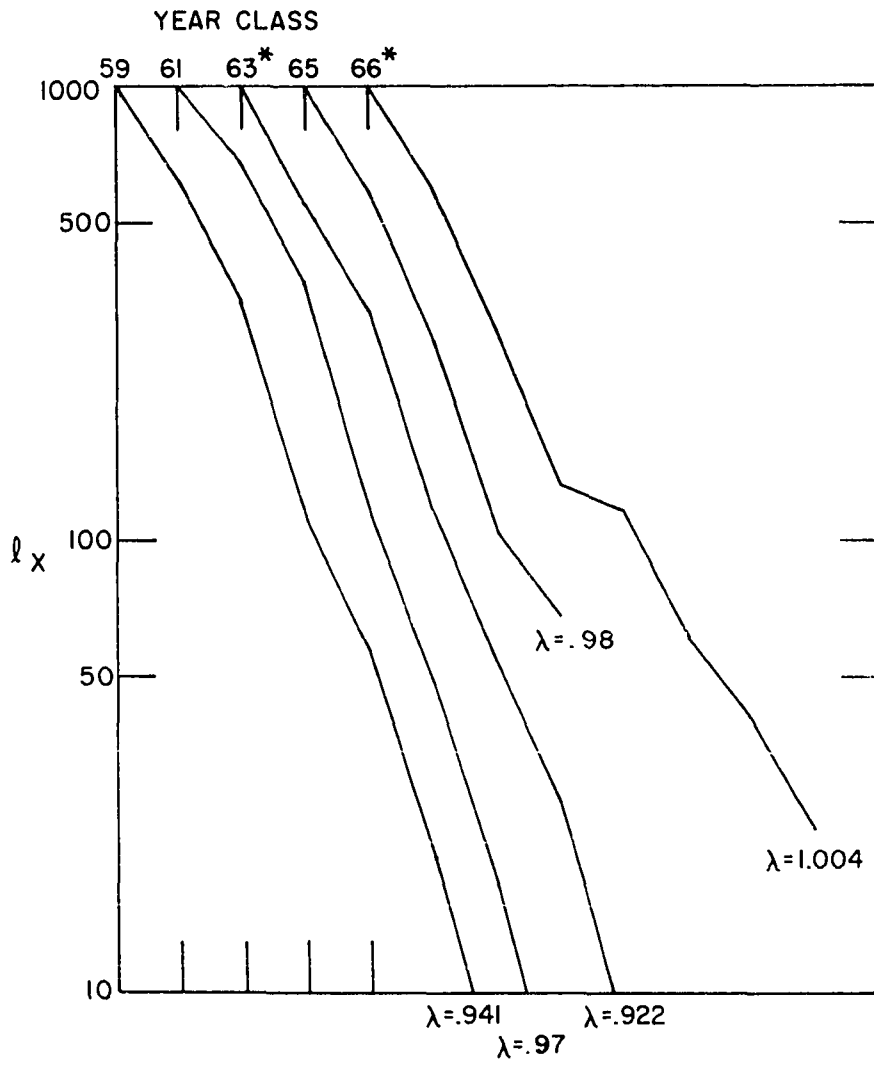


Figure 26b. Trends in population change for region three, western Iowa, as expressed by estimates of lambda

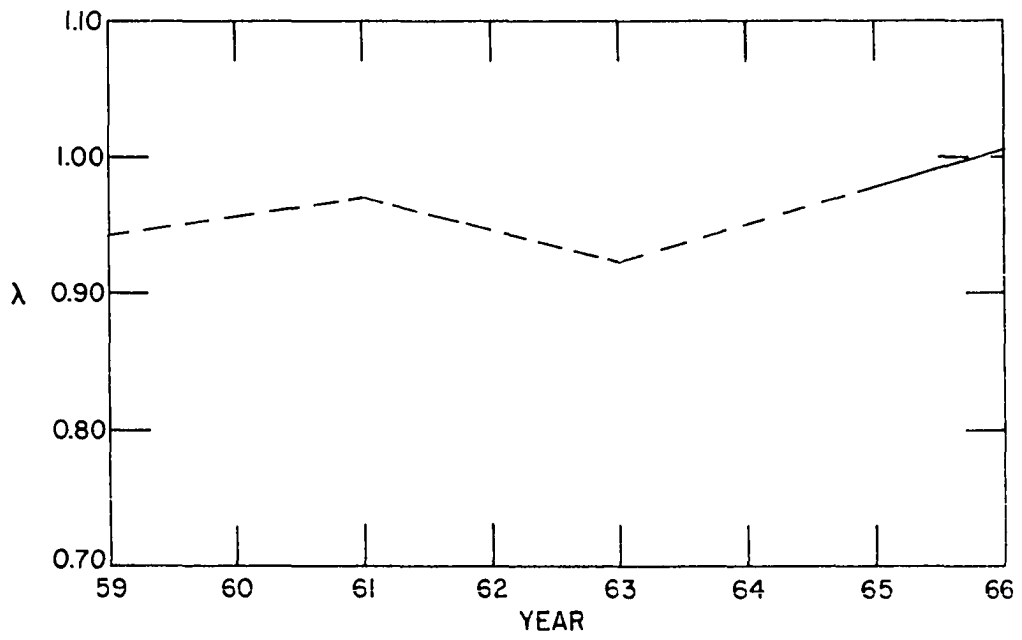


Figure 27a. Survivorship (l_x) curves for stable, time-specific populations of region four, southern Iowa, with estimates of lambda

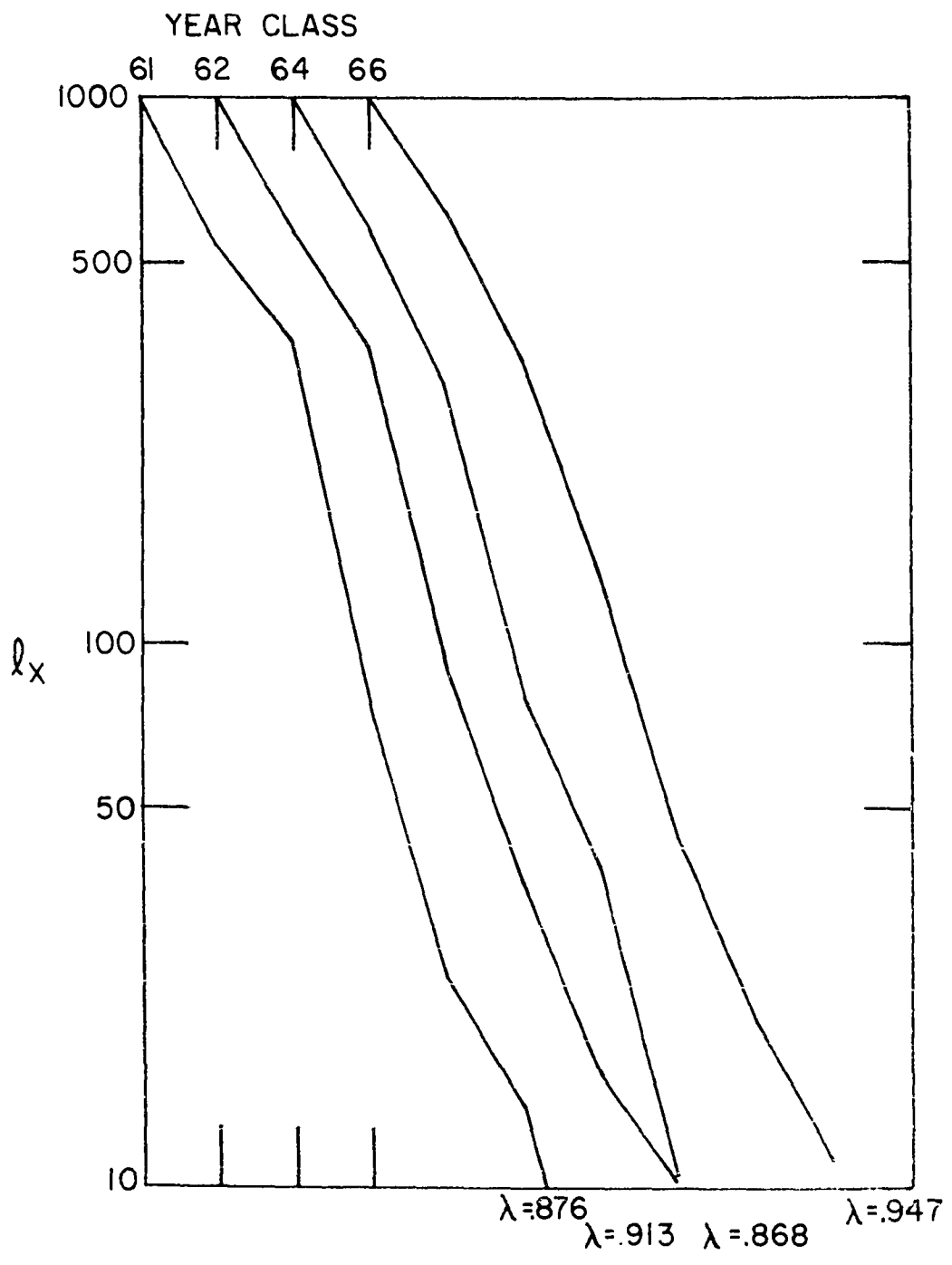
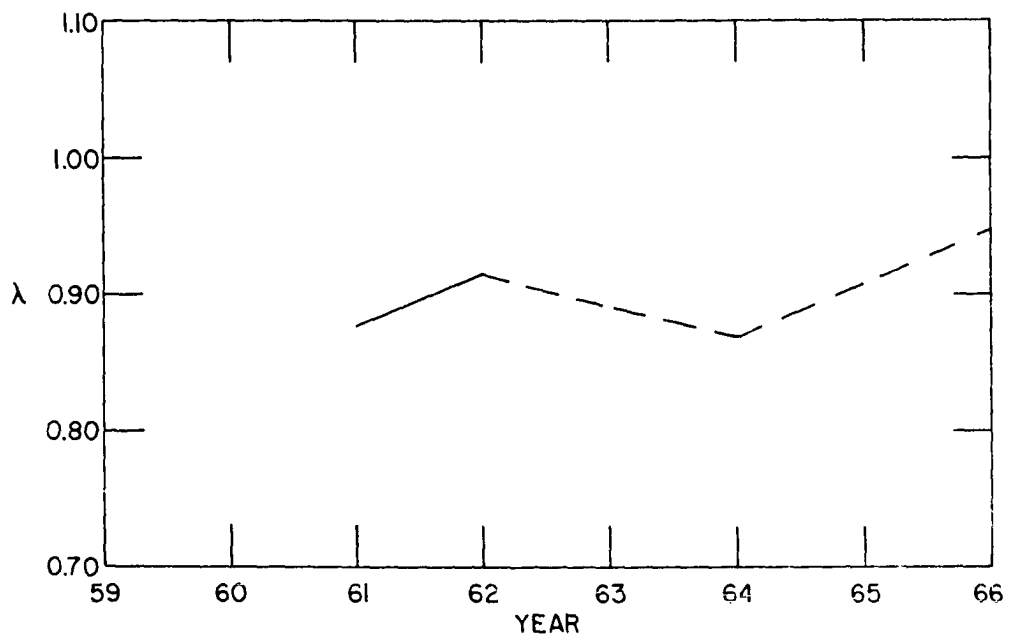


Figure 27b. Trends in population change for region four, southern Iowa, as expressed by estimates of lambda



Zonal divisions

Zone one--northern prairie This zone is composed of a different subdivision of counties than that termed northern prairie under Region two. It is smaller and represents only north-central agricultural land. These plots (Figure 28a and b) show a possible small decline in 1961 and 1962 with approximately a 5% annual increase from 1963 to 1966.

The effect on the distribution for 1963 of curtailment of permits and a shorter season is quite obvious. The population accumulated some older deer and increased approximately 5%.

Zone two--long zone The rate of increase of this primary population representing approximately 85% of the statewide population began to decline in 1961 and in 1963 a small reduction in total numbers is apparent. In 1964, the data indicate about a 10% decline in numbers. The decline was short with 1965 and 1966 showing 4-6% increases in numbers. The 1966 data are better and indicate about 4% annual increase possible. Data plots are in Figure 29a and b.

