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POPULATION BIOLOGY OF THE BLACK-TAILED JACKRABBIT (*LEPUS CALIFORNICUS*) IN NORTHERN UTAH

by

L. Charles Stoddart

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Resources Sciences

Approved:

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Logan, Utah

1972

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I am indebted to Jack E. Gross for use of data which he collected on the jackrabbit population during three years previous to my study.

L. Charles Stoddart

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ABSTRACT

Population Biology of the Black-tailed Jackrabbit (*Lepus californicus*) in Northern Utah

by

L. Charles Stoddart, Doctor of Philosophy

Utah State University, 1972

Major Professor: Dr. Frederic H. Wagner
Department: Wildlife Resources

Population biology of the black-tailed jackrabbit population on a 250-square-mile area in Curlew Valley, northern Utah, was studied from 1962-70. During this period the fall population density index increased from 40.0 in 1962, to 60.6 in 1963, decreased progressively to a low of 21.2 in 1967, then increased the following 3 years to a high of 185.0 in 1970.

Breeding was synchronous with four conception periods each year; in some years a fifth conception period was evident. The first conception period occurred about the last half of January; other periods followed at 40-day intervals indicating a 40-day gestation period and postpartum estrus with subsequent conception. Over the 9 years of study, the mean percentages of females breeding during the five conception periods were 88, 99, 100, 70, and 11 percent, respectively. The mean number of ova ovulated per breeding female for the five periods was 1.9, 5.1, 6.4, 4.9, and 3.6, respectively.

During the period of decreasing density, 1963-67, the yearly mean number of ova ovulated per female surviving the breeding season

ranged from 13.2-19.3, but varied independently of density. During the 3 consecutive years of density increase, 1968-70, however, the number of ova ovulated per female decreased progressively from 19.8 in 1968 to 14.2 in 1970.

Mortality rates of the total population from October-March remained relatively constant (mean: 63 percent) during the years of population decline, but dropped to 33 percent during the first year of population increase (1968). March-October mortality of adults decreased to 9 percent during the first year of population increase from a previous mean of 73 percent, and juvenile mortality from parturition to fall census, decreased from a mean of 68 percent to 38 percent.

The effects of variations in mortality rates on population density have overshadowed the effects of the relatively less extreme variations in natality rates. As a result the pattern of density change was almost entirely a result of changes in mortality rates.

Changes in mortality rates of adults and juveniles were well correlated with the coyote/rabbit ratio on the study area. Exceptions occurred with juvenile mortality rates at the relatively high rabbit densities observed in 1969-70. During these two years, juvenile mortality rates from parturition to fall census (61 and 68 percent, respectively) were greater than could be accounted for by coyote predation. The factor or factors responsible for the increased juvenile mortality are not known.

Observed annual density changes were described with the mathematical model:

$$N_{t+1} = N_t(1 - 37.8 - 988x_1)(1 + 11.2 - 1130x_2 - 0.0581x_3 + 42000x_2^2 + 0.00115x_3^2)$$

where N_t is the number of animals at the end of October, N_{t+1} is the number of animals at the end of the following October, x_1 is the coyote/rabbit ratio from October-March, x_2 is the coyote/rabbit ratio from March-October, and x_3 is the mean number of rabbits per square mile from March-October. The model accounts for 99 percent of the observed change in rabbit density from 1968-70.

(175 pages)

INTRODUCTION

A study of the black-tailed jackrabbit (Lepus californicus) population in a 250-square-mile area of Curlew Valley in northwestern Utah has been in progress since 1962, carried out by students and staff of Utah State University. The long-term objective of the study is to understand the intrinsic and extrinsic mechanisms involved in population growth and decline in order to: (1) develop a predictive simulation model describing the effects of variation in environmental factors on rabbit density over extended periods of time; (2) describe the role of the rabbit population in energy flow through the ecosystem in the area; and (3) add to our knowledge concerning the general problem of population regulation; i.e., maintenance of a long-term equilibrium density.

After the first three years of the study, 1962-64, Gross (1967) reported on methodology used, and described the relationship of mortality and natality rates to observed changes in density.

The objectives of the work reported herein were to: (1) estimate population density in October and March of each year using a strip census method and to analyze alternative methods for interpreting the strip census data; (2) continue, with some modification of methods, the study of the joint role of mortality during three life history stages--juveniles from birth-October, adults from March-October, and population from October-March--and natality in determining rabbit density changes; and (3) develop a mathematical model of annual density change using results from nine years of the above study, 1962-70.

METHODS

Study Area

A 250-square-mile area, henceforth called "the study area," (Figure 1) was located in the southern half of Curlew Valley, an intermountain basin of about 1,200 square miles which is divided approximately in half by the Utah-Idaho border. A one-square-mile sub-area was located on the lower north slope of the Wildcat Hills in approximately the center of the study area (Figure 1). This area, which will henceforth be called the "drive-count area," was established for an intensive study of jackrabbit density (cf. Gross, 1967).

Climate, vegetation, and topography in Curlew Valley have been described in detail by Rusch (1965) and Gross (1967). Vegetation in the study area falls within what Fautin (1946) termed the Northern Desert Shrub Biome and what a number of authors have referred to as "The Great Salt Lake Desert." The general aspect of the vegetation is a shrub type with big sagebrush (*Artemisia tridentata*) and associated grasses and forbs dominating over half of the area including the drive-count area. Other distinguishable types are shadscale (*Atriplex confertifolia*) shrub zone, greasewood (*Sarcobatus vermiculatus*) shrub zone, and limited acreages of agricultural land and exotic range-grass seedings which cover approximately 25 percent, 15 percent, and 5 percent of the area, respectively.

Precipitation within the study area ranges from 8-10 inches annually and falls mostly between fall and spring. Snow cover is usual in winter with several inches accumulating on the level.

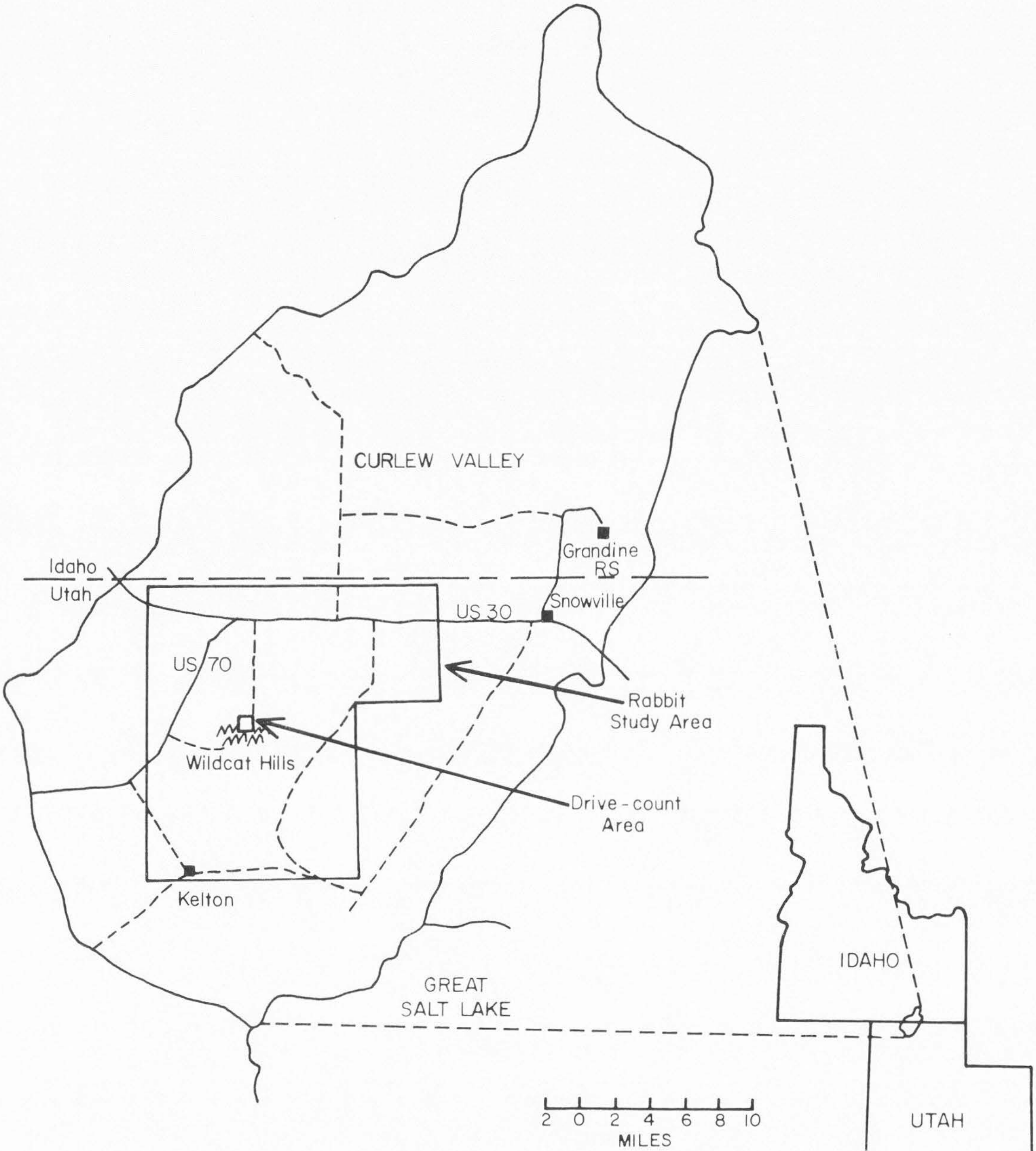


Figure 1. Location and boundaries of Curlew Valley, Curlew Valley study area, and drive-count area.