Six zone plan

This plan was adopted for 1967 and data have been processed in this way but only the northern prairie zone exhibited stable populations and adequate sample size. This plan was adopted partially to protect the fourth zone, the east central river breaks area. The results of protection are not available

Figure 28a. Survivorship (l_x) curves for stable, time-specific populations of zone one, northern prairie, with estimates of lambda

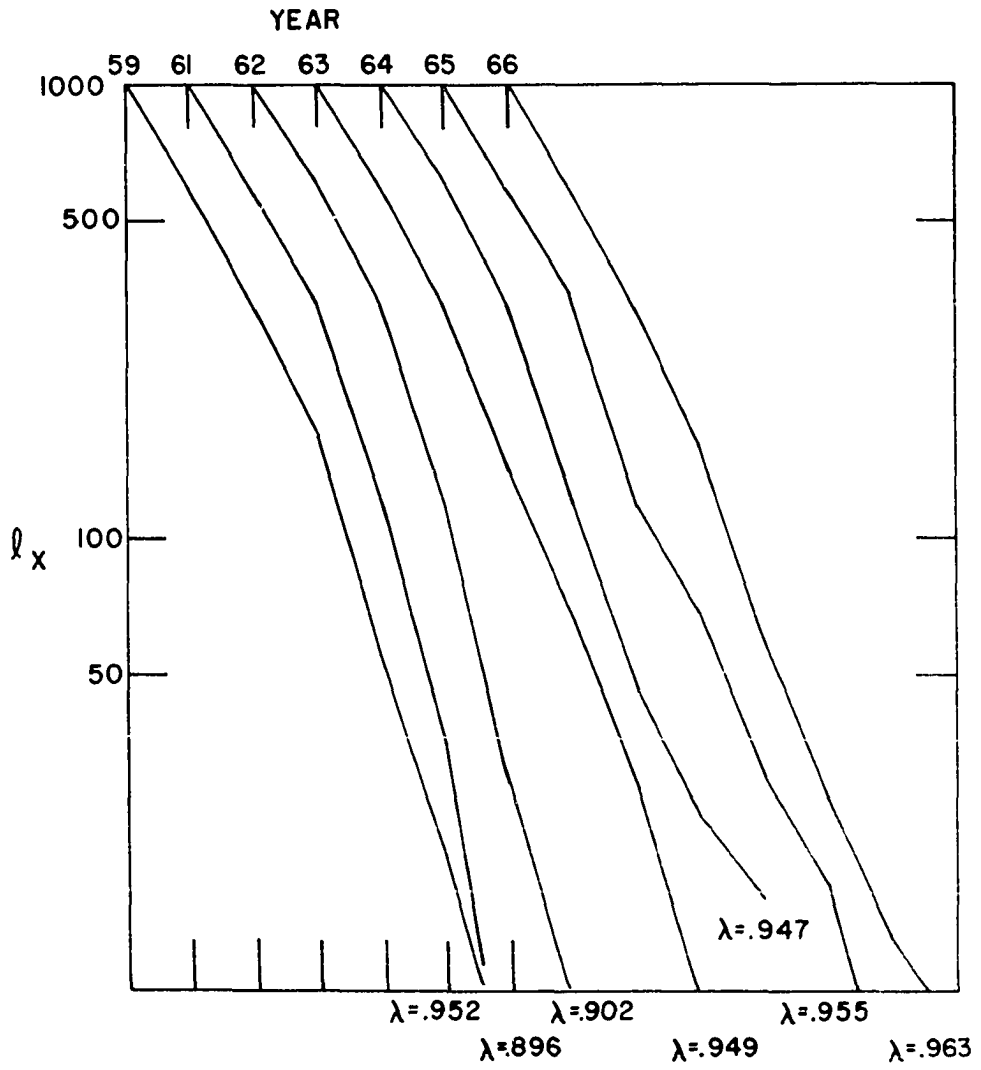


Figure 28b. Trends in population change for zone one,
northern prairie, as expressed by estimates
of lambda

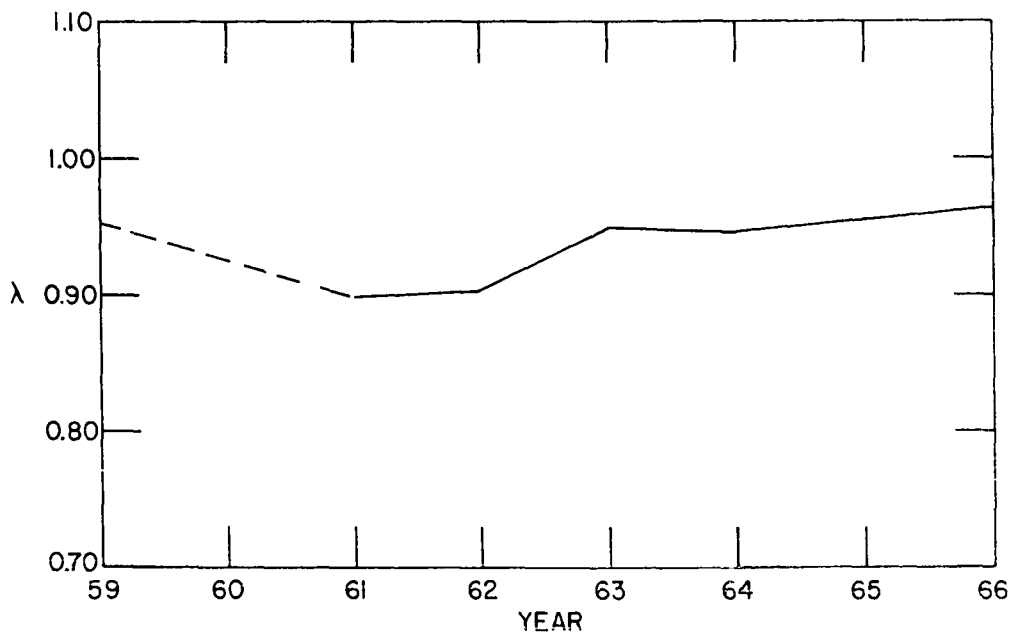


Figure 29a. Survivorship (l_x) curves for stable, time-specific populations of zone two, southern Iowa, with estimates of lambda

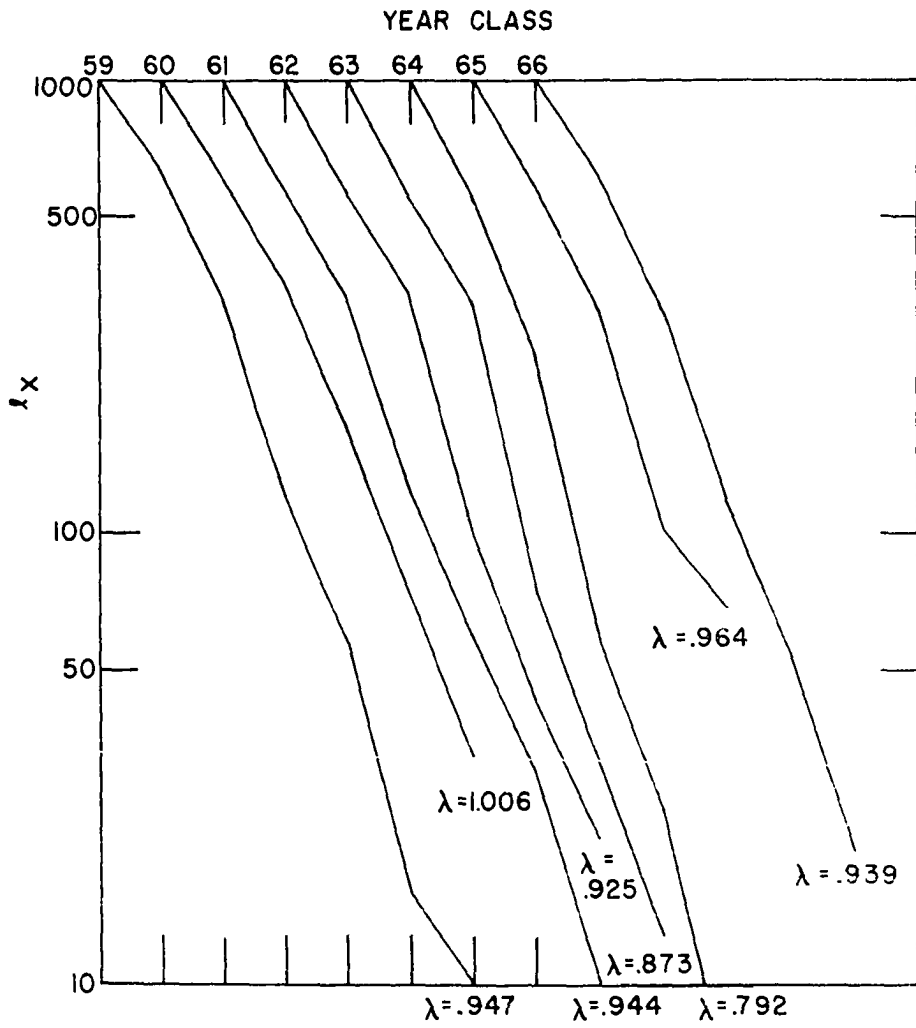
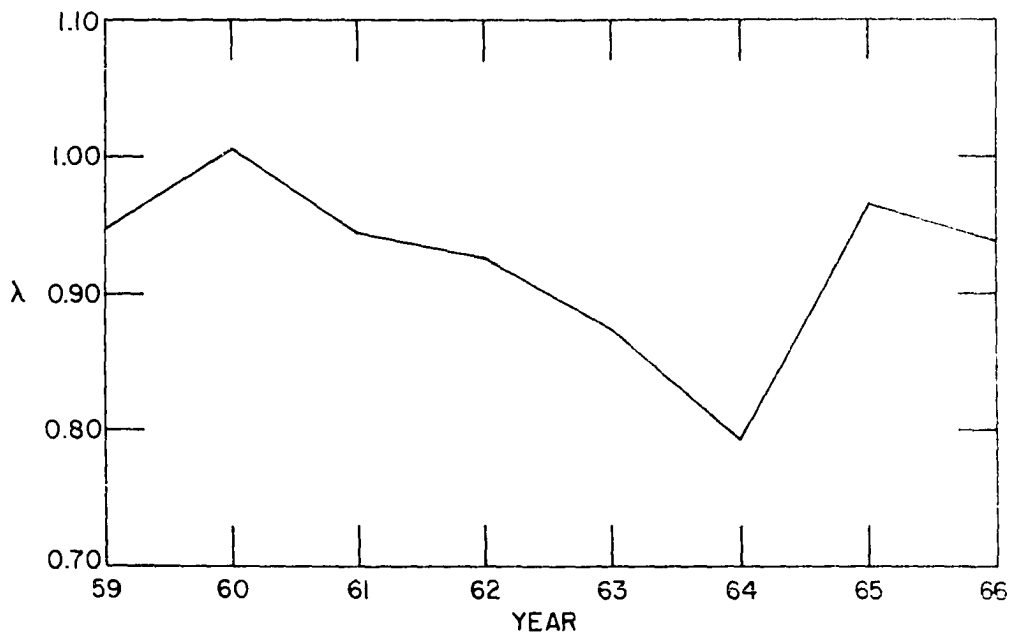


Figure 29b. Trends in population change for zone two, southern Iowa, as expressed by estimates of lambda



from this study. The lack of adequate data would indicate extremely low numbers of deer in this large area during the whole eight year period.

General

Although the Lotka analysis did reveal nearly every population was declining, the bias's in the data may not justify such a large adjustment factor as $.10 \pm .02$ to be added to these results. This is an unacceptably subjective judgment. It is apparent that to harvest female deer at a rate so close to recruitment is folly.

Sex specific trends

The trends in buck populations, statewide are plotted in Figure 30, for time specific analysis. Figure 31 illustrates the trend in female population changes, statewide and time specific, and Figure 32 illustrates results of age-specific analysis.

Male population changes were in opposing directions from 1960-1963. The male population was increasing while the female population was decreasing. There was a sharp decline in both populations in 1964 of about 5%. They both recovered and in 1965 and 1966 both populations were gaining from 1-4% annually.

Figure 30. Trends in population change for stable, time-specific populations of males, statewide, as expressed by lambda

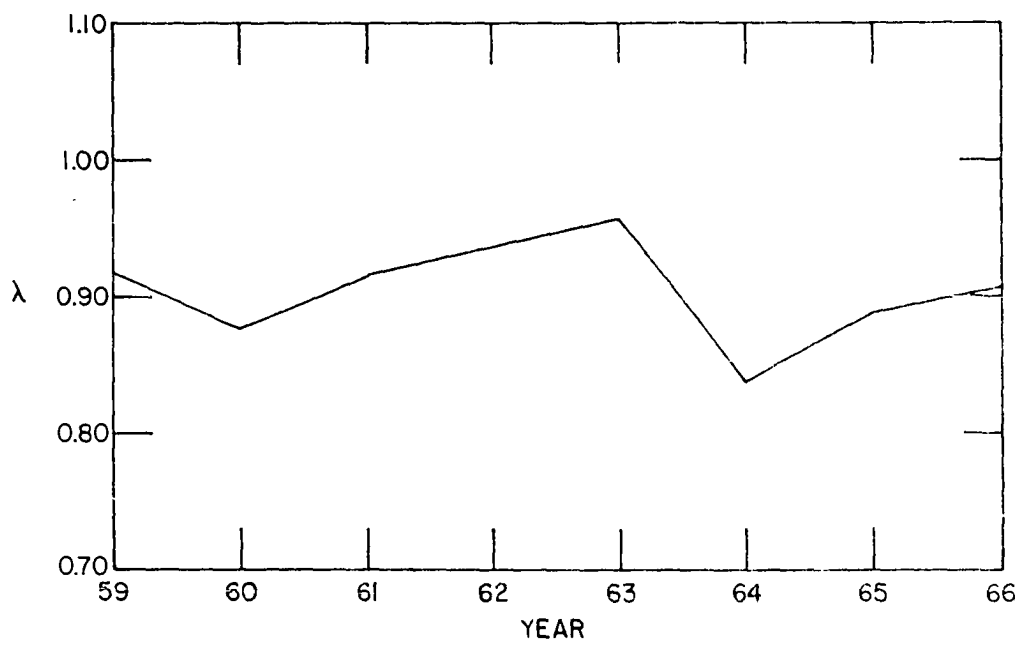


Figure 31. Trends in population change for stable, time-specific populations, female, statewide, as expressed by lambda

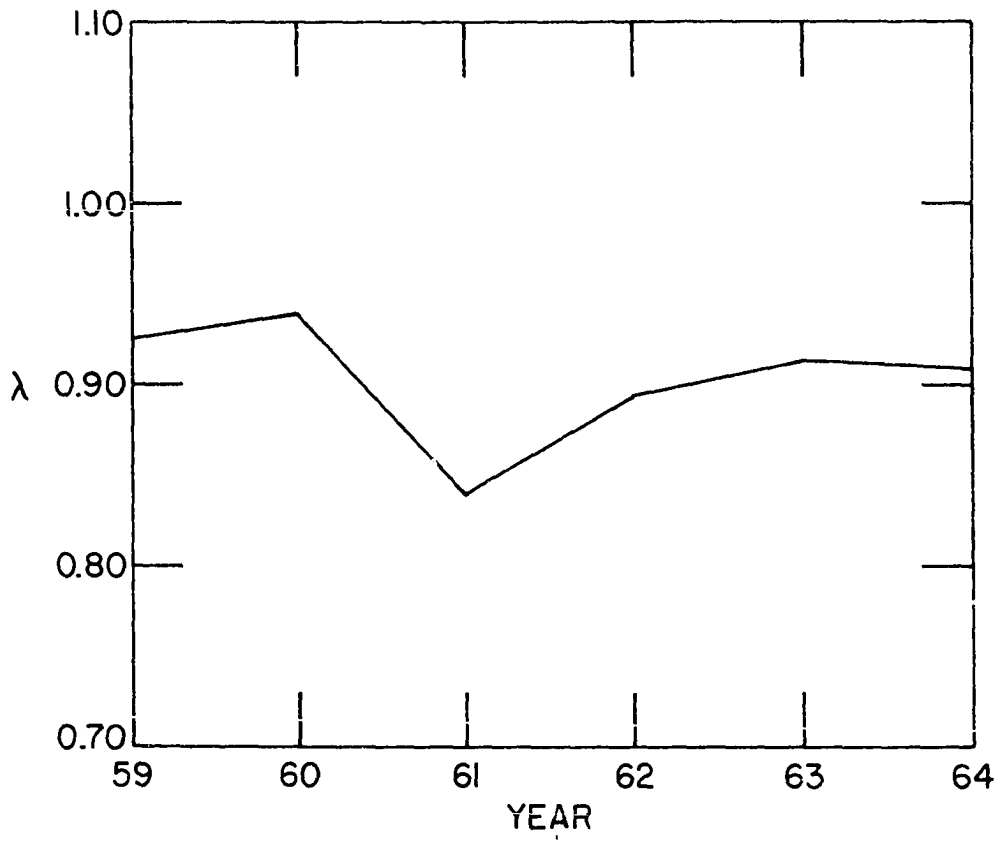
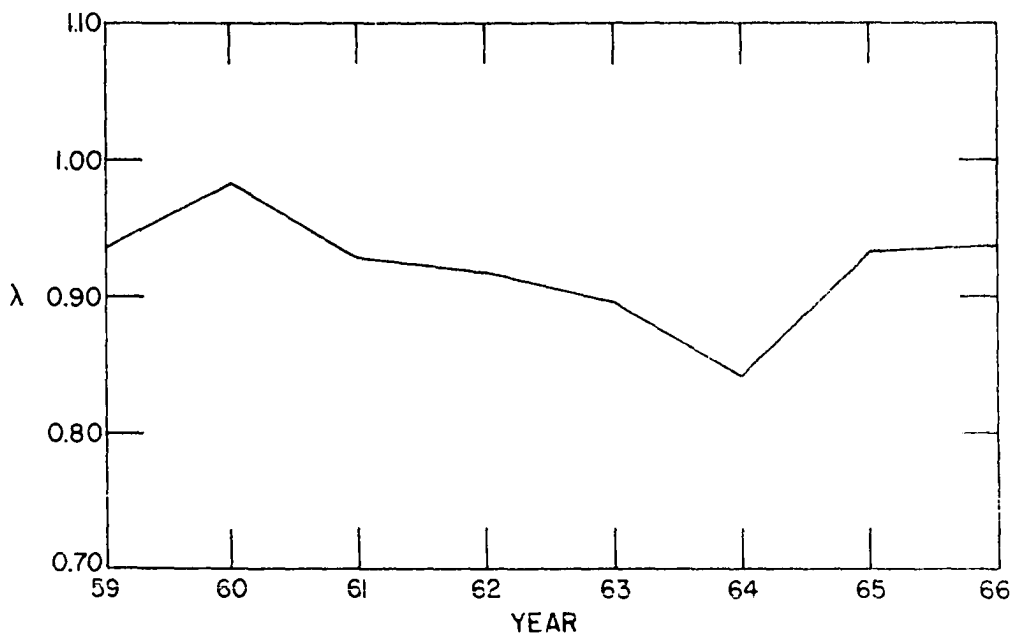


Figure 32. Trends in population change for stable, age-specific populations, female, statewide, as expressed by lambda



RECOMMENDATIONS

The management of white-tailed deer for either control of the species or the perpetuation of breeding stock for hunting purposes has been practiced without a sound scientific base in theory. As has been shown, most management practices either have no scientific basis with the trial and error method of determining allowable kill being used or are in conflict with accepted and existing population theory such as Lotka's theory of stable age-distributions. Iowa has been exploiting the white-tailed deer population to its limit of productivity (Nixon, 1968), and must utilize the most sophisticated techniques available to assure the prevention of an over-harvest. It is believed that the results of this study show that techniques employed have not been sufficiently precise to measure the proportion harvested.

It is believed appropriate that the following steps be taken in order that management be based on existing knowledge.

1. Population analysis techniques based on Lotka's theory of stable age-distributions be applied in the management of Iowa deer herds; i.e., that the intrinsic rate of natural increase, r , and the anti-logarithm of r , λ , be the basis for expressing level of exploitation.

2. In order to implement the above analysis technique, sampling and systematic bias must be removed in the collection of data which are used to determine l_x , (the probability of

survival to age x), and m_x , (the age-specific schedule of fertility).

3. The trend of herd reduction through hunting as revealed by this study, must be reversed.

4. Because extensive data are required and the analysis is tedious, computer analysis should be the method of choice in the processing of deer data for management purposes.

Implementation

There is seldom a difference in objective between biologists and others responsible for managing game species. However, disagreement frequently develops as to how best to achieve objectives. Because the biologist who is most intimately involved frequently has the best insight into the effect of specific management proposals, it is suggested that the following points be considered to best achieve objectives listed in the above recommendations.

1. It is quite apparent that the kill levels of the years up to 1966 are too great in much of Iowa. To be consistent with a prime obligation to provide hunting opportunity, it would be best to reduce the kill of antlerless deer only. As the female component is the key to maintenance of a population, it is thought to be the best of alternatives to increase the probabilities of survival of this component. Because complete preservation is neither possible or desirable, it is recommended that the kill of antlerless deer be controlled by

permitting the taking of them by every third, fourth, or fifth permit holder. The frequency of antlerless deer permits would depend on the status of the population in the various management zones. A small change in the l_x of the fawn and 1-1/2 year class would cause populations in all zones to increase. The result would be more females, young, and yearling bucks which in Iowa are frequently prized 6 to 8 pointers. Many more total permits could be authorized under this system and thus provide greater hunting opportunity as well as make maximum use of the resource. A satisfactorily accurate forecast could be made by running the available computer programs with expected l_x values to determine effect of various rates of issuing antlerless deer permits. Any desired level of increase could be obtained through precalculation.

2. The best way to remove sampling bias from the l_x probability data would be a mandatory check by biologists of all antlerless deer rather than just a sample of them. This is recommended for at least the first year. Age data from female deer could be taken at locker plants during the season of implementation and compared with data from the mandatory check.

Locker checks for antlered deer should be continued as increased hunting pressure on this component will reduce its age base even further than at present. Ultimately, it is the hunter satisfaction with success here that will determine the number of permits that can be authorized in total. Increased

efforts should be expended in areas of lower deer population and the statewide sample should be assembled by stratification on a pro-rata basis to the kill in each zone.

The principal systematic bias in the l_x probabilities lies in the execution of the Severinghaus aging technique. The present alternative is the dental annuli technique which is currently in use in all parts of Minnesota and Wisconsin. It is considered valid and appropriate but depends on a painstaking execution of the histo-technique involved. It is recommended that research be renewed to test and to implement this technique for aging deer in Iowa.

3. The efficiency of data collection and the validity of data on county of kill could be much improved. It is recommended that a pre-numbered tag be provided as an integral part of the license which the hunter is required to affix to the head when delivering to a locker plant. The hunter would enter the name of the county of kill and his own name. The sample size has been greatly reduced per unit effort in the past by lack of identification of heads in locker plants. Also, locker personnel introduce additional bias by varying policies on carcass handling, especially head removal.

4. Data used in this study to obtain an estimate of m_x , the age-schedule of fertility, were seriously biased at its point of collection. Evidence of bias is apparent when the foetal counts increase significantly as the gestation period

progresses. Further, it is inadequate due to sample size which permitted only a schedule of two age classes, fawn and adult, to be assembled. An m_x value should be obtained for each age class that will appear in the population sample.

It is suggested that it is possible to reduce this bias by having all road-killed female deer dying between March 1 and June 1 brought to a biology field station for examination. Data collected by other than professionally trained personnel is not suitable, or likely to produce acceptable estimates of fertility in Iowa deer herds.