Census Techniques

In order for my model to give a quantitative description of changes in rabbit numbers and for future use of the rabbit data in energy-flow analysis, I have estimated absolute numbers. In understanding the relationships of the various demographic parameters to changes in animal numbers, however, it is necessary only to have an index of population density. Since an absolute count is logistically unfeasible in a large study area, absolute densities were estimated (as described below) by combining index measurements with absolute counts, herein called "drive counts," from the drive-count area.

Line transects

Density indexes were obtained through the use of line transects. In early April and late October of each year, 78 randomly distributed, square transects 1/4 mile on a side (cf. Gross, 1967) were walked. The four sides are henceforth called "transect legs" or simply "legs." As the transects were walked, the transect leg and the direct distance at time of flush from the observer to the point of flush, henceforth called the "flushing distance," were recorded for each rabbit flushed. Starting in fall, 1966, the angle, henceforth called the "flushing angle," formed by the transect line and a line from the observer to the point where the animal was located, was measured to the nearest degree. On these transects the perpendicular distance from the transect line to the point from which the animal was flushed, henceforth called the "lateral distance," was calculated by multiplying the flushing distance by the sine of the flushing angle. Four of the 78 transects were located in the drive-count area for use in absolute density estimates as described below.

During the course of the study, the original 78 transects were reduced to 70 because some native habitats where transects were located were cultivated.

Drive-counts

Drive-counts are the numbers of animals driven from the drive-count area by crews of men. The area was divided into sub-areas 1/4 mile wide by 1 mile long which were driven separately. The procedure (cf. Gross, 1967) produced counts which I think were close to the absolute numbers of animals on the square mile.

Drive-counts were related through regression analysis to results from the four transects walked in the drive-count area. The purpose was twofold: (1) transect results from the study area could be converted with the regression equation into crude estimates of absolute numbers of rabbits; and (2) any long-term changes in jackrabbit flushing behavior which affect transect results would become apparent through a change in the linear relationship of the regression equation.

Field Collections and Gross Autopsy

Rabbits were collected from the study area to provide data on reproductive rates and chronology, and on sex, age, and weight structure of the population. Collections were made each month except November. The collections were made at night from a pickup truck with the use of a spotlight and shotgun or .22 rifle.

In December-April, 50 rabbits were collected each month. In May and June when juveniles began to appear in the collections, the number was increased so that approximately 50 adults were still obtained. Finally, the monthly collection was increased to 100 animals in July-October when the population was composed of a high percentage of juveniles. Animals were brought to the laboratory within a few hours after collection and frozen at 0 C.

From 1962-68, animals were collected during the last half of each month. During this period, 2-4 nights of hunting were usually required to make a collection; as a result, rabbits were collected on only a few nights of each month.

Jackrabbit breeding was found to be synchronous (see below). Starting in January, 1969, rabbit collections during the breeding season were scheduled so that a collection would be made about mid-way between the peak conception periods of the breeding season, a time when most females would be visibly pregnant. Therefore, collections were made about every 40 days rather than on a monthly basis.

From 1962-68 rabbits were collected from areas where they could most readily be obtained; no attempt was made to get a random sample over the study area. The areas from which animals were collected varied from month to month and from one year to the next. During 1969-70, a single collecting area composed of approximately 10 miles of roadside near the center of the study area, was specified from which all rabbit collections were taken.

Usually within 30 days after collection the animals were thawed, weighed (Appendix B), and a gross autopsy performed (cf. Gross, 1967). A humerus was removed from each animal for use in determining population age structure (Gross and Gross, 1966). Entire reproductive tracts of females, testes of males, adrenals from both sexes, and an eye lens from each rabbit were removed and fixed in 10 percent formalin. Starting in February, 1969, one aspect of this procedure was modified. Instead of the eye lens being removed from the carcass after freezing, an entire eyeball was removed from each animal prior to freezing and fixed in 10 percent formalin (cf. Friend, 1967).

Laboratory Analyses

Uterine and fetal analyses

After uteri were fixed in formalin, those from visibly pregnant females, as shown by uterine swelling, were dissected. Healthy and resorbing fetuses were counted. Healthy fetuses were aged from a table relating fetal weight and morphology with age (cf. Gross, 1967). Conception dates for all visible litters were determined with the use of fetal ages by backdating from the date of collection. The sex of fetuses 32 days old or older was determined by internal examination of the shape and location of the gonads (Gross, 1967).

Ovarian analysis

Ovaries were examined for two reasons: (1) corpus luteum counts were used as estimates of ovulation rates; and (2) size of corpora lutea and corpora albicantia aided in determining the reproductive status of nonvisibly pregnant females. Each ovary was sliced into 1/32-inch-thick longitudinal sections with a razor blade. Corpora lutea were counted and their cross-sectional diameter measured.

The most frequently recognized bodies in the ovaries were follicles, corpora lutea and corpora albicantia; the three could be distinguished readily. Follicles and corpora lutea were generally about the same color, but could be separated in two ways:

(1) follicles were generally 1 mm or less in diameter, whereas the smallest corpora lutea were 2 mm in diameter; and (2) rupture sites were evident for corpora lutea, but not present in the case of follicles.

Corpora lutea and corpora albicantia could be separated by color and texture. Corpora lutea in preserved ovaries were usually a medium brown color with a somewhat granular texture. Corpora albicantia from recently postpartum females, as determined by the presence of a large flaccid uterus, had already turned a whitish color and were solid or dense in texture (cf. Lechleitner, 1959). As the corpora albicantia aged they maintained their solid texture, became yellow, steadily decreased in size, and usually became irregular in shape.

Reproductive-condition Criteria in Females not Visibly Pregnant

Females not visibly pregnant were placed into four groups: (1) pregnant, but not yet implanted or with embryos not yet visible; (2) postpartum with no postpartum ovulation as yet; (3) pseudopregnant; and (4) nonbreeding.

Criteria used for classing nonpregnant females were as follows:

1. Corpora lutea in ovaries of pregnant females were found to grow from about 2mm at the time of ovulation to 8-10 mm at the end of the gestation period. I found that by the time the embryos implanted and became visible as uterine swellings, about 7 days postovulation (cf. Lechleitner, 1959), corpora lutea had reached 6 mm in diameter. This was consistant with Lechleitner's (1959) data which show corpus luteum diameters of 5-6 mm by implantation time. On the basis of

these findings, females with no visible fetuses but with corpora lutea less than 6 mm in diameter were classed as being pregnant in the first 7 days postovulation.

2. Immediately following parturition, corpora albicantia were about 8-10 mm in diameter and the uterus was stretched and flaccid. The uterus contracted to its nonpregnant size within a few days, but the corpora albicantia persisted, decreasing in size at about the same rate that they grew as corpora lutea (cf. Lechleitner, 1959). Hence, the postpartum condition was recognizable from the uterine appearance and/or the presence of corpora albicantia.

3. In the domestic rabbit, if conception does not follow ovulation, pseudopregnancy occurs for about one-half the normal gestation period; during this time functional corpora lutea persist (Hughes and Myers, 1966). Brambell (1944) found evidence that the same condition occurs with total litter loss before mid term. Assuming that the same condition occurs in jackrabbits, I classed females with no visible fetuses but with corpora 6 mm or larger in diameter as pseudopregnant.

4. A female was classed nonbreeding if no corpora lutea or large corpora albicantia were found in the ovaries.

Age Criteria

It was necessary to have some means for separating adults and juveniles in the monthly collections in order to calculate mortality and natality rates in the jackrabbit population. From 1962-68, two criteria were used for this separation. The first was the presence or absence of epiphysial cartilage at the proximal end of the humerus.

Considerable variability may exist in the age at which the replacement of epiphysial cartilage by bone is complete in juvenile jackrabbits (Connally et al., 1969). Replacement in some animals may be complete by 7 months of age and perhaps earlier. By October (a month of particular importance in my study because the fall census was conducted in this month), some juveniles might have been as old as 9 months; thus erroneous results could have been obtained in fall using this method alone.

Therefore, in fall, the above method of separating adults and juveniles was supplemented with a second criterion, the weight of the dry eye lens. As mentioned, eye lenses were frozen before drying and weighing in 1962-68. The precision with which the lenses could be processed was greatly reduced because this procedure causes partial breakdown of lens tissue and increases fragility (Friend, 1967). As a result, by fall, some overlap occurred in the lens weight groups of the two age classes. However, with combined use of both these techniques, probably few animals were erroneously classed.

During 1969-70 when unfrozen lenses were dried and weighed, rabbits were aged with the use of lens weights only.

Since the breeding season in Curlew Valley was confined within a calendar year it was convenient to class rabbits collected within the calendar year of their birth as juveniles. By definition, then, all juveniles in the population became adults on January 1 of the year following their birth.

Testis and Adrenal Weights

Weights of testes, excluding the epididymis, and adrenals were recorded. The purposes were: (1) to determine what annual changes, if any, existed in the weight of these organs and how they related to onset and cessation of the breeding season; and (2) to determine whether the weights varied between years with changes in population density or other population parameters. Results are shown in Appendixes A and C.

Mortality Measurement

Using the census and autopsy results, I calculated mortality rates over four stages or time periods in the life history of the jackrabbit: (1) preparturition; (2) postpartum to fall census; (3) total population from fall to spring census; and (4) adult population from spring to fall census.

Mortality was also determined using a telemetric technique designed to measure rates and causes of mortality (Stoddart, 1970).