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APPENDIX A. COMPUTER PROGRAMS


```

IF(IANAP)310,310,207
307 CONTINUE
    DN 70 IW=1,NY
    M=NY*8-1W
    WRITE(3,5005)
5005 FORMAT('11')
C
C
C
    WPK ON ONE POPIN AT A TIME
50 ENMR
51 ENMR
52 ENMR
    DN 20 J=1,NZ
    DN 20 K=1,3
    READ(1,999)(YY(I),I=1,10)
999 FORMAT(10F9.0)
    NY=10
    DN 90 I=1,10
    IF(YY(I))81,81,80
    90 CONTINUE
    81 NY=I-1
C
C
C
    TRANSFORM
51 ENMR
52 ENMR
    WRITE(3,5000)J,K,(YY(I),I=1,NN)
5000 FORMAT('0 FOR ZONE',15,'AND SEX',13,'THE UNTRANSFORMED FREQ. ARE /
    110F10.2)
    DN 6 I=1,NV
    IF(YY(I).LE.0.0)YY(I)=1.0
    6 YY(I)=ALOG10(YY(I))
    NV2(J,K)=NV-2
    20 CALL BEG(X,YY,NV,
    3(J,K),RL(J,K,1),PL(J,K,2),32(J,K,3),
    182(J,K,2),4(J,K),S(J,K),T(J,K),RR(J,K))
57 ENMR
58 ENMR
    THE ARRAYS:R=SLOPE:RL,RR-LEFT AND RIGHT LIMITS ARE ALL 8X3ENMR
59 TO HOLD THE PARAMETERS FOR ALL ZONE SEX:Q,M:S:A CONTAINS INT. ENMR
60 S HAS SUM(SQ.PEV FROM BEG.):T HAS T TEST STATISTIC
    ENMR
61 ENMR
    NV=11 OR LESS IF THERE ARE ZEROS AT THE END
    ENMR
71

```

```

C
C          OUTPUT
C
      WRITE(3,2000) W , TANAP
2000 FORMAT('1 OUTPUT FOR      YEAR',I5,' FOLLOWS IN ORDER OF  ZONES
1   FOR THE THREE SEX GROUPS,USING ANALYSIS PLAN',I5,' FOR IX'//)
C
      DO 30 J=1,N7
      WRITE(3,2001)J,DATLAB
2001 FORMAT('0',40X,'  ZONE ',I5      //32A4//)
C
      WRITE(3,2002)SEX1,A(J,1),R(J,1),RL(J,1,2),BL(J,1,1),STAR,BR(J,1,1)
1,RR(J,1,2),S(J,1),NM2(J,1),T(J,1),RR(J,1),SEX2,A(J,2),B(J,2),
1BL(J,2,2),
2BL(J,2,1),STAR,BR(J,2,1),BR(J,2,2),S(J,2),NM2(J,2),T(J,2), RR(J,2)
1,SEX3,
3A(J,3),R(J,3),RL(J,3,2),BL(J,3,1),STAR,BR(J,3,1),BR(J,3,2),S(J,3),
4NM2(J,3),T(J,3),RR(J,3)
8888 FORMAT(3I5,3F10.4)
      DO 71 K=1,3
      B(J,K)=10.0**B(J,K)
      DO 71 L=1,2
      RL(J,K,L)=10.0**RL(J,K,L)
71  BR(J,K,L)=10.0**BR(J,K,L)
      WRITE(2,8888)TANAP,W,J , R(J,1),R(J,2),R(J,3)
      WRITE(3,2010)(R(J,M),BL(J,M,2),BL(J,M,1),STAR,BR(J,M,1),BR(J,M,2),
1V=1,3)
2010 FORMAT('0'//10X,' TRANSFORMED R VALUES AND C.I.'//3(10X,3F12.4,A4,
22F12.4//))
      GO CONTINUE
C
2002 FORMAT(3(2A4,F10.3,2X,F10.3,2F10.3,1X,A4,3F10.3,4X,I2,8X,F10.3,
1F10.4//))
      DO 40 K=1,3
      DO 40 J=1,P
40  IT(J,K)=0
      DO 41 J=1,10

```

```

ENWR 73
ENWR 74
ENWR 75
ENWR 81
ENWR 85
ENWR 87
ENWR 88
ENWR 89
ENWR 90
ENWR 91
ENWR 92
ENWR 93

```

```

41 YY(J)=0.0
70 CONTINUE
304 GO TO 301
310 STOP
END
SUBROUTINE REG(X,Y,N,B,BL5,BL9,PR5,PR9,A,SSDEV,S,RR)
DIMENSION X(N),Y(N),T(9,2)
DATA T/12.706,4.303,3.182,2.776,2.571,2.447,2.365,2.306,2.262,
163.657,9.925,5.841,4.604,4.032,3.707,3.499,3.355,3.250/
ENMR 129 ENMR 130 ENMR 99 ENMR 100 ENMR 101 ENMR 102 ENMR 103 ENMR 104 ENMR 105 ENMR 106 ENMR 107 ENMR 108 ENMR 109 ENMR 110 ENMR 111 ENMR 112 ENMR 113 ENMR 114 ENMR 115 ENMR 116 ENMR 117 ENMR 118 ENMR 119 ENMR 120 ENMR 97 ENMR 98 ENMR 99
COMPUTE SUM X , SUM Y , XBAR,YBAR
SXX=0.0
SUMX=0.0
SUMY=0.0
DO I =1,N
SUMX=SUMX+X(I)
SUMY=SUMY+Y(I)
ENMR 101 ENMR 102 ENMR 103 ENMR 104 ENMR 105 ENMR 106 ENMR 107 ENMR 108 ENMR 109 ENMR 110 ENMR 111 ENMR 112 ENMR 113 ENMR 114 ENMR 115 ENMR 116 ENMR 117 ENMR 118 ENMR 119 ENMR 120 ENMR 97 ENMR 98 ENMR 99
XBAR=SUMX/N
YBAR=SUMY/N
SDY=0.0
SDX=0.0
COMPUTE S SQUARED DEVIATIONS
DO I =1,N
SDX=SDX+(X(I)-XBAR)*(X(I)-XBAR)
SDY=SDY+(Y(I)-YBAR)*(Y(I)-YBAR)
2 SDXY=SDXY + (X(I)-XBAR)*(Y(I)-YBAR)
COMPUTE: A=SDXY/SDX
A=YBAR-B*XBAR
SSDEV=SSDY-R*SDXY
SSYX=(SSDEV)/(N-2)
SSR=SSYX/SSDX
ENMR 94 ENMR 95 ENMR 96

```

C	SR=SQR(T(SSB))	ENWR 100
C	S=B/SB THE T TEST STAT FOR H:R=0	ENWR 101
C	BL5,RL9,RR5,RR9=B+-T*SB WHERE T HAS N-2 D.F	ENWR 102
C		ENWR 103
	NM2=N-2	ENWR 104
	T5=T(NM2,1)	ENWR 105
	T9=T(NM2,2)	ENWR 106
C		ENWR 107
C	T5 AND T9 ARE THE TABULAR T VALUES FOR	ENWR 108
C	95 AND 99 % C.I. WITH (N-2) D.F.	ENWR 109
C		ENWR 110
	R=SDXY/SSDX	ENWR 111
	A=YB-R*XB	ENWR 112
	SSDEV=SSDY-R*SDXY	ENWR 113
C		ENWR 114
	SSYX=SSDEV/NM2	ENWR 115
	SSR=SSYX/SSDX	ENWR 116
	SR=SQR(SSB)	ENWR 117
	S=B/SB	ENWR 118
C		ENWR 119
C		ENWR 120
	BL5=B-T5*SR	ENWR 121
	BR5=B+T5*SR	ENWR 122
	RL9=B-T9*SR	ENWR 123
	RR9=B+T9*SR	ENWR 124
	RR=B*SDXY/SSDY	
C		ENWR 125
	RETURN	ENWR 125
	END	

```

C          RATIOS PROGRAM
C
C          DIMENSION X(10),CUM(5),RAT(8,4,3),IYR(8),Z(8,3)
C          DATA IYR/1959,1960,1961,1962,1963,1964,1965,1966/
C
C          CUM(1)=ALL DEFER,CUM(2)=ALL ADULT,CJM(3)=2 1/2 & OLDER
C
C          CUM(4)=3 1/2 & OLDER,CUM(5)=4 1/2 & OLDER
C
500 READ(1,100) IANAP,NZ
      DO 50 I=1,8
        DO 50 J=1,4
          DO 50 K=1,3
            50 RAT(I,J,K)=0.0
          100 FORMAT(2I5)
            IF(IANAP)333,333,5
              5 CONTINUE
                DO 20 J=1,NZ
                  DO 20 K=1,3
                    WRITE(3,1234)
                    1234 FORMAT('1')
                      DO 30 IY=1,8
                        READ(1,101) X
                        WRITE(3,102)(X(LL),LL=1,10)
                        102 FORMAT(' ',10F12.3)
                          SUM=0.0
                            DO 10 I=1,10
                              10 SUM=SUM+X(I)
                                CUM(1)=SUM
                                  CJM(2)=SUM-X(1)
                                    CUM(2)=CJM(2)-X(2)
                                      CUM(4)=CUM(2)-X(3)
                                        CUM(5)=CUM(4)-X(4)
C
C          RAT(IY,1,2)=CUM(2)/CUM(1)
          RAT(IY,1,3)=RAT(IY,1,2)

```

```

IF(CUM(2).EQ.0.0) GO TO 30
RAT(IY,1,1)=X(1)/CUM(2)
RAT(IY,2,2)=CUM(3)/CUM(2)
RAT(IY,3,2)=CUM(4)/CUM(2)
RAT(IY,4,2)=CUM(5)/CUM(2)
RAT(IY,2,3)= CUM(3)/CUM(2)
IF(CUM(3).EQ.0.0) GO TO 30
RAT(IY,2,1)=X(2)/CUM(3)
RAT(IY,3,3)=CUM(4)/CUM(3)
IF(CUM(4).EQ.0.0)GO TO 30
RAT(IY,3,1)=X(3)/CUM(4)
RAT(IY,4,3)=CUM(5)/CUM(4)
IF(CUM(5).EQ.0.0) GO TO 30
RAT(IY,4,1)=X(4)/CUM(5)
20 CONTINUE
DO 40 IY=1,8
DO 40 IT=1,3
ZZ=0.0
DO 80 IN=1,4
80 ZZ=ZZ+RAT(IY,IN,IT)
40 Z(IY,IT)=ZZ*.25
101 FORMAT(10F8.0)

```

C
C
C

TABLES AND CARD OUTPUT

```

200 FORMAT(3I5/12(8F9.6/))
WRITE(2,200)IANAP,J,K,(((RAT(I,L,M),I=1,8),L=1,4),M=1,3)
WRITE(3,103)IANAP,J,K,((IYR(I),(RAT(I,L,M),L=1,4),Z(I,M),I=1,8),
IM=1,3)
103 FORMAT('0',20X,'DESCRIPTION OF POPULATION:AV.PLAN',I2,' ZONE',I2,'
1 SFX',I2///10X,
1YFAR',5X,'FAWN/ADULT',5X,'1 1/2 /2 1/2 & OLDER',5X,'2 1/2 /3 1/2 &
2 OLDER',5X,'3 1/2 /4 1/2 & OLDER'/8( 9X,I5,4X,F10.6,8X,F10.6,16X,
3F10.6,16X,F10.6,9X,F10.6)///
4 //10X,'YEAR',5X,'ADULTS/TOTAL DEER',5X,'2 1/
4? & OLDER/ADULTS',5X,'3 1/2 & OLDER/ADULTS',5X,'4 1/2 & OLDER/ADUL
STS'/8( 9X,I5,6X,F10.6,14X,F10.6,14X,F10.6,14X,F10.6,9X,F10.6)///

```



```
5                                     ///10X,'Y
YEAR',5X,'ADULTS/TOTAL DEER',5X,'2 1/2& OLDER/ADULTS',5X,'3 1/2& OL
IDER/2 1/2& OLDER',5X,'4 1/2& OLDER/3 1/2& OLDER'/8(9X,I5,6X,F10.6,
114X,F10.6,14X,F10.6,17X,F10.6,9X,F10.6/),'1')
20 CONTINUE
   GO TO 500
333 STOP
   END
```

```

C          PROGRAM TO PLOT 'B' VALUES
C
C          DIMENSION EX(6,3,8),X(8),Y(8),NZ(9),DATL( 5),DATLAB(6,3,5),XL(5),
1YL(5),GL(5)
C          READ(1,102)XL,YL
102  FORMAT(10A4)
C          READ(1,101)((DATLAB(I,J,K),K=1,5),J=1,3),I=1,6)
101  FORMAT(5(15A4/1),15A4)
C          FOR ANY APLAN THERE ARE UP TO 6 ZONES,3 SEX GROUPS AND
C
C          8 YEARS OF EX VALUES-
C
C          DATA X/1959.0,1960.0,1961.0,1962.0,1963.0,1964.0,1965.0,1966.0/,NZ
1/6,2,2,2,2,0,4,1,1/
C          DO 1000 IANAP=1,9
C          IF(IANAP.EQ.6.OR.IANAP.EQ.8) GO TO 1000
C          READ(1,102)GL
C          JZ=NZ(IANAP)
C
C          DO 10 LL=1,8
C          LY=9-LL
C          DO 10 J=1,JZ
10  READ(1,100)(EX(J,K,LY),K=1,3)
100  FORMAT(15X,3F10.0)
C
C          DO 20 I=1,J7
C          DO 20 J=1,3
C
C          DO 15 K=1,8
15  Y(K)=EX(I,J,K)
C
C          DO 16 K=1,5
16  DATL(K)=DATLAB(I,J,K)
C
C          XSS=5.5
C          CALL GRAPH(8,X,Y,J,20,XSS,6.0,0.00,0.0,0.20,0.0,XL,YL,GL,DATL)
C