RESULTS

Population Density

Field biases in census technique

If all factors or biases affecting the number of rabbits counted on the transects, except rabbit density, remain constant from one census to another, the number of rabbits counted will serve as a relative estimate of density (cf. Hayne and Eberhardt, 1954). If any factor changes between census periods and thereby alters the level of bias, that factor must be corrected for. I have examined three factors for changing levels of bias: (1) flushing behavior; (2) observer behavior; and (3) duplicate counting of individual rabbits on different legs of the transect.

Flushing behavior. Frequency distribution of flushing distances from all spring censuses pooled and all fall censuses (except 1970) pooled (Figure 2) suggest shorter flushing distances in fall than in spring. (Unweighted mean flushing distances in fall and spring were 23.1 and 31.0 yards respectively.) I found the distributions to be significantly different at the 1 percent probability level by the Kolmogorov-Smirnov test. This is a bias that tends to increase the spring count relative to the fall count and needs correction if fall and spring counts are to be compared.

In addition to interseasonal variations in flushing distances, differences within the same season were evident between years (cf. Figure 3 for the extremes). These variations between years were evidently associated in part, at least, with variations in

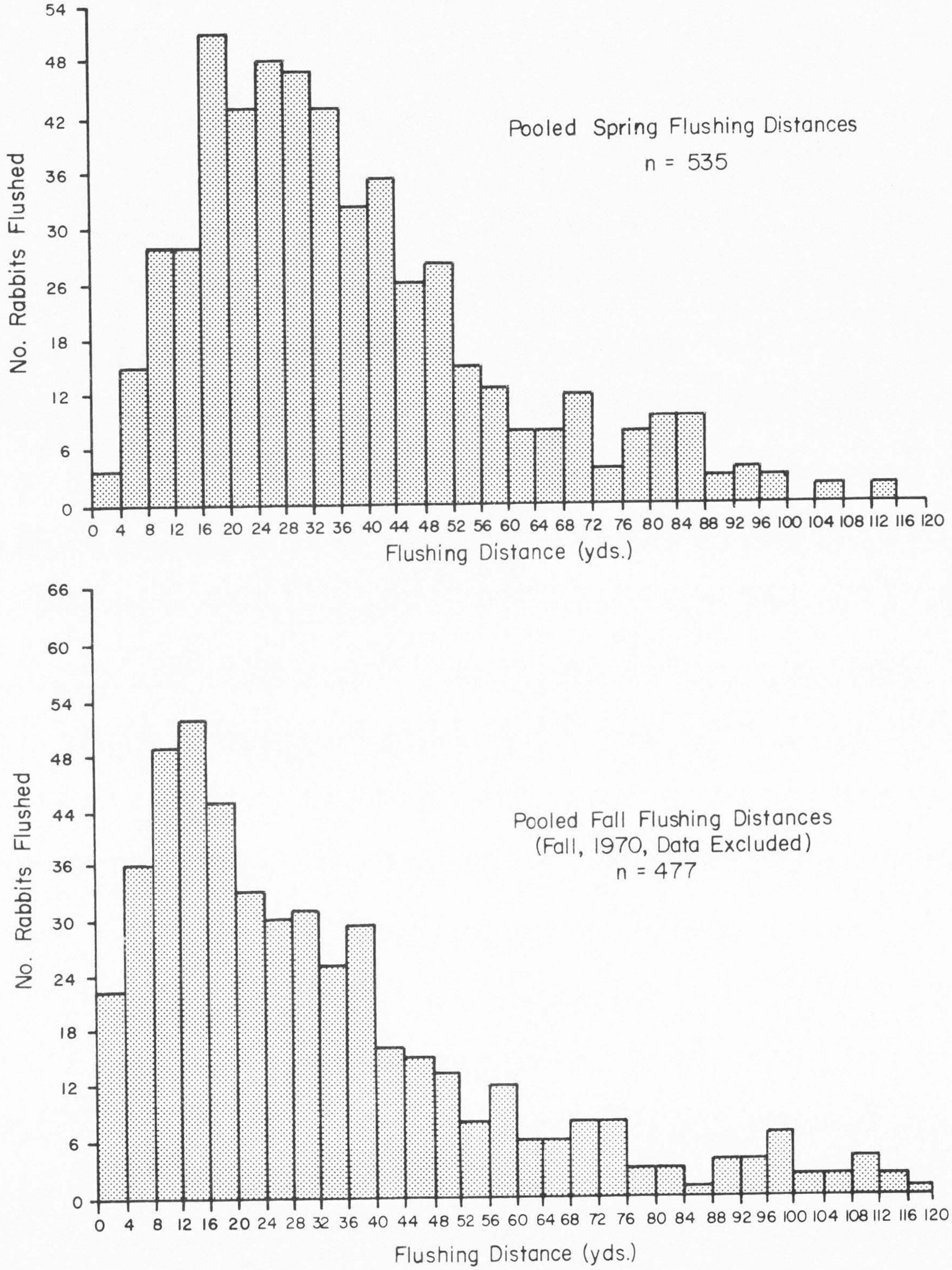


Figure 2. Frequency distribution of flushing distances from all spring censuses pooled and all fall census (except 1970) pooled.

density as flushing distances were correlated with density (Figure 4).

Using the Kolmogorob-Smirnov test, I found the distribution of flushing distances in fall, 1970, (Figure 3) to be significantly different at the 1 percent probability level from the pooled fall distribution of flushing distances (1962-69) in Figure 2. Because of the difference between these two distributions, which can be explained on the basis of increased flushing distance with density (Figure 4), I excluded fall, 1970, data from the pooled fall distribution of flushing distances (Figure 2).

Since fall and spring distributions of flushing distances were found to be different, a separate regression equation was calculated for spring and fall flushing distances (Figure 4). The fall and spring correlations were significant at the 0.5 percent and 5 percent probability levels respectively. Apparently, the factor or factors responsible for the difference between fall and spring distributions of flushing distances were independent of density, since the slopes of the two regression lines are nearly the same (0.253 and 0.234 for spring and fall respectively).

Observer behavior. The distributions of flushing angles obtained by one observer, 1969-70, and by another, 1966-68, (Figure 5) are different at the 0.1 percent probability level (Kolmogorov-Smirnov test). The continuous curves in Figure 5 are cosine curves which represent the expected distribution of flushing angles provided the flushing behavior of the animals is independent of the observer's angle of approach. Since the frequency distribution of angles observed in 1969-70 was obtained during years when spring and fall densities were the highest so far recorded, it might be argued that

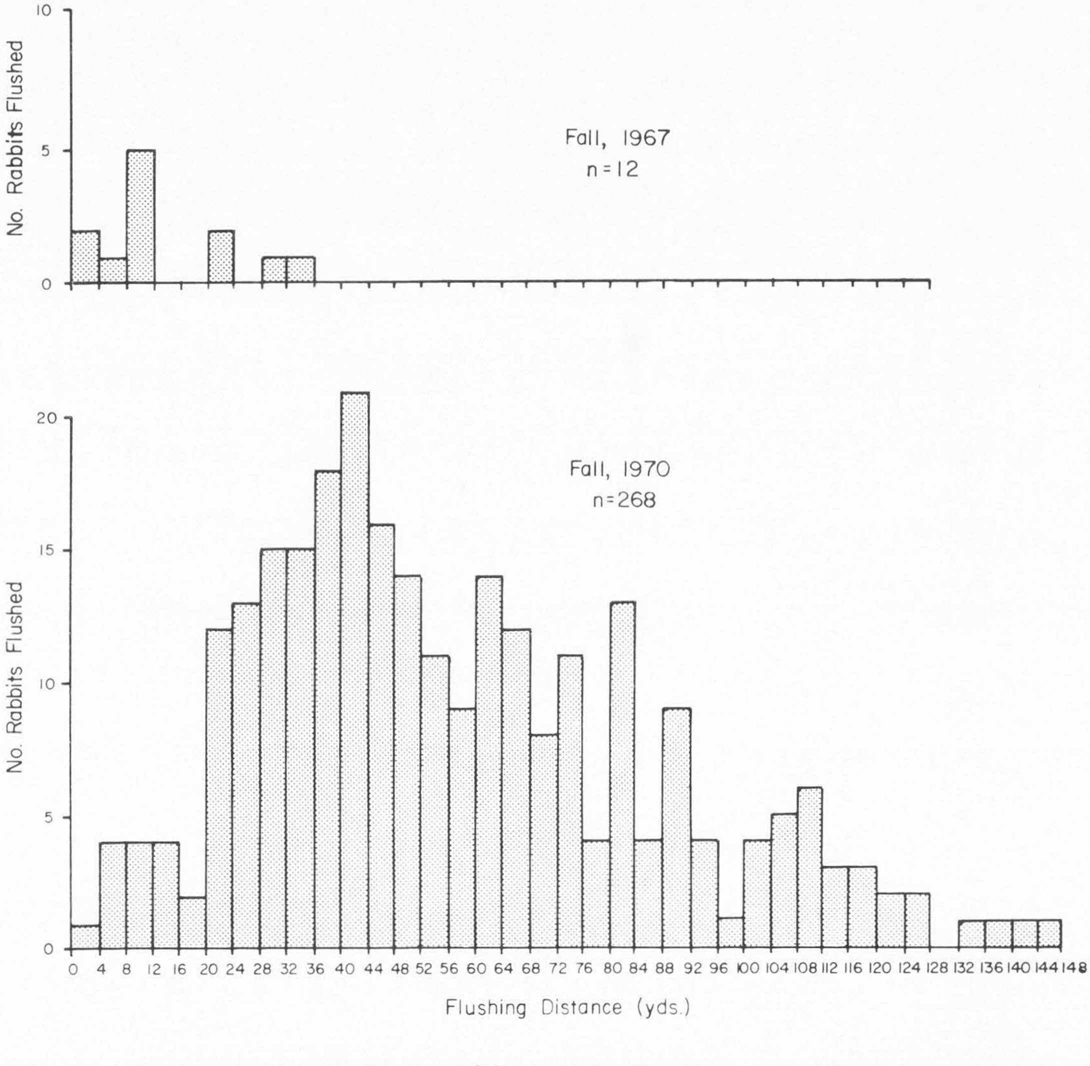


Figure 3. Comparison of fall, 1967, distribution of flushing distances with fall, 1970, distribution of flushing distances.