```

```
20 WRITE(3,200)IANAP,I,J
200 FORMAT('0 PLOT FOR AP',I2,' ZONE',I2,' SEX',I2,' EXECUTED')
C
C
C
C
C
1000 CONTINUE
STOP
END
```

C
C

STIMULATED HUNT PROGRAM

DIMENSION ICKM(15),JCKF(15),MFHS(15),MHS(15),JCKM(15),JCKF(15)
DIMENSION AA(4),SSY(5),SS3(5),IPP(15)
INTEGER REC(15),AFS(15),FFHS(15),AS(15)
DATA ICKM,ICKE,PEC,AFS,MFHS,MHS,AS,JCKM,JCKF,FFHS/150#0/
DATA AA/0.8,0.85,0.9,0.95/,SSY/0.45,0.50,0.55,0.6,0.65,0.7/,SS3/
10.35,0.40,0.45,0.50,0.55/,IPP/1180,1095,985,898,490,190,75,40,25,
215,7,0,0,0-0/

C
C
C
C
C
C

INPUT PARAMETERS

INPUT INITIAL POPULATIONS(EQUAL NO. OF M AND F.)

C

AI=1.84
FI=1.22
IA=4
A=AA(IA)
INIT=5
DO 1 ISSY=INIT,6
SYM=SSY(ISSY)
SYF=SYM
SIM=SYM
SIF=SYM
INN=2
DO 1 ISS3=INN,F
S3M=SS3(ISS3)
S3F=S3M
SM=0.5#SYM
SF=SM

3 DO 4 I=1,15
ICKM(I)=IPP(I)

C

```

4 ICKF(I)=ICKM(I)
C
WRITE(3,301)A,FI,AI,SYM,S1M,S3M,SYF,S1F,S3F,SM,SF,ICKM,ICKF
301 FORMAT('1',10X,'PARAMETERS FOR THIS RUN:A=',F5.2,' IF=',F5.2,' IA=
1',F5.2,' SYM,S1M,S3M',3F6.2,' SYF,S1F,S3F',3F6.2/31X,' SM=',F6.3,'
2SF=',F6.3//40X,'INITIAL POPULATIONS'/2(10X,15'6/1)
C
C
C COMPUTE OTHER COLUMNS
C DO 48 LL=1,15
C
5 REC(I)=ICKF(I)*FI
C
6 DO 7 I=2,15
7 REC(I)=ICKF(I)*AI
C
8 AFS(1)=ICKF(1)*SYF*1.0476
9 AFS(2)=ICKF(2)*S1F*1.0476
10 AFS(3)=ICKF(3)*S3F*1.0476
C
11 DO 12 I=4,15
12 AFS(I)=ICKF(I)*S3F*1.0476
C
13 DO 15 I=1,15
14 MFHS(I)=REC(I)*SM*0.9524
15 FFHS(I)=REC(I)*SF*1.0476
C
16 MHS(1)=ICKM(1)*SYM*0.9524
17 MHS(2)=ICKM(2)*S1M*0.9524
18 MHS(3)=ICKM(3)*S1M*0.9524
C
19 DO 20 I=4,15
20 MHS(I)=ICKM(I)*S3M*0.9524
C
21 DO 22 I=1,15
22 AS(I)=A*(AFS(I)+MHS(I))

```

```

C
C          SUM FAWN SURVIVORS
C
C
C 23 SFM=0.0
C 24 SFF=0.0
C
C 25 DO 27 I=1,15
C 26 SFM=SFM+MFHS(I)
C 27 SFF=SFF+FFHS(I)
C
C 28 JCKM(1)=SFM*A*0.9524
C 29 JCKF(1)=SFF*A*1.0476
C
C 30 DO 33 I=2,15
C 31 IM1=I-1
C 32 JCKM(I)=AS(IM1)*0.5*0.9524
C 33 JCKF(I)=AS(IM1)*0.5*1.0476
C
C          .
C          OUTPUT
C
C
C 200 FORMAT(3Y1,15I5/15I5,15)
C 24 WRITE(2,200)IA,JSSY,ISSZ,JCKM,JCKF,LL
C    NN=15
C    DO 55 I=1,15
C    IF(ICKF(I).EQ.0.AND.JCKF(I).EQ.0)GO TO 52
C    GO TO 55
C 52 NN=I-1
C    GO TO 56
C 55 CONTINUE
C 56 CONTINUE
C    WRITE(3,310)
C 310 FORMAT('0',25X,'SIMULATED HUNT TABLE'//)
C    DO 60 I=1,NN
C 60 WRITE(3,311)(ICKM(I),ICKF(I),REC(I),AFS(I),MFHS(I),FFHS(I),MHS(I),
C    1AS(I),JCKM(I),JCKF(I))

```

```
311 FORMAT(10X,10I10)  
WRITE(3,312)LL  
312 FORMAT('0',40X,'END OF GENERATION',I4)
```

```
C  
C  
C  
C  
C
```

```
STORE JCKM,JCKF INTO ICKM,ICKF AND RECYCLE
```

```
36 DO 47 I=1,15  
37 ICKM(I)=JCKM(I)  
38 ICKF(I)=JCKF(I)  
39 JCKM(I)=0  
40 JCKF(I)=0  
41 REC(I)=0  
42 AFS(I)=0  
43 MHS(I)=0  
44 MFHS(I)=0  
45 FFHS(I)=0  
46 AS(I)=0  
47 CONTINUE  
IF(ICKM(1).EQ.0) GO TO 1  
48 CONTINUE  
1 CONTINUE  
STOP  
END
```

C
C
C
C
C
C

LARSON(20 NOV 69) PROGRAM FOR LAMBDA ZERO

BASED ON T.ALSD FOR COMPUTING STABLE AGE DIST'N

DIMENSION TAB(10,8,3), LP(5),NZ(5),NY(5),NN(3),T(3),RZ(3),RM(13),CC(3),DATLAB(32),DX(10),XX(10),CCC(3)

REAL LAMBDA(?)

REAL LAMBAA

704 FORMAT(10(1X,2F4.0,FF.3,F4.3,4F6.5,3X,2F4.0,
2 FF.3,F4.3,4F6.5,3X,2F4.0,
1F5.3,F4.3,4F6.5//)

705 FORMAT('O T,RZERO,R(M),LAMBDA(ZERO)*1/3(5X,4F8.5)//)

DO 75 I=1,10

DO 75 J=1,8

DO 75 K=1,3

75 TAB(I,J,K)=0.0

READ(1,7777)DATLAB

7777 FORMAT(20A4)

C
C
C
C

INPUT DX1000 COLUMN FROM LIFE TABLE AND EXTEND UNTIL LAST
ENTRY IS UNITY-THEN SUM AND PUT ON TOTAL=1000 BASIS

C

DATA LP/1,2,7,0,8/,NZ/6,2,4,1,1/,NY/8,8,8,2,4/

DO 1000 IANAP=1,5

IAP=LP(IANAP)

NYR=NY(IANAP)

NZN=NZ(IANAP)

DO 1000 I=1,NYP

IYR=1958+I

IF(NYP.EQ.4)IYP=IYR+5

DO 1000 J=1,NZN

DO 900 K=1,3

C

READ(1,2000)DX


```

2000 FORMAT(10F8.0)
DO 10 L=1,10
  LL=L
  IF(L.GT.8)GO TO 5
  IF(DX(L).LT.1.0) GO TO 6
  4 TAB(L,1,K)=DX(L)
  GO TO 10
  6 LLD=DX(L-1)*.41+.5
  DX(L)=LLD
  IF(DX(L).LT.1.0)GO TO 12
  GO TO 4
  5 ML=TAB(L-1,1,K)*0.41+0.50
  IF(ML.LT.1)GO TO 12
  TAB(L,1,K)=ML
C
10 CONTINUE
12 NN(K)=LL-1
C
C
C
  IJM=0
  ISS=NN(K)
  DO 20 L=1,ISS
  20 IJM=IJM+TAB(L,1,K)
C
  SUM=IJM
  DO 30 L=1,ISS
  30 TAB(L,2,K)=TAB(L,1,K)/SUM*1000.0
C
  41 IMS=0
  DO 40 L=1,ISS
  IMP=TAB(L,2,K)
  TAB(L,2,K)=IMP
  40 IMS=IMS+IMP
  IF(I*MS.EQ.1000)GO TO 50
C
  ID=1

```

```

IF(IMS.GT.1000)ID=-1
XD=IMS-1000
XD=ABS(XD)
IDD=XD
IF(IDD.GT.4)GO TO 51
DO 52 L=1,IDD
52 TAB(L,2,K)=TAB(L,2,K)+ID
GO TO 60
51 IDL=IDD/2
ID=ID*2
DO 54 L=1,IDL
54 TAB(L,2,K)=TAB(L,2,K)+ID
ID=ID/2
LM=IDL+1
IF(2#IDL.LT.IDD)TAB(LM,2,K)=TAB(LM,2,K)+ID
GO TO 41

C
60 CONS=1000.0
DO 70 L=1,ISS
TAB(L,3,K)=(CONS-TAB(L,2,K))
CONS=TAB(L,3,K)
70 TAB(L,3,K)=CONS*0.001

C
TAB(1,4,K)=0.67
DO 80 L=2,ISS
80 TAB(L,4,K)=0.057

C
DO 90 L=1,ISS
90 TAB(L,5,K)=TAB(L,4,K)*TAB(L,3,K)

C
DO 100 L=1,ISS
100 TAB(L,6,K)=TAB(L,5,K)*L

C
S5=0.0
S6=0.0
DO 120 L=1,ISS

```

```

S5=S5+TAB(L,5,K)
120 S6=S6+TAB(L,6,K)
T(K)=S6/S5
RZ(K)=S5
RM(K)=ALOG(S5)/T(K)
LAMRDA(K)=EXP(RM(K))
LAMBA=LAMRDA(K)
D0 130 L=1,ISS
TAB(L,7,K)=TAB(L,3,K)/LAMBA**L
S=1.0
D0 140 L=1,ISS
SS=SS+TAB(L,7,K)
GCCX=1.0/SS
D0 150 L=1,ISS
TAB(L,8,K)=TAB(L,7,K)*GCCX
CC(K)=GCCX
LP=MAXO(NN(1),NN(2),NN(3))
900 CONTINUE
IF(1.0/ST.1.0P.J.GT.1) GO TO 200
WRITE(3,700)
700 FORMAT(1I1)
200 WRITE(2,701)IAP,IYR,J
701 FORMAT(10I1,15X,1ANALYSIS PLAN,13I1,
YEAR,15I1,ZONE,13/)
WRITE(3,702)PATLAB
702 FORMAT(32A4)
WRITE(3,703)CC
703 FORMAT(38X,F5.4,38X,F5.4,38X,F5.4)

```

```

      WRITE(3,704) (((TAR(I1,I2,I3),I2=1,8),I3=1,3),I1=1,LLP)
C
      WRITE(3,705) (T(K),RZ(K),PM(K),LAMBDA(K),K=1,3)
      WRITE(2,898) IAP, JVR, J, CC
      898 FORMAT(3I10,10X,3F10.5)
      888 FORMAT(10F8.4)
      WRITE(2,888) (((TAR(K1,K2,K3),K1=1,10),K2=2,8,6),K3=1,3)
      DO 79 KK=1,10
      DO 79 KKK=1,8
      DO 79 KKKK=1,3
      79 TAB(KK,KKK,KKKK)=0.0
1000 CONTINUE
      STOP
      END