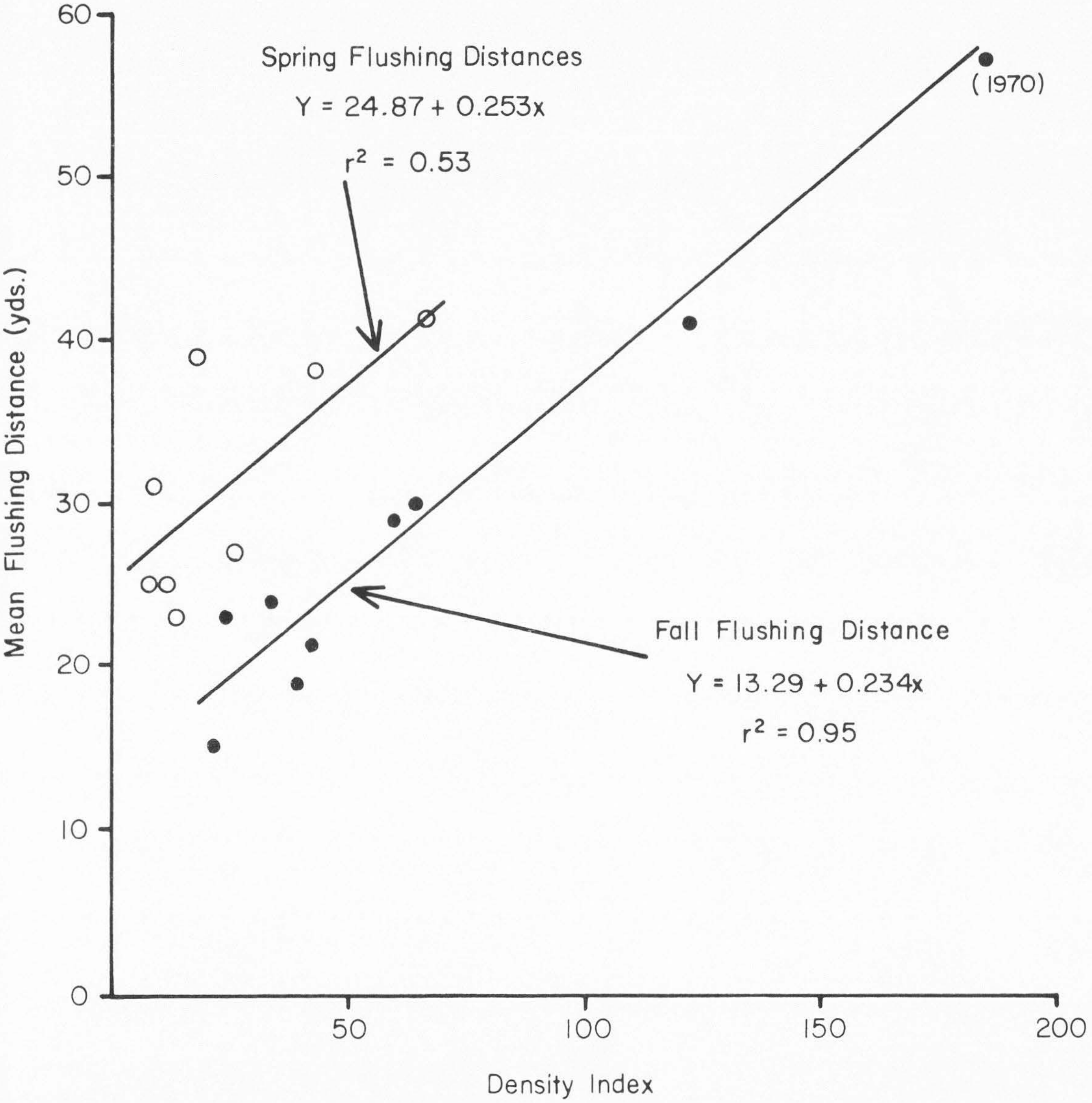
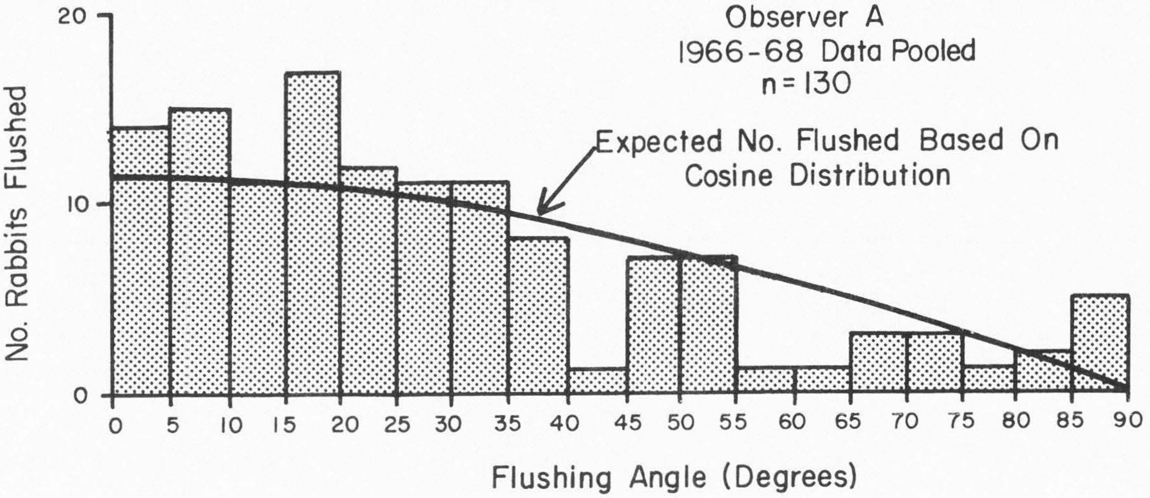
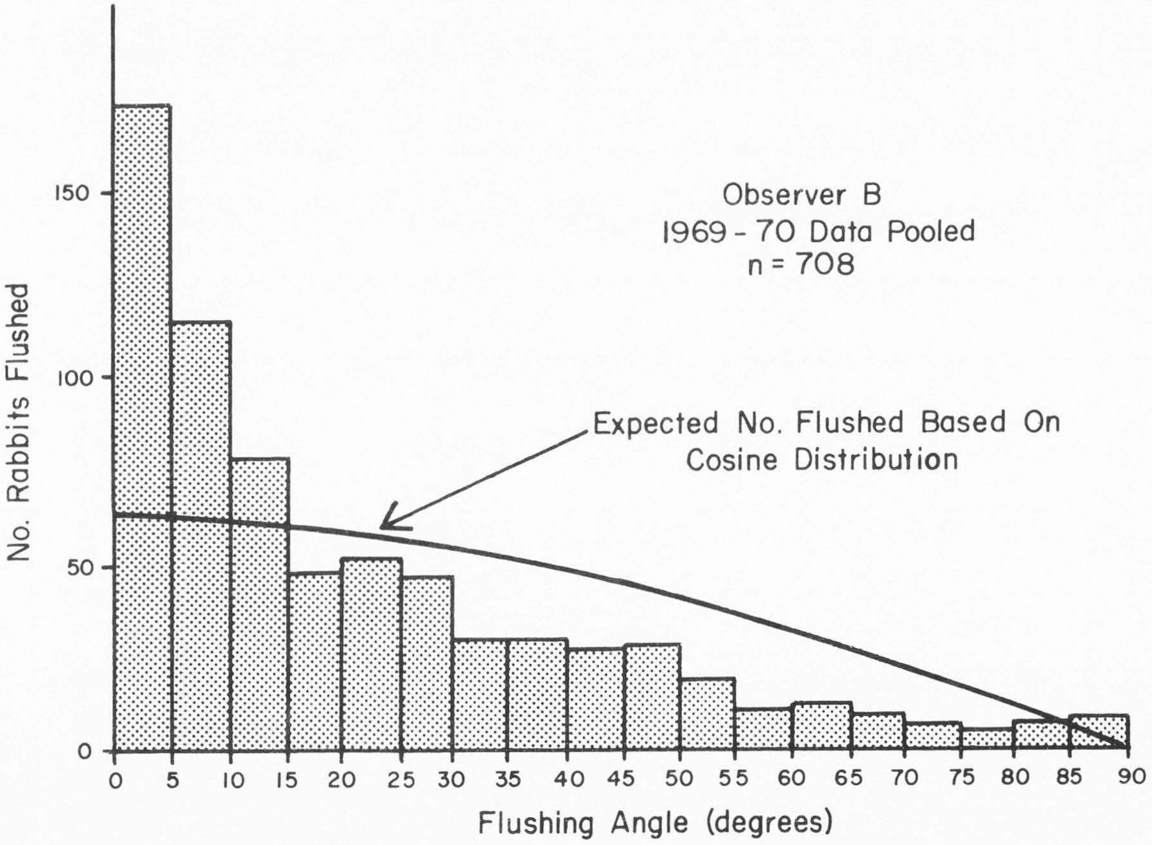


Figure 4. Linear regression of the mean flushing distance in spring and mean flushing distance in fall on density index. Data are from all transects over the study area.