```

C	LARSON PROGRAM FOR LIFE TABLES (IOWA DEER)	ENW	2
C	(F.N.WEST PROGRAMMER ISU JULY 1969)	ENW	3
C		ENW	4
C	DATA ARE OBS ON SEX, AGE AND COUNTY OF KILL (TO BE	ENW	5
C	CONVERTED TO ZONE)	ENW	6
C		ENW	7
C			
	DIMENSION ZDN(99), I(3), TSLTA(11,7,8,3), IT(3,8), DATLAB(32)		
	DIMENSION MM(6)		
	DATA TSLTA/1848#0.0/	ENW	8
	INTEGER ZDN		
	INTEGER THOU		
	THOU=1000		
	READ(1,1000)DATLAB		
1000	FORMAT(20A4)		
1302	READ(1,4001)IANAP,NZ		
	IF(IANAP.EQ.0)STOP		
C	ZDN(99) CONTAINS THE CODES FOR THE 99 COUNTIES (ANALY.PLANENW	ENW	10
C	I(3) CONTAINS THE CURRENT OBSERVATION	ENW	11
C	TSLTA(J,K,L,M) = THE TIME SPECIFIC LIFE TABLES (11 X 7)	ENW	12
C	WITH THE THIRD DIMENSION GIVING ZONE, AND THE FOURTH, SEXENW	ENW	13
C		ENW	14
C	SEX CODE: MALE=1, FEMALE=2, COMB=3	ENW	15
C		ENW	16
C		ENW	19
C	READ NUMBER OF ZONES (CALLED NZ), ZONE CODE (ZDN), IYEAR	ENW	20
C		ENW	21
C		ENW	24
C	SET UP AGE CLASSES IN TSLTA(J,1,K,M), J=1,11, K=1,NZ; M=1,3	ENW	25
C		ENW	26
	104 DO 1 J=1,11		
	DO 1 K=1,NZ		
	DO 1 M=1,3	ENW	29
	1 TSLTA(J,1,K,M)=J	ENW	30
C		ENW	31
C	READ DATA CARDS 1 AT A TIME UNTIL A BLANK CARD IS HIT TO	ENW	32
C	INDICATE THE END OF A YEAR COUNT NUMBER OF MALE, NO. OF	ENW	33

C	FEMALE, AND NUMBER OF ALL COMPUTE COL 2 (DEATHS), AND CHECK	ENW	34
C	TOTALS. IT1=NO. OF FEMALES, IT2=NO. OF MALES, IT3=COMBINED	ENW	35
C		ENW	36
	302 READ(1,4001)IYFAR		
	IF(IYEAR.EQ.0)STOP		
	IYY=IYEAR-1900		
	4001 FORMAT(2I5)		
	ICLK=0		
	DD 6 M=1,NZ		
	DD 6 N=1,3		
	6 IT(N,M)=0	ENW	39
C		ENW	40
C	IY=0 MEANS END OF THIS YEAR(BLANK CARD)	ENW	41
	3 READ(1,1001)IY,I		
	1001 FORMAT(I2,5X,I1,2I2)	ENW	43
	IF(IYY-IY)2,2,4		
	2 IF(I(3).GE.100)I(3)=99		
	IF(I(3).LE.0)I(3)=1		
	IS=I(1)	ENW	45
	IA=I(2)	ENW	46
	ICT=I(3)		
	IF(IS.LE.0)IS=1		
	IF(IS.GE.4)IS=2		
	IF(IA.LE.0)IA=1		
	IF(IA.EQ.62)IA=2		
	IF(IA.GE.12)IA=11		
C	ICOUN=COUNTY(CODED VALUE 1 TO NZ)	ENW	42
C	IA=AGE CODE, IS=SEX, 1 OR 2		
	ICOUN=1		
	IT(1S,ICOUN)=IT(1S,ICOUN)+1	ENW	51
	IT(3,ICOUN)=IT(3,ICOUN)+1	ENW	52
C		ENW	53
C		ENW	54
C	THE PREVIOUS STATEMENTS CHOSE THE CORRECT ZONE	ENW	55
C	CODE FROM THE VECTOR ZON AND UPDATE TOTALS	ENW	56
C	TSLTA(IA,2,ICOUN,1S)=TSLTA(IA,2,ICOUN,1S)+1.0	ENW	58
	TSLTA(IA,2,ICOUN,3)=TSLTA(IA,2,ICOUN,3)+1.0	ENW	59

	GO TO 3	ENW	60
	4 CONTINUE	ENW	61
C		ENW	62
C	WE NOW HAVE ALL THE OBS. FOR THIS YEAR:CHECK FIRST 2 ADD	ENW	63
C	UP TO THIRD FOR EACH ZONE	ENW	64
C	COMPUTE COL 3,4,5,6,7	ENW	68
C	3:COL 2/COL 2 TOTAL *1000	ENW	69
C		ENW	70
C	4:BEGIN WITH 1000 AND DECREASE BY ONE STEP LAGGED ELEMENT	ENW	71
C	IN COL 3.	ENW	72
C		ENW	73
C	5:COL 3 DIV.BY COL 4 TIMES 1000	ENW	74
C		ENW	75
C	6:(COL 4 ENTRY + NEXT ENTRY IN COL 4)/2.0	ENW	76
C	7:SUM COL.6 JP TO AND INCL ENTRY AND DIV.BY COL 4	ENW	78
C		ENW	79
C		ENW	80
C		ENW	81
C	DO 5,M=1,N7	ENW	82
C	DO 5 N=1,3	ENW	83
C			
	JD=0		
	DO 80 J=1,11		
	IF(TSLTA(J,2,M,N))81,81,82		
91	JD=JD+1		
	GO TO 80		
87	JD=0		
80	CONTINUE		
	NN=11-JD		
	IF(N-2)90,91,91		
91	MM(M)=NN		
90	CONTINUE		
	IF(NV)190,190,191		
190	WRITE(3,192)M,N,NN,IYEAR,IY,IYY,IT		
192	FORMAT('1 NN LF 0',6I5/24I5)		
	STOP		
191	CONTINUE		

C				
C				
	DO 7 J=1, NN		ENW	84
			ENW	86
	IF (IT(N, M)) 17, 17, 18			
	17 WRITE(3, 170) M, N, IT(N, M), NN			
	170 FORMAT('1 ', 4I5)			
	GO TO 7			
	18 TSLTA(J, 2, M, N) = TSLTA(J, 2, M, N) / IT(N, M) * 1000.			
	7 CONTINUE			
	TSLTA(1, 4, M, N) = 1000.0		ENW	87
	DO 8 J=2, NN			
	JM1 = J - 1			
	8 TSLTA(J, 4, M, N) = TSLTA(JM1, 4, M, N) - TSLTA(JM1, 3, M, N)		ENW	89
			ENW	90
			ENW	91
	DO 9 J=1, NN			
	IF (TSLTA(J, 4, M, N)) 19, 19, 20			
	19 WRITE(3, 171) M, N, TSLTA(J, 4, M, N), NN			
	171 FORMAT('1 TSLTA(J, 4, M, N) IN 9 ', 2I5, F14.6, I5)			
	GO TO 9			
	20 TSLTA(J, 5, M, N) = TSLTA(J, 3, M, N) / TSLTA(J, 4, M, N) * 1000.0		ENW	92
	9 CONTINUE			
			ENW	93
	DO 10 J=1, NN		ENW	94
	JP1 = J + 1		ENW	95
	10 TSLTA(J, 6, M, N) = (TSLTA(J, 4, M, N) + TSLTA(JP1, 4, M, N)) * 0.5		ENW	96
	SUM = 0.0		ENW	97
	DO 11 J=1, NN			
	11 SUM = SUM + TSLTA(J, 6, M, N)		ENW	98
	DO 12 J=1, NN		ENW	100
	IF (TSLTA(J, 4, M, N)) 121, 121, 122			
	121 WRITE(3, 172) M, N, TSLTA(J, 4, M, N), NN			
	172 FORMAT('1 IN 12 ', 2I5, F14.6, I5)			
	GO TO 12			
	122 TSLTA(J, 7, M, N) = SUM / TSLTA(J, 4, M, N)		ENW	101
	12 SUM = SUM - TSLTA(J, 6, M, N)		ENW	103
			ENW	104


```

C          OUTPUT NEXT BY COUNTY(ZONE CODED)          ENW  102
C                                                    ENW  105
C                                                    ENW  106
C                                                    ENW  107
5 CONTINUE
  WRITE(3,2005)IYEAR,IANAP
2005 FORMAT('1      THE OUTPUT FOR YEAR',I5,' USING ANALYSIS PLAN',I3,'
1FOLLOWS')
  DO 15 M=1,N7
    NN=MM(M)
    WRITE(2,2010)IYEAR,IANAP,M,(((TSLTA(J,K,M,N),J=1,10),K=2,7),N=1,3)
2010 FORMAT(3I5/3(6(10F8.2/)))
    WRITE(3,2001)M          ENW  109
2001 FORMAT('0',25X,'TABLES FOR ZONE CODE=',I2//22X,'MALES',25X,'FEMALE'ENW  110
1S',37X,'COMBINED'//)    ENW  111
    WRITE(3,2002)DATLAB    ENW  112
    WRITE(3,2003)(((TSLTA(J,K,M,N),K=1,7),N=1,3),J=1,NN)    ENW  113
    WRITE(3,2006)IT(1,M),THOU,IT(2,M),THOU,IT(3,M),THOU
2006 FORMAT('0TOTAL',I7,I8,32X,I5,I6,32X,I5,I6)
2003 FORMAT(11(4X,F3.0,5F6.0,F6.2,5X,F3.0,5F6.0,F6.2,5X,F3.0,5F6.0,F6.2)ENW  114
1/)          ENW  116
15 CONTINUE
  DO 50 I1=1,11
  DO 50 I2=2,7
  DO 50 I3=1,8
  DO 50 I4=1,3
50 TSLTA(I1,I2,I3,I4)=0.0
  GO TO 302
310 STOP
2002 FORMAT(32A4)          ENW  116
  END                      ENWR 127

```

```

C          LARSON PROGRAM FOR LIFE TABLES(TOWA DEER)          ENW      2
C          (E.N.WEST PROGRAMMER ISU JULY 1969)                ENW      3
C                                                                ENW      4
C          DATA ARE OBS ON SEX,AGE AND COUNTY OF KILL(TO BE  ENW      5
C          CONVERTED TO ZONE)                                    ENW      6
C                                                                ENW      7
C                                                                E
C          DIMENSION ZON(99),      TSLTA(11,7,8,3),IT(3,8),DATLAB(32)
C          DIMENSION FMT(20)
C          DIMENSION MM(6)
C          DIMENSION TABLE(8,17,6,3)
C          DATA TSLTA/1848#0.0/          ENW      9
C          ZON(99) CONTAINS THE CODES FOR THE 99 COUNTIES(ANALY.PLANENW 10
C          I(3)      CONTAINS THE CURRENT OBSERVATION          ENW      11
C          TSLTA(J,K,L,M) = THE TIME SPECIFIC LIFE TABLES(11 X 7) ENW      12
C          WITH THE THIRD DIMENSION GIVING ZONE,AND THE FOURTH, SEXENW 13
C          SEX CODE: MALE=1, FEMALE=2, COMB=3                  ENW      15
C                                                                ENW      14
C                                                                ENW      16
C                                                                ENW      17
C                                                                ENW      18
C          INTEGER ZON
C          INTEGER THOU
C          THOU=1000
C          READ(1,1000)DATLAB
1000  FORMAT(20A4)
C
C          READ NUMBER OF ZONES(CALLED NZ),ZONE CODE(ZON),IYEAR ENW      19
C                                                                ENW      20
C                                                                ENW      21
C          301 READ(1,3001) IANAP,NZ
C              DO 201 I=1,8
C              DO 201 J=1,17
C              DO 201 K=1,6
C              DO 201 L=1,3
C          201 TABLE(I,J,K,L)=0.0
C              IND=0
C          3001 FORMAT(2I5)
C              IF(IANAP.EQ.0) GO TO 310
104  DO 1 J=1,11