Observer A
1966-68 Data Pooled
n = 130
Expected No. Flushed Based On Cosine Distribution
No. Rabbits Flushed
0
10
20
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
Flushing Angle (Degrees)

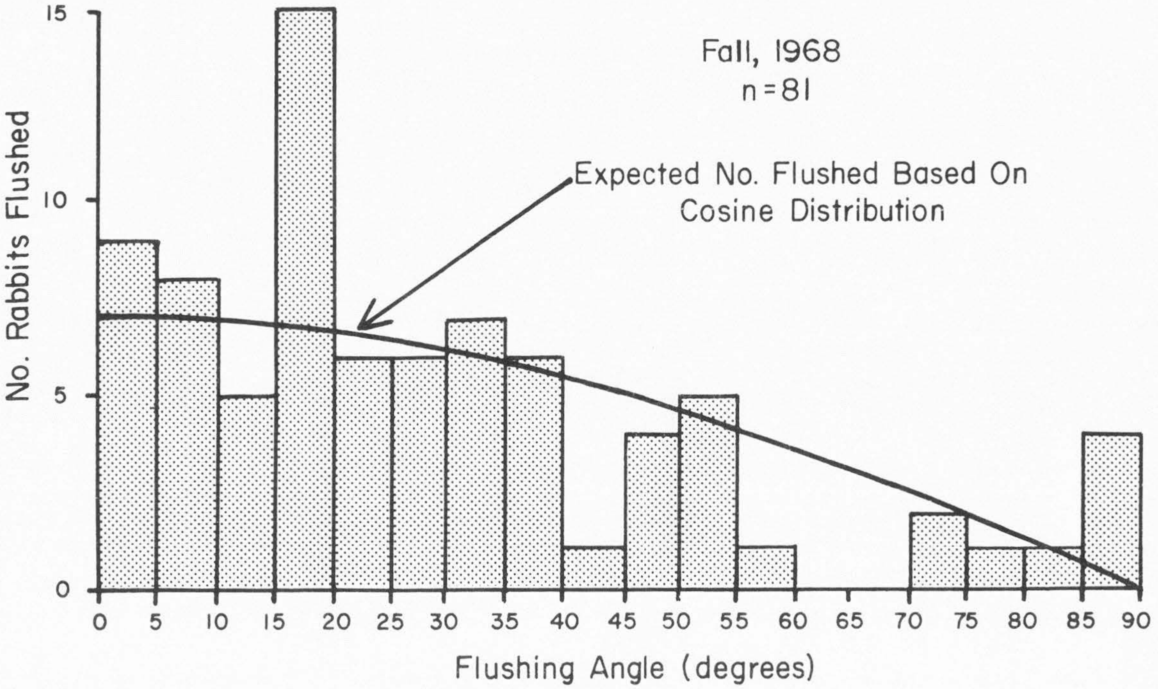

Observer B
1969 - 70 Data Pooled
n = 708
Expected No. Flushed Based On Cosine Distribution
No. Rabbits Flushed
0
50
100
150
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
Flushing Angle (degrees)

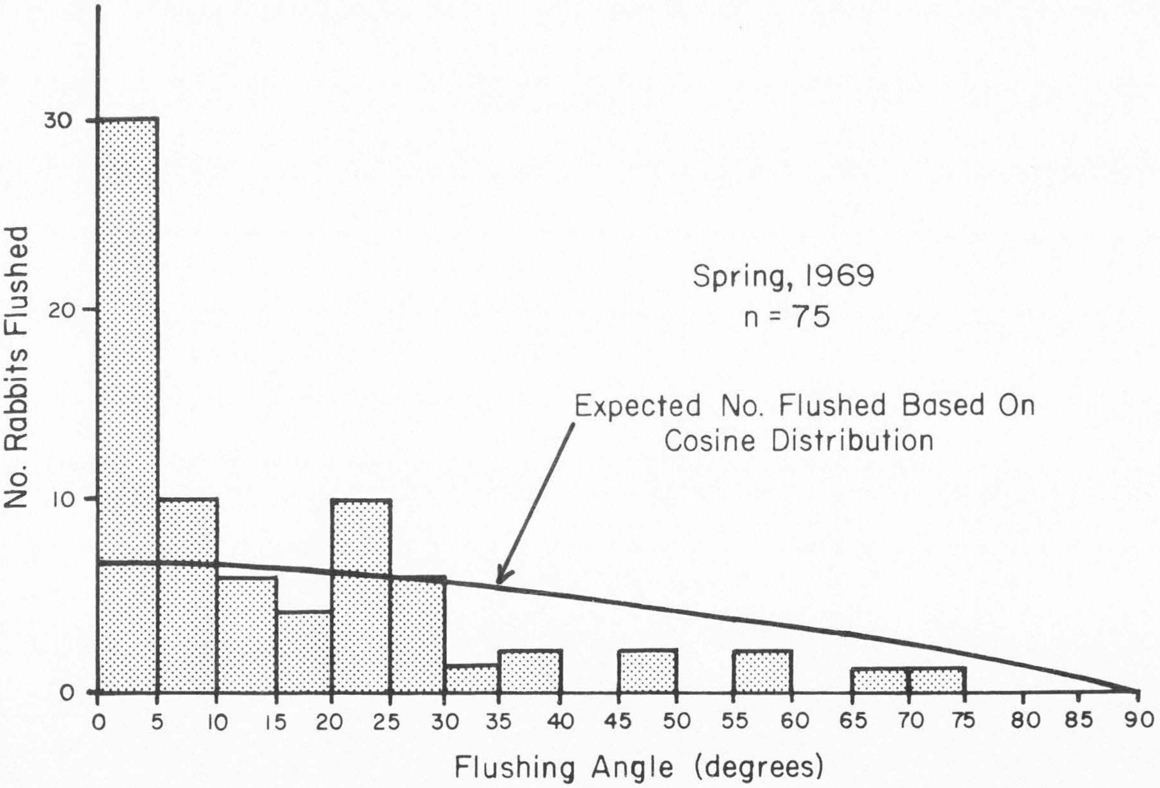
the distributions were affected by density. This is probably not the case since a comparison of spring, 1969, with the higher density of fall, 1968, shows this same trend (Figure 6).

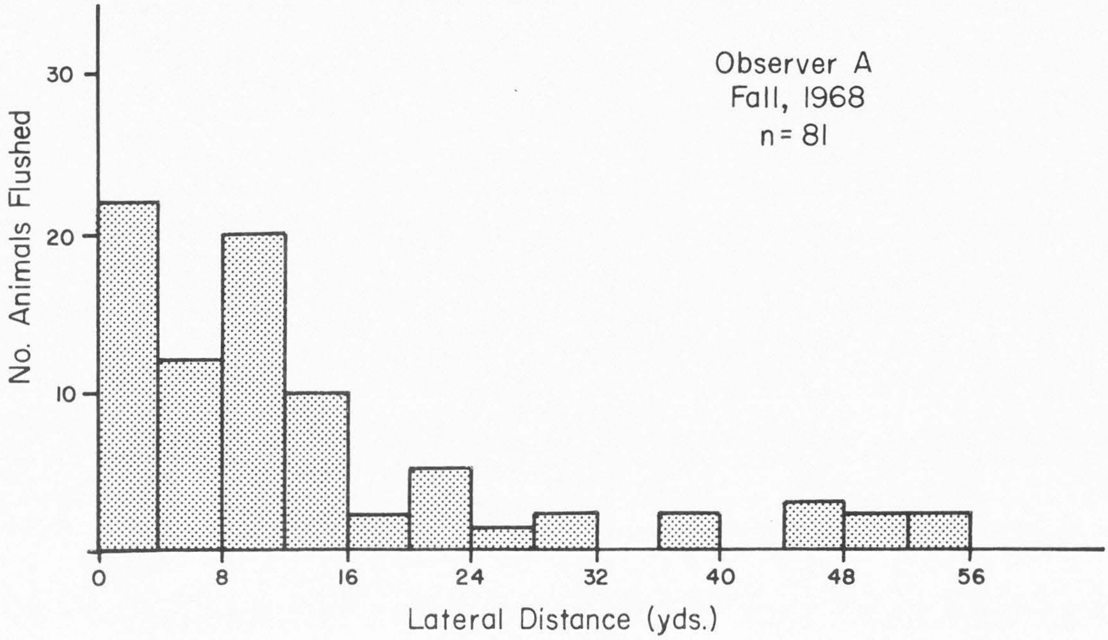
It is also informative to look at the distributions of observed lateral flushing distances. The distributions of lateral distances observed in fall, 1968, by one observer and spring, 1969, by another observer are shown in Figure 7. These distributions were found to be different at the 20 percent probability level (Kolmogorov-Smirnov test). An important point is the frequency of animals observed in the 4-yard interval immediately adjacent to the transect line. Although the spring, 1969, density estimate was 75 percent of the fall, 1968, density estimate, 50 percent more animals were observed in the 0-4 yard interval in spring, 1969. The number of animals in the 0-4 yard interval in spring, 1969, is significantly larger than in fall, 1968, at the 7.0 percent probability level ($\chi^2 = 3.07$). The increased number of animals observed in the 0-4 yard interval is likely not a result of changes in animal density. The only logical explanation for this increase is a difference in observer bias.

Hence, there is evidence of variation between observer; this variation needs correcting if transects walked by different observers are to be compared.

Duplicate counts of the same rabbit. In any type of line-transect census, an animal can be flushed more than once. This possibility may be enhanced by the square shape of the transects. A rabbit flushed on one leg could conceivably run to another where he is flushed again. This phenomenon would not necessarily introduce error into the indexes unless its frequency varied between censuses.


Fall, 1968
n=81
Expected No. Flushed Based On Cosine Distribution
No. Rabbits Flushed
15
10
5
0
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90
Flushing Angle (degrees)


Spring, 1969
n = 75
Expected No. Flushed Based On Cosine Distribution
No. Rabbits Flushed
30
20
10
0
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90
Flushing Angle (degrees)



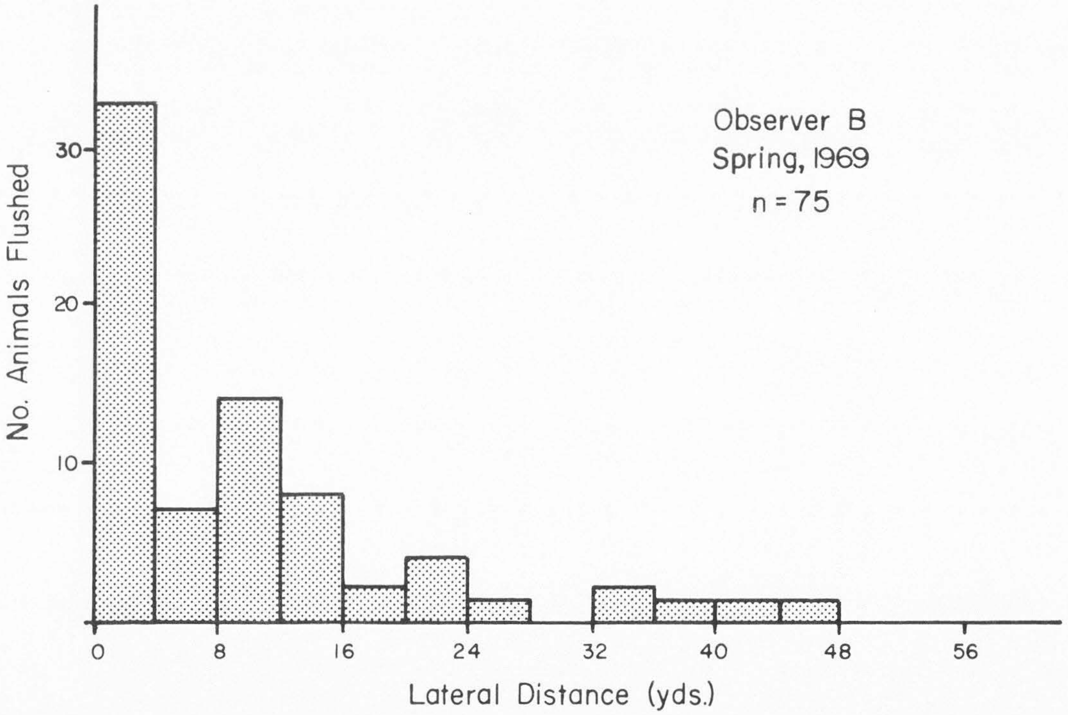


Figure 7. Distribution of lateral distances observed in spring, 1969, and in fall, 1968.

In order to establish whether or not the phenomenon existed, I explored the problem in the following way. All of the transects walked from fall, 1965, to fall, 1970, were pooled and divided into groups according to the number of rabbits flushed per transect. During this period, 115 transects were walked which contained a single rabbit ($n = 1$). Subdivision of this group according to which of the four legs contained the single rabbit produced 33, 32, 28, and 22 transects with the rabbit on leg 1, 2, 3, and 4 respectively. This is different from the expected even distribution at the 30 percent probability level (χ^2 test).

A second group of transects was then pooled on which two or more rabbits were flushed ($n > 1$), and on which (1) all but the last rabbit was seen on leg 1; and (2) the last (n^{th}) rabbit may have been flushed on any of the four legs. The frequency on legs 1, 2, 3, and 4 of the n^{th} rabbits was then compiled. This proved to be 8, 9, 9, and 9 respectively on the 35 transects involved. This distribution is not statistically different ($\chi^2 = 1.30$) from the expected frequency distribution of 10.05, 9.73, 8.51, and 6.69 determined from the distribution of rabbits on transect legs observed on 1-rabbit transects. The rationale for this test is that the n^{th} rabbits should have the same relative distribution as the single rabbits on 1-rabbit transects. If a rabbit flushed on leg 1 runs to another leg and is subsequently flushed, the distribution of the n^{th} rabbits should be different from that of the single rabbits. The fact that it does not differ, while not confirming that duplicate flushes did not occur, does not provide any evidence that they did.

The distribution of 885 rabbits observed over transect legs 1, 2, 3, and 4 for all transects pooled was 233, 245, 240, and 167 respectively. This is significantly different at the 0.5 percent probability level ($\chi^2 = 18.06$) from an expected even distribution.

The reason for this uneven distribution and the decline in rate of rabbits observed on successive legs on the 1-rabbit transects (above) is not known. It may stem from a tendency for rabbits to hear the observer on the first part of the transect and to sneak away unseen from the latter legs. Or, it could stem from observer fatigue and decline in alertness as he walks the transect. Whatever the reason, it is a potential source of error, but one on which I have no evidence for variation with population density. The rabbit distribution by legs (46, 53, 49, and 32 on leg 1, 2, 3, and 4 respectively) obtained by one observer during the period fall, 1965, to fall, 1968, when densities were relatively low, and that obtained by a second observer (187, 192, 191, and 135 on leg 1, 2, 3, and 4 respectively) in 1969-70 when densities were higher, were compared and found to be nearly the same ($\chi^2 = 0.5$).

Analytical interpretation of transect data

Two basic census procedures were explored for a means of correcting the line-census data for the existing biases discussed above: (1) use of the distribution of observed lateral distances; and (2) use of the observed flushing distances.

Method based on the distribution of lateral distances. Eberhardt (1968) has suggested the use of a continuous "sighting probability" function $\gamma(x)$ which defines the probability of sighting an animal that exists in the field as a function of x, the lateral distance of the animal from the transect line. An example of a sighting probability curve is shown in Figure 8. Presumably the shape of the curve is assumed and then tested against actual field data. It can be tested, since the form chosen for $\gamma(x)$ should be the same as the distribution of observed lateral distances.

If W is defined as one unit of distance, then the area under the curve, A_x, found by integrating $\gamma(x)$ from 0-1, represents the proportion of animals seen on the transects, while the shaded area (Figure 8) represents the proportion not seen. The total area under the horizontal, dashed line equals 1.0, and if n is the number of animals observed, then $\frac{1}{A_x}$ n equals the estimated number of animals present in an area with width equal to W and length equal to the length of the transect. The form of $\gamma(x)$ is all important; once it is selected, n is the only factor that is measured during a census. The density estimate is independent of the actual lateral distances of the observed animals.

If, as Eberhardt assumed, the probability of seeing an animal at or near the transect line is 1.0, and this probability decreases to 0.0 at some distance, W, then $\gamma(x)$ can be replaced by a frequency of sighting function, f(x). In practice, frequency of sighting as a function of lateral distance is not a continuous function; the function must be determined empirically from a histogram of the observed data with intervals of some finite size (Figure 9).

Eberhardt (personal communications) questions how one knows what proportion of the animals in the first interval are actually seen. If the width of an interval is reduced to the point where one is

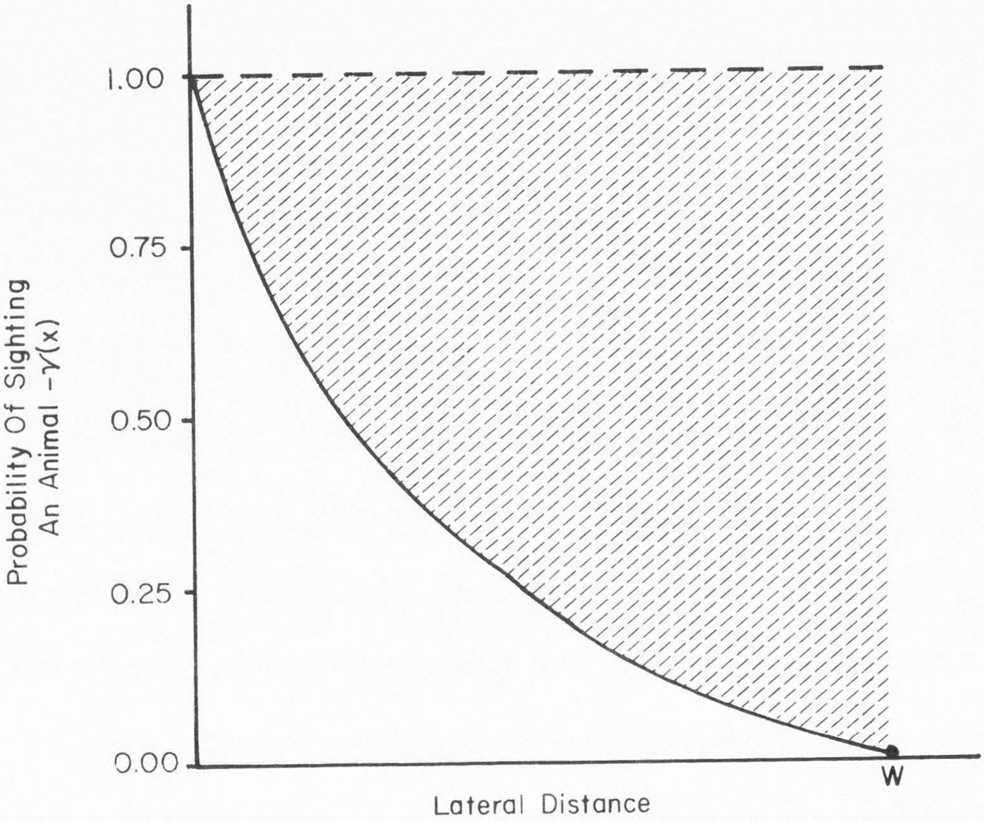


Figure 8. An example of a sighting probability curve. The sighting probability function, $\gamma(x)$, defines the probability of sighting an animal that exists in the field as a function of x, the lateral distance of the animal from the transect line.