```

C		ENW	24
C	SET UP AGE CLASSES IN TSLTA(J,1,K,M), J=1,11,K=1,NZ;M=1,3	ENW	25
C		ENW	26
	DO 1 K=1,N7	ENW	28
	DO 1 M=1,3	ENW	29
	1 TSLTA(J,1,K,M)=J	ENW	30
	DO 5 M=1,N7	ENW	37
	DO 6 N=1,3	ENW	38
	6 IT(N,M)=0	ENW	39
	DO 300 K=1,N7		
	DO 300 L=1,3		
	DO 300 I=5,8		
	IPP=I+9		
	300 READ(1,3000)(TABLE(I,J,K,L),J=I,IPP)		
	3000 FORMAT(10F8.0)		
	DO 303 K=1,N7		
	DO 303 L=1,3		
	DO 303 I=2,8		
	IM=I-1		
	DO 303 J=1,IM		
	JP=2*I-J		
	IF(JP.GT.17) GO TO 303		
	TABLE(I,J,K,L)=TABLE(I,JP,K,L)		
	303 CONTINUE		
C			
	ID=3		
	DO 210 ICOL=5,8		
	ID=ID+1		
	DO 207 I1=ICOL,8		
	IP=I1-ID		
	DO 207 I3=1,N7		
	DO 207 I4=1,3		
	207 TSLTA(IP,2,I3,I4)=TABLE(I1,ICOL,I3,I4)		
	DO 507 I1=1,N7		
	DO 507 I2=1,3		
	SUM=0.0		
	DO 508 I3=1,8		

```

508 SUM=SUM+TSLTA(I3,2,I1,I2)
507 IT(I2,I1)=SUM
C          COMPUTE COL 3,4,5,6,7          ENW 68
C          3:COL 2/COL 2 TOTAL *1000      ENW 69
C          ENW 70
C          4:BEGIN WITH 1000 AND DECREASE BY ONE STEP LAGGED ELEMENT ENW 71
C          IN COL 2.                      ENW 72
C          ENW 73
C          5:COL 3 DIV.BY COL 4 TIMES 1000 ENW 74
C          ENW 75
C          6:(COL 4 ENTRY + NEXT ENTRY IN COL 4)/2.0 ENW 76
C          ENW 77
C          7:SUM COL.6 UP TO AND INCL ENTRY AND DIV.BY COL 4 ENW 78
C          ENW 79
C
C          NOW TO TSLTA CODING
C
C          ENW 80
C          ENW 81
C          DD = M=1,N7                     ENW 82
C          DD = N=1,3                     ENW 83
C
C          JD=0
C          DD 80 J=1,11
C          IF(TSLTA(J,2,M,N)) 81,81,82
81 JD=JD+1
GO TO 80
82 JD=0
80 CONTINUE
NN=11-JD
IF(N-3) 90, 91, 91
91 MM(M)=NN
90 CONTINUE
C
C          DD 7 J=1,MM                     ENW 84
IMPY =TSLTA(J,2,M,N)/IT(N,M)*1000.

```

	7	TSLTA(J,3,M,N)=IMPPY		
		ISSS=0		
		DO 777 J=1,NN		
	777	ISSS=ISSS+TSLTA(J,3,M,N)		
		IF(ISSS.GE.1000) GO TO 778		
		IDD=1000-ISSS		
		DO 776 J=1,IDD		
	776	TSLTA(J,3,M,N)=TSLTA(J,3,M,N)+1.0		
C			ENW	86
	778	TSLTA(1,4,M,N)=1000.0		
		DO 8 J=2,10		
		JM1=J-1		
	8	TSLTA(J,4,M,N)=TSLTA(JM1,4,M,N)-TSLTA(JM1,3,M,N)		
C			ENW	89
			ENW	90
		DO 9 J=1,NN		
	9	TSLTA(J,5,M,N)=TSLTA(J,3,M,N)/TSLTA(J,4,M,N)*1000.0		
C			ENW	91
			ENW	92
		DO 10 J=1,NN		
		JP1=J+1		
	10	TSLTA(J,6,M,N)=(TSLTA(J,4,M,N)+TSLTA(JP1,4,M,N))*0.5		
		SUM=0.0		
		DO 11 J=1,NN		
	11	SUM=SUM+TSLTA(J,6,M,N)		
		DO 12 J=1,NN		
		TSLTA(J,7,M,N)=SUM/TSLTA(J,4,M,N)		
	12	SUM=SUM-TSLTA(J,6,M,N)		
C			ENW	93
			ENW	94
			ENW	95
			ENW	96
			ENW	97
			ENW	98
			ENW	99
			ENW	100
			ENW	101
			ENW	102
C			ENW	103
C			ENW	104
C		OUTPUT NEXT BY COUNTY(ZONE CODED)	ENW	102
C			ENW	105
C			ENW	106
	5	CONTINUE	ENW	107
		IYEAR=ICOL+1958		
		IYR=IYEAR		
		WRITE(3,2005)IYR,IANAP		
	2005	FORMAT('1 FAWNS BORN IN THE YEAR',I5,' USING ANALYSIS PLAN',I3)		
		DO 15 M=1,NZ		
		NN=MM(M)		
			ENW	108

```

      IY=IYFAR
      WRITE(2,2010)IY,IANAP,M,(((TSLTA(J,K,M,N),J=1,10),K=2,7),N=1,3)
2010  FORMAT(3I5/2(6(10F8.2/)))
      WRITE(3,2001)M
      2001  FORMAT('0',25X,'TABLES FOR ZONE CODE=',I3//22X,'MALES',35X,'FEMALE'
1S',37X,'COMBINED'//)
      WRITE(3,2002)DATLAB
      WRITE(3,2003)(((TSLTA(J,K,M,N),K=1,7),N=1,3),J=1,NN)
      WRITE(3,2006)IT(1,M),THPU,IT(2,M),THQJ,IT(3,M),THQU
2006  FORMAT('TOTAL',I7,I8,32X,I5,I6,32Y,I5,I6)
2003  FORMAT(11(4X,F3.0,5F6.0,F6.2,5X,F3.0,5F6.0,F6.2,5X,F3.0,5F6.0,F6.2)ENW 114
1/)
      ENW 116
      15  CONTINUE
      DO 50 I1=1,11
      DO 50 I2=2,7
      DO 50 I3=1,8
      DO 50 I4=1,3
      50  TSLTA(I1,I2,I3,I4)=0.0
210  CONTINUE
      GO TO 301
      310  STOP
2002  FORMAT(32A4)
      ENW 116
C
      END

```

APPENDIX B. LIFE TABLES

Table 9. Life tables

Symbolism:

x = Age interval

D'_x = Deaths within age interval

D_x = Deaths per 1000

l_x = Survivors at beginning of interval or
probability of attaining age x

Q_x = Death rate per 1000

L_x = Average number living within age interval

E_x = Mean expectation of life

c_x = Calculated stable age distribution

Table 9 (Continued)

x	D' _x	D _x	l _x	Q _x	L _x	E _x	c _x
Analysis Plan #9 - Zone 1 (Continued)							
1964 n' = 393							
0-1	432	498	1000	.498	751	1.21	.44210
1-2	256	294	502	.586	355	0.91	.27386
2-3	181	208	208	1.000	104	0.50	.16272
3-4							.07186
4-5							.03111
5-6							.01284
6-7							.00471
7-8							.00086
<u>Males</u>							
Analysis Plan #9 - Zone 1							
1959 n' = 339							
0-1	385	403	1000	.403	799	1.61	
1-2	270	284	597	.476	455	1.35	
2-3	161	168	313	.537	229	1.13	
3-4	99	103	145	.710	94	0.85	
4-5	32	33	42	.786	26	0.71	
5-6	9	9	9	1.000	5	0.50	
6-7	0	0	0	.000	0	0.00	
7-8	0	0	0	.000	0	0.00	
1960 n' = 421							
0-1	462	450	1000	.450	775	1.53	
1-2	258	251	550	.456	425	1.37	
2-3	175	170	299	.569	214	1.10	
3-4	94	91	129	.705	84	0.89	
4-5	30	28	38	.737	24	0.82	
5-6	9	8	10	.800	6	0.70	
6-7	2	2	2	1.000	1	0.50	
1961 n' = 421							
0-1	449	453	1000	.453	774	1.47	
1-2	278	281	547	.514	407	1.28	
2-3	161	162	266	.609	185	1.10	
3-4	63	63	104	.606	73	1.04	
4-5	26	26	41	.634	28	0.87	
5-6	15	15	15	1.000	8	0.50	

Table 9 (Continued)

x	D' _x	D _x	l _x	Q _x	L _x	E _x	C _x
Analysis Plan #9 - Zone 1 (Continued)							
1962 n' = 452							
0-1	403	430	1000	.430	785	1.51	
1-2	272	290	570	.509	425	1.27	
2-3	152	162	280	.579	199	1.06	
3-4	75	79	118	.669	79	0.83	
4-5	37	39	39	1.000	20	0.50	
1963 n' = 470							
0-1	413	454	1000	.454	773	1.40	
1-2	261	287	546	.526	403	1.15	
2-3	149	163	259	.629	178	0.87	
3-4	88	96	96	1.000	48	0.50	
1964 n' = 469							
0-1	483	491	1000	.491	755	1.14	
1-2	373	378	509	.743	320	0.76	
2-3	129	131	131	1.000	66	0.50	

Table 9 (Continued)

x	D' _x	D _x	l _x	Q _x	L _x	E _x	C _x
Analysis Plan #2 - Zone 2							
1959 n' = 146							
0-1	54	370	1000	.370	815	1.68	.43970
1-2	45	308	630	.489	476	1.38	.29219
2-3	29	199	322	.617	223	1.22	.15654
3-4	9	62	123	.500	92	1.39	.06169
4-5	6	41	62	.667	41	1.28	.03121
5-6	1	7	21	.333	17	1.83	.00926
6-7	1	7	14	.500	10	1.50	.00611
7-8	0	0	7	.000	7	1.50	.00258
8-9	1	7	7	1.000	3	0.50	.00068
1960 n' = 219							
0-1	88	402	1000	.402	799	1.79	.44500
1-2	52	237	598	.397	479	1.66	.26353
2-3	41	187	361	.519	267	1.42	.15686
3-4	21	96	174	.553	126	1.42	.07378
4-5	9	41	78	.529	57	1.56	.03167
5-6	1	5	37	.125	34	1.75	.01380
6-7	5	23	32	.714	21	0.93	.01199
7-8	1	5	9	.500	7	1.00	.00255
8-9	1	5	5	1.000	2	0.50	.00085
1961 n' = 204							
0-1	88	431	1000	.431	784	1.66	.44390
1-2	48	235	569	.414	451	1.53	.26626
2-3	42	206	333	.618	230	1.26	.16400
3-4	13	64	127	.500	96	1.50	.06444
4-5	6	29	64	.462	49	1.50	.03246
5-6	4	20	34	.571	25	1.36	.01720
6-7	1	5	15	.333	12	1.50	.00629
7-8	1	5	10	.500	7	1.00	.00400
8-9	1	5	5	1.000	2	0.50	.00141

Table 9 (Continued)

x	D' _x	D _x	l _x	Q _x	L _x	E _x	C _x
Analysis Plan #2 - Zone 2 (Continued)							
1966 n' = 261							
0-1	104	398	1000	.398	801	1.62	.44110
1-2	77	295	602	.490	454	1.36	.28220
2-3	50	192	307	.625	211	1.19	.15295
3-4	16	61	115	.533	84	1.33	.06119
4-5	9	34	54	.643	36	1.29	.03059
5-6	1	4	19	.200	17	1.70	.01206
6-7	2	8	15	.500	11	1.00	.01091
7-8	2	8	8	1.000	4	0.50	.00683
8-9							.00218
Analysis Plan #7 - Zone 2							
1959 n' = 62							
0-1	25	403	1000	.403	798	1.58	.44170
1-2	18	290	597	.486	452	1.31	.28092
2-3	10	161	306	.526	226	1.08	.15576
3-4	7	113	145	.778	89	0.72	.08188
4-5	2	32	32	1.000	16	0.50	.02623
5-6	0	0	0	.000	0	0.00	.00980
6-7							.00304
7-8							.00064
1961 n' = 106							
0-1	47	443	1000	.443	778	1.63	.44390
1-2	23	217	557	.390	448	1.53	.26565
2-3	22	208	340	.611	236	1.19	.17396
3-4	9	85	132	.643	90	1.29	.07181
4-5	3	28	47	.600	33	1.70	.02641
5-6	1	9	19	.500	14	2.50	.01036
6-7	0	0	9	.000	9	3.50	.00489
7-8	0	0	9	.000	9	2.50	.00226
8-9	0	0	9	.000	9	1.50	.00081
9-10	1	9	9	1.000	5	0.50	.00000