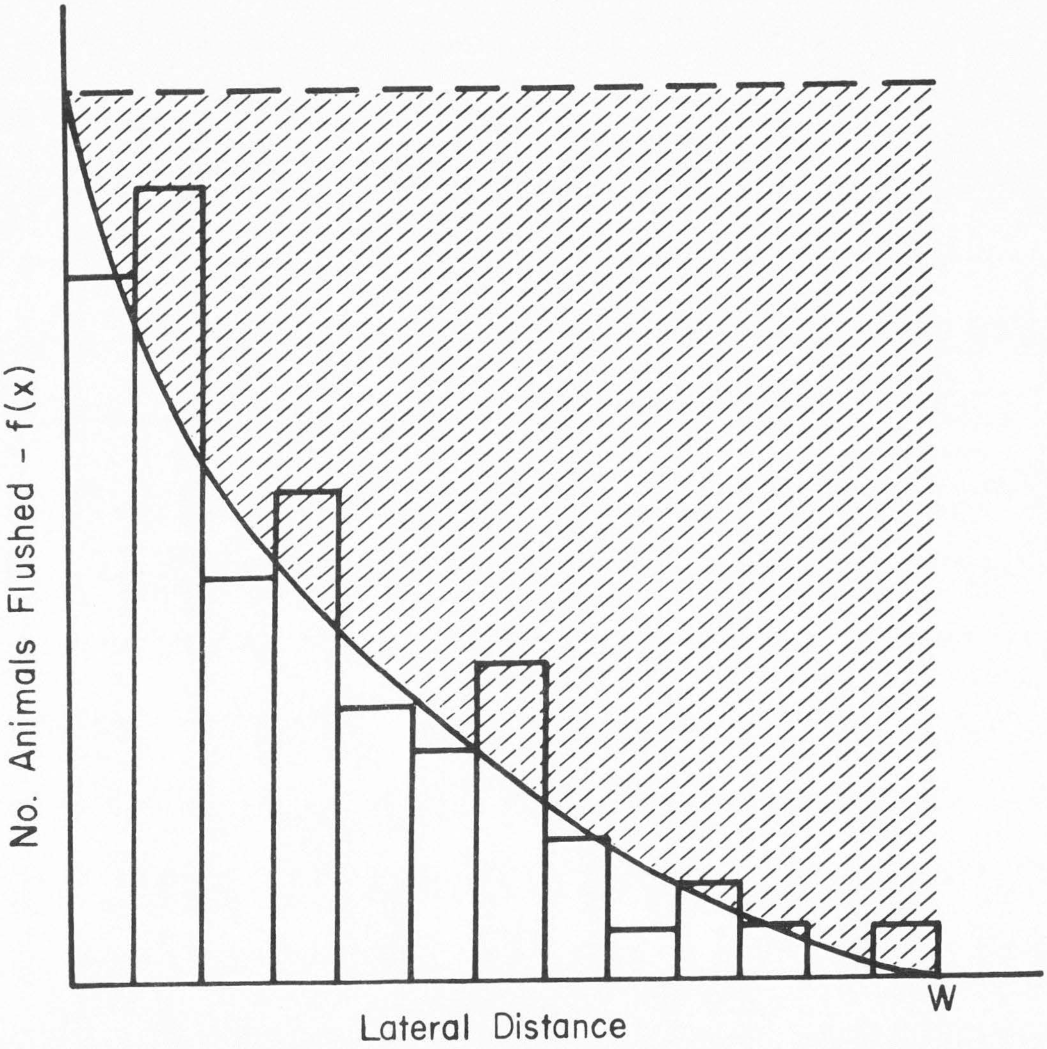


Figure 9. An example of a histogram of observed lateral distances. The continuous line is a frequency of sighting curve and is determined empirically from the data shown in the histogram.

virtually assured of seeing all the animals in the first interval, then he suspects that the sample size will generally be small and the sampling error large. However, if the method is to be used as an index to density and the proportion in the first strip that is missed remains constant, this is no longer an objection.

The above procedure of empirically determining f(x) from a histogram of the observed lateral distances was used by Anderson and Pospahala (1970). After determining f(x) they integrated to obtain the area under the curve, A_x, as did Eberhardt with $\gamma(x)$. To obtain a population estimate for the area, they used the equation:

$$\frac{A_T}{A_x}\, n = \text{population estimate} \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (1)$$

where A_T equals the area below the horizontal dashed line, and n equals the number of animals observed.

However, equation (1) appears to me to be a <u>non sequitur</u>. The distribution, f(x), represents the best, continuous fit to the histogram which contains sampling error. Since f(x) is the best estimate of the frequency distribution, the area under f(x) and not n would seem to be the best estimate of the number of animals to be seen under ideal conditions. Equation (1) in my opinion should be:

$$\frac{A_T}{A_x}\, A_x = A_T = \text{total population of area} \; . \; . \; . \; (2)$$

The population of the censused area can then be obtained by determining A_T from W and from the intercept of f(x) with the frequency axis. Equation (2) eliminates the need for integrating f(x) since A_x cancels out of the equation.

Animal numbers per unit area (density) rather than total population of the censused area is the parameter of interest. Density is independent of W and depends only on the intercept of f(x) with the frequency axis. Therefore, the form of f(x) is unimportant except at x = 0.0, and the problem then reduces to finding the intercept. This can be accomplished simply by inspection of the data, which is essentially the method of Kelker (1945), or by mathematically fitting a curve, f(x), to the data as in Figure 9 and evaluating f(x) at x = 0.0.

Method based on flushing distances. Equations for estimating population density based on observed flushing distances--specifically those of King (cf. Leopold, 1933:151), Hayne (1949), Gates *et al.* (1968), and Gates (1969), are of the form $\hat{D} = n/2LW$ (Gates *et al.*, 1968). $\hat{D}$ is the estimated absolute density, n is the number of animals observed, and L is the length of transect walked. W is the only factor that varies between equations of the above authors and is an estimate of the effective width of the transect.

Results of the computer simulations of Gates *et al.* (1968) indicated the methods of Gates *et al.* and Gates were the only ones that gave unbiased estimates of absolute density. King's equation differs from the above two only by a constant and therefore provides an equally good estimate of relative density. The difference between the equations of Gates *et al.* and Gates is that W in the latter is based on the more conveniently measured flushing distances, whereas the former is based on lateral distances. Both of these methods have the advantage over other methods in that equations are provided for estimating variance of density estimates.

Gates et al. assumed the exponential function:

$$P_Y = e^{-\lambda_1 Y} \quad . \quad (3)$$

in relating the probability, P_Y, of observing an animal as a function of lateral distance, Y, where λ_1 is some unknown constant. Using this function they derived an expression for the probability, P, of observing an animal, given that it is in the census area:

$$P = 2L/\lambda_1 A \quad . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \quad (4)$$

where L is the length of the transect and A is the area censused.

To get λ_1 in terms of flushing distance instead of lateral distance, Gates assumed that the probability-density function of flushing distances, r, given Y is:

$$f(r/Y) = \lambda_2 e^{-\lambda_2 (r-Y)} \quad . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \quad (5)$$

Using equations (4) and (5) and letting $\lambda_1 = \lambda_2 = \lambda$, Gates derived a joint density function of flushing distances and the number of observed animals, n. With this function he was able to obtain the following maximum-likelihood estimators:

$$\hat{\lambda} = (2n-1)/\Sigma r \quad . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \quad (6)$$

and

$$\hat{N} = n/\hat{P} \quad . \quad (7)$$

where $\hat{P} = 2L/A\hat{\lambda}$. An estimate of the variance of $\hat{N}$ as derived by Gates is:

$$V(\hat{N}) = n/\hat{P} \ [\frac{3n - 2}{2(n-1)\hat{P}} - 1] \quad . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \quad (8)$$

The variance of $\hat{N}$ estimated by Equation (8) is that found on a single transect and is due to variance in $\hat{\lambda}$ and the number, n, of animals observed.

Gates showed that if $\lambda_1 = \lambda_2$, the flushing angles will have a cosine frequency distribution with a mean of 32.7°. This is the same result Hayne (1949) obtained using the assumption that each animal has a particular flushing distance which is independent of the observer's angle of approach. Figure 5 shows the observed frequency distributions of flushing angles and the expected cosine distributions when $\lambda_1 = \lambda_2$. The 1966-68 (obtained by one observer, A) and the 1969-70 (obtained by a second observer, B) flushing-angle frequency distributions were found to be significantly different from a cosine distribution at the 5 percent and 0.1 percent levels, respectively (Kolmogorov-Smirnov test). The mean flushing angles in the 1966-68 period and in the 1969-70 period were 30.0° and 21.8° respectively.

It might be concluded, then, that λ_1 did not equal λ_2. If the census method is used only as an index, this inequality is not important since there will be a constant bias as long as the ratio of λ_1 to λ_2 remains constant. Apparently the ratio did not remain constant. The fit of P_Y, Equation (3), to the observed results (Figure 10 and 11), where the λ's were calculated from Equation (6) with 1966-68 pooled data and 1969-70 pooled data, was better in 1966-68 than in 1969-70. The 1966-68 distribution of lateral distances was not significantly different from the expected distribution, P_Y, at the 20 percent level, whereas, the 1969-70 distribution was different at the 1 percent probability level (Kolmogorov-Smirnov test).