Table 9 (Continued)

x	D' _x	D _x	l _x	Q _x	L _x	E _x	C _x
Analysis Plan #7 - Zone 4 (Continued)							
1964 n' = 208							
0-1	88	423	1000	.423	788	1.50	.43760
1-2	60	288	577	.500	433	1.24	.29026
2-3	43	207	288	.717	185	0.98	.16654
3-4	9	43	82	.529	60	1.21	.05412
4-5	6	29	38	.750	24	1.00	.02924
5-6	1	5	10	.500	7	1.50	.00886
6-7	0	0	5	.000	5	1.50	.00612
7-8	1	5	5	1.000	2	0.50	.00587
8-9							.00135
1966 n' = 171							
0-1	67	392	1000	.392	804	1.62	.44100
1-2	49	287	608	.471	465	1.34	.28446
2-3	34	199	322	.618	222	1.08	.16070
3-4	15	88	123	.714	79	1.02	.06744
4-5	4	23	35	.667	23	1.33	.02355
5-6	0	0	12	.000	12	2.00	.01156
6-7	1	6	12	.500	9	1.00	.00671
7-8	1	6	6	1.000	3	0.50	.00387
8-9							.00068
Analysis Plan #9 - Zone 1							
1959 n' = 205							
0-1	79	385	1000	.385	807	1.65	.44010
1-2	61	298	615	.484	466	1.37	.28892
2-3	38	185	317	.585	224	1.19	.15849
3-4	16	78	132	.593	93	1.17	.06919
4-5	8	39	54	.727	34	1.14	.02894
5-6	1	5	15	.333	12	1.83	.00682
6-7	1	5	10	.500	7	1.50	.00465
7-8	0	0	5	.000	5	1.50	.00213
8-9	1	5	5	1.000	2	0.50	.00076

Table 9 (Continued)

x	D'_x	D_x	l_x	Q_x	L_x	E_x	c_x
Analysis Plan #9 - Zone 1 (Continued)							
1966 n' = 408							
0-1	167	409	1000	.409	795	1.61	.44160
1-2	116	284	591	.481	449	1.37	.27881
2-3	74	181	306	.592	216	1.18	.15472
3-4	31	76	125	.608	87	1.17	.06783
4-5	14	34	49	.700	32	1.20	.02876
5-6	1	2	15	.167	13	1.83	.00983
6-7	2	5	12	.400	10	1.10	.00919
7-8	3	7	7	1.000	4	0.50	.00701
8-9							.00225
<u>Males</u>							
Analysis Plan #9 - Zone 1							
1959 n' = 286							
0-1	110	385	1000	.385	808	1.61	
1-2	89	311	615	.506	460	1.30	
2-3	51	178	304	.586	215	1.12	
3-4	25	87	126	.694	82	1.00	
4-5	7	24	38	.636	26	1.14	
5-6	3	10	14	.750	9	1.25	
6-7	0	0	3	.000	3	2.50	
7-8	0	0	3	.000	3	1.50	
8-9	1	3	3	1.000	2	0.50	
1960 n' = 392							
0-1	181	462	1000	.462	769	1.49	
1-2	106	270	538	.502	403	1.34	
2-3	54	138	268	.514	199	1.20	
3-4	36	92	130	.706	84	0.98	
4-5	11	28	38	.733	24	0.97	
5-6	3	8	10	.750	6	1.25	
6-7	0	0	3	.000	3	2.50	
7-8	0	0	3	.000	3	1.50	
8-9	1	3	3	1.000	1	0.50	

Table 9 (Continued)

x	D' _x	D _x	$\frac{1}{x}$	Q _x	L _x	E _x	C _x
Analysis Plan #9 - Zone 1 (Continued)							
1961 n' = 361							
0-1	162	449	1000	.449	776	1.56	
1-2	93	258	551	.467	422	1.42	
2-3	58	161	294	.547	213	1.23	
3-4	30	83	133	.625	91	1.10	
4-5	13	36	50	.722	32	1.11	
5-6	1	3	14	.200	12	1.70	
6-7	2	6	11	.500	8	1.00	
7-8	2	6	6	1.000	3	0.50	
8-9	0	0	0	.000	0	0.00	
9-10	0	0	0	.000	0	0.00	
1962 n' = 424							
0-1	171	403	1000	.403	798	1.63	
1-2	118	278	597	.466	458	1.39	
2-3	74	175	318	.548	231	1.16	
3-4	42	99	144	.689	94	0.96	
4-5	13	31	45	.684	29	0.97	
5-6	4	9	14	.667	9	1.00	
6-7	1	2	5	.500	4	1.00	
7-8	1	2	2	1.000	1	0.50	
1963 n' = 533							
0-1	220	413	1000	.413	794	1.66	
1-2	145	272	587	.463	451	1.48	
2-3	86	161	315	.512	235	1.33	
3-4	50	94	154	.610	107	1.20	
4-5	17	32	60	.531	44	1.28	
5-6	9	17	28	.600	20	1.17	
6-7	3	6	11	.500	8	1.17	
7-8	2	4	6	.667	4	0.83	
8-9	1	2	2	1.000	1	0.50	

Table 9 (Continued)

x	D'_x	D_x	l_x	Q_x	L_x	E_x	c_x
Analysis Plan #9 - Zone 1 (Continued)							
1964 $n' = 671$							
0-1	324	483	1000	.483	759	1.43	
1-2	175	261	517	.504	387	1.31	
2-3	102	152	256	.593	180	1.13	
3-4	42	63	104	.600	73	1.04	
4-5	20	30	42	.714	27	0.86	
5-6	6	9	12	.750	7	0.75	
6-7	2	3	3	1.000	1	0.50	
7-8	0	0	0	.000	0	0.00	
1965 $n' = 228$							
0-1	84	368	1000	.368	816	1.54	
1-2	85	373	632	.590	445	1.15	
2-3	34	149	259	.576	184	1.09	
3-4	17	75	110	.680	72	0.90	
4-5	6	26	35	.750	22	0.75	
5-6	2	9	9	1.000	4	0.50	
6-7	0	0	0	.000	0	0.00	
7-8	0	0	0	.000	0	0.00	
1966 $n' = 464$							
0-1	199	429	1000	.429	786	1.56	
1-2	139	300	571	.525	421	1.35	
2-3	60	129	272	.476	207	1.29	
3-4	41	88	142	.621	98	1.02	
4-5	17	37	54	.680	36	0.86	
5-6	7	15	17	.875	10	0.62	
6-7	1	2	2	1.000	1	0.50	
7-8	0	0	0	.000	0	0.00	

APPENDIX C. COMPUTER MATRIX FOR
INPUT OF COUNTY OF KILL

Table 10. Computer matrix for input of county of kill data to analysis plans

County number	Management plans			
	1 1967 zoning	2 1966 zoning	7 Mustard's regions	9 Statewide except res. data
01	2	2	4	1
02	2	2	3	1
03	5	2	1	1
04	3	2	4	1
05	1	2	3	1
06	4	1	2	1
07	4	1	2	1
08	2	1	2	1
09	6	1	2	1
10	4	2	2	1
11	6	1	2	1
12	6	1	2	1
13	6	1	2	1
14	2	1	2	1
15	1	2	3	1
16	4	2	4	1
17	6	1	2	1
18	6	1	2	1
19	6	2	2	1
20	2	2	4	1
21	6	1	2	1
22	5	2	1	1
23	4	2	4	1
24	1	2	3	1
25	2	1	2	1
26	3	2	4	1
27	2	2	4	1
28	4	2	2	1
29	3	2	4	2
30	6	1	2	1
31	4	2	1	1
32	6	1	2	1
33	5	2	1	1
34	6	1	2	1
35	6	1	2	1
36	1	2	3	1
37	2	1	2	1
38	4	1	2	1
39	2	2	4	1
40	6	1	2	1
41	6	1	2	1
42	4	1	2	1

Table 10 (Continued)

County number	Management plans			9 Statewide except res. data
	1 1967 zoning	2 1966 zoning	7 Mustard's regions	
43	1	2	3	1
44	3	2	4	1
45	6	2	2	1
46	6	1	2	1
47	1	1	2	1
48	4	1	4	1
49	4	2	4	1
50	4	1	4	1
51	3	2	4	1
52	4	1	4	1
53	4	2	4	1
54	3	2	4	1
55	6	1	2	1
56	3	2	4	1
57	4	2	2	1
58	3	2	4	1
59	3	2	4	1
60	6	1	3	1
61	2	2	4	1
62	3	2	4	1
63	3	2	4	1
64	4	1	4	1
65	1	2	3	1
66	6	1	2	1
67	1	2	3	1
68	3	2	4	1
69	1	2	3	1
70	4	2	4	1
71	6	1	2	1
72	6	1	2	1
73	1	2	3	1
74	6	1	2	1
75	6	1	3	1
76	6	1	2	1
77	4	1	2	1
78	1	2	3	1
79	4	1	4	1
80	2	2	4	1
81	6	1	2	1
82	4	2	4	1
83	1	2	3	1
84	6	1	3	1
85	4	1	2	1

Table 10 (Continued)

County number	1 1967 zoning	Management plans		9 Statewide except res. data
		2 1966 zoning	7 Mustard's regions	
86	4	1	4	1
87	2	2	3	1
88	2	2	4	1
89	3	2	4	1
90	3	2	4	1
91	3	2	4	1
92	4	2	4	1
93	3	2	4	1
94	6	1	2	1
95	6	1	2	1
96	5	2	1	1
97	1	2	3	1
98	6	1	2	1
99	6	1	2	1

APPENDIX D. SAMPLE CALCULATION OF $c(t, x)$,
THE STABLE AGE-DISTRIBUTION

$c(t,x)$ = proportion of individuals in age group x

$$= \frac{\lambda^{-x} l_x}{\sum_{y=0}^w \lambda^{-y} l_y}$$

where w = upper limit of reproductive life for species.

Composite data for 1959-1966, $n = 2853$ females

<u>Age</u>	<u>l_x</u>	<u>λ^{-x}</u>	<u>$\lambda^{-x} l_x$</u>	<u>$c(t,x)$</u>
0	1.000		1.000	.4257
1	.570	1.1919	.6794	.2892
2	.301	1.4206	.4276	.1820
3	.091	1.6932	.1541	.0656
4	.026	2.0181	.0525	.0223
5	.010	2.4054	.0241	.0103
6	.004	2.8669	.0114	.0049
			<hr/>	<hr/>
			2.3491	1.0000

APPENDIX E. SAMPLE CALCULATION OF LAMBDA

Sample Calculation of Lambda for Composite Distribution
of Females 1959-1966, n' = 2853, Classes
Extended to Account for 10 Age Classes

n = 2903

Age	D'_x	D_x	l_x	m_x	$l_x m_x$	$l_x m_x x$
0			1.0000			
1	1226	422.3	.5777	.630	.36395	.36395
2	767	264.2	.3125	.957	.30002	.60004
3	600	206.7	.1068	.957	.10221	.30663
4	185	63.7	.0431	.957	.04125	.16500
5	75	25.8	.0173	.957	.01656	.08280
6	30*	10.3	.0070	.957	.00670	.04080
7	12*	4.1	.0029	.957	.00278	.01946
8	5*	1.7	.0012	.957	.00115	.00920
9	2*	.7	.0005	.957	.00048	.00432
10	1					
	<u>2903</u>	<u>999.5</u>			<u>.83510</u>	<u>1.59220</u>

T = mean length of a generation

$$= \frac{\sum l_x m_x x}{\sum l_x m_x} = \frac{1.5922}{.8351} = 1.90659$$

$$R_0 = \sum l_x m_x = .83510 = e^{rT}$$

$$r = \frac{\lg R_0}{T} = \frac{\lg 8.351 - \lg 10}{1.90659} = \frac{2.12238 - 2.30259}{1.90659}$$

$$r = \frac{-.18021}{1.90659} = \underline{\underline{-.09452}}$$

$$\lambda = \text{antilog } r = \underline{\underline{.910}}$$

* Estimated at .4 preceding class.