It appears to me from looking at the distributions of flushing distances (Figure 12) during the two periods and referring back to Figures 10 and 11 and Equations (3) and (5) that λ_1 in Equation (3) increased and λ_2 in Equation (5) decreased between the two periods.

A remaining problem is to determine the cause of these observed differences and the subsequent necessary modification, if any, of $\hat{\lambda}$ in Equation (6) to correct for them. All the observed differences can be accounted for if the angular distribution of observation time changed between observers so that observer B spent more time observing at small angles and less time at the larger angles than did observer A. Since the expected angular frequency of sighting is a cosine distribution, observer B, spending more time observing at small angles, would be expected to see more rabbits with a subsequent smaller mean flushing angle than observer A under like conditions.

The rabbits observer B saw would also probably have relatively larger flushing distances for two reasons: (1) Rabbits seen by observer A at large angles will have relatively short flushing distances (the mean flushing distances between 0°-30° and between 60°-90° were 28.5 and 12.7 yards respectively) since rabbits apparently do not flush, or at least are not readily seen, at large lateral distances. (2) The proportion of rabbits flushing at small angles that would be seen by observer B but missed by observer A is not independent of flushing distance; it is likely that the more distant rabbits are most easily missed by observer A. This might be inferred from the two distributions in Figure 12. The above two reasons likely account for some unknown part of the observed positive correlation of flushing distance with density (Figure 3).

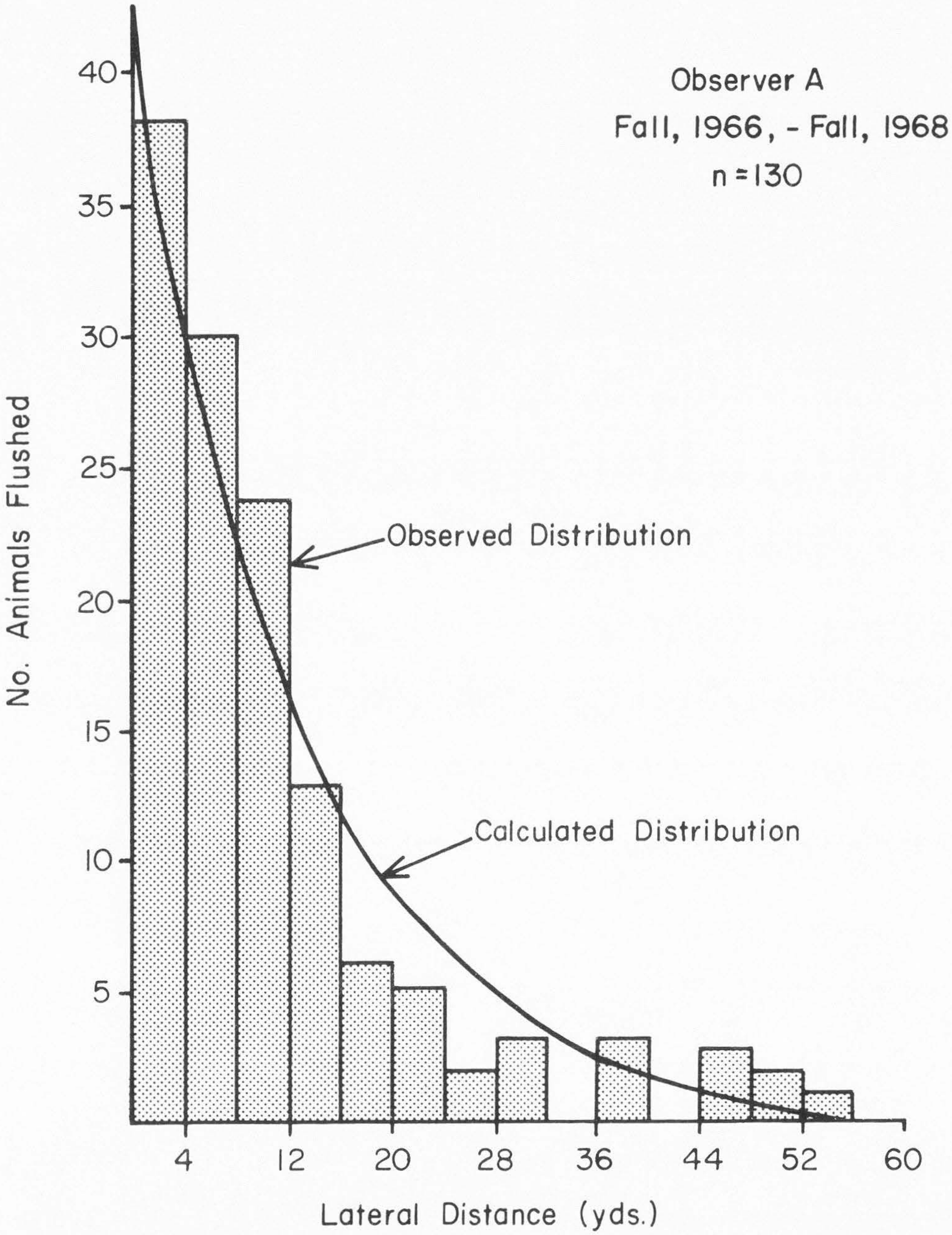


Figure 10. Histogram of observed lateral distances from transects walked in fall, 1966, to fall, 1968. The solid line is the theoretical probability of observing an animal as a function of lateral distance.

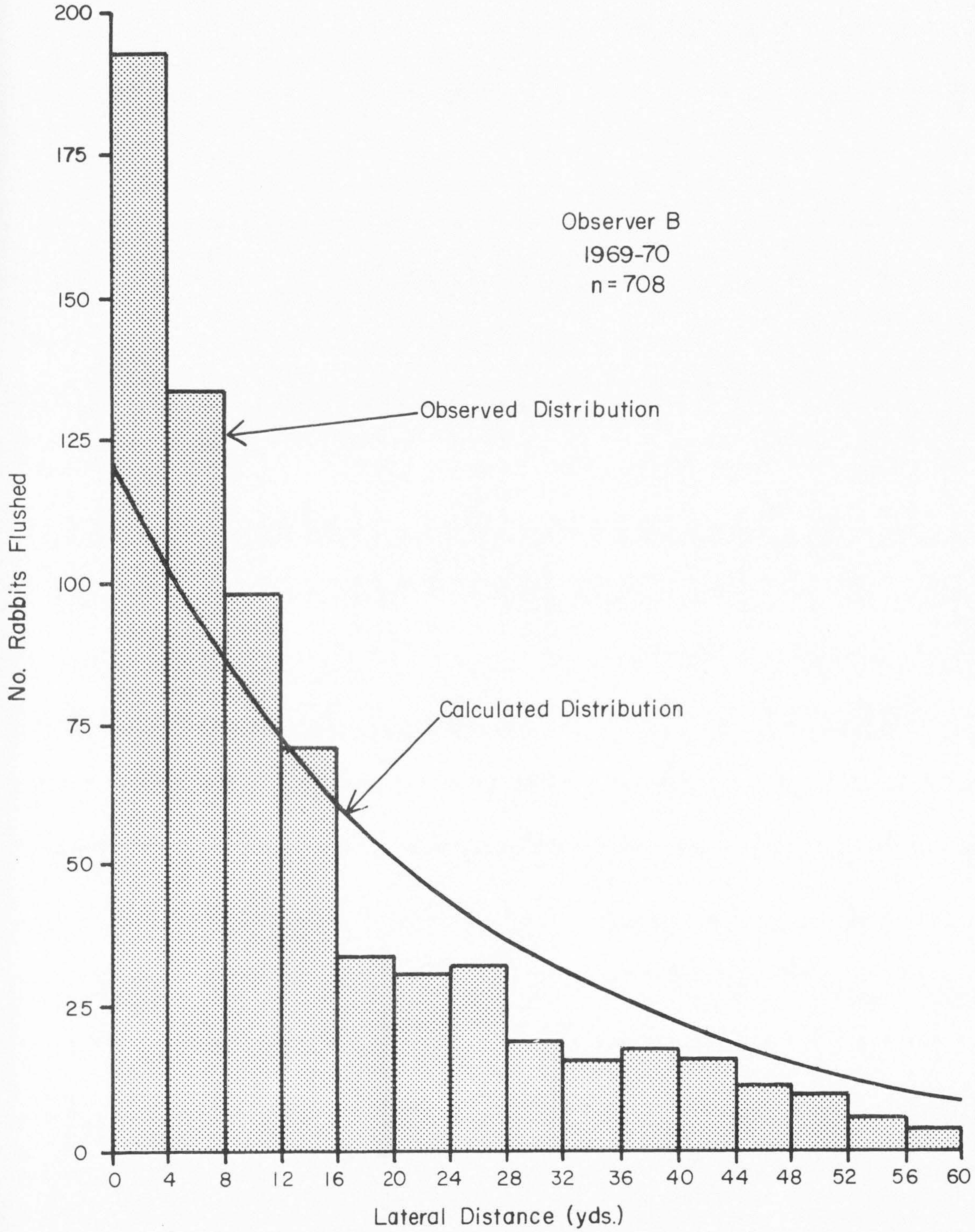


Figure 11. Histogram of observed lateral distances from transects walked in 1969-70. The solid line is the theoretical probability of observing an animal as a function of lateral distance.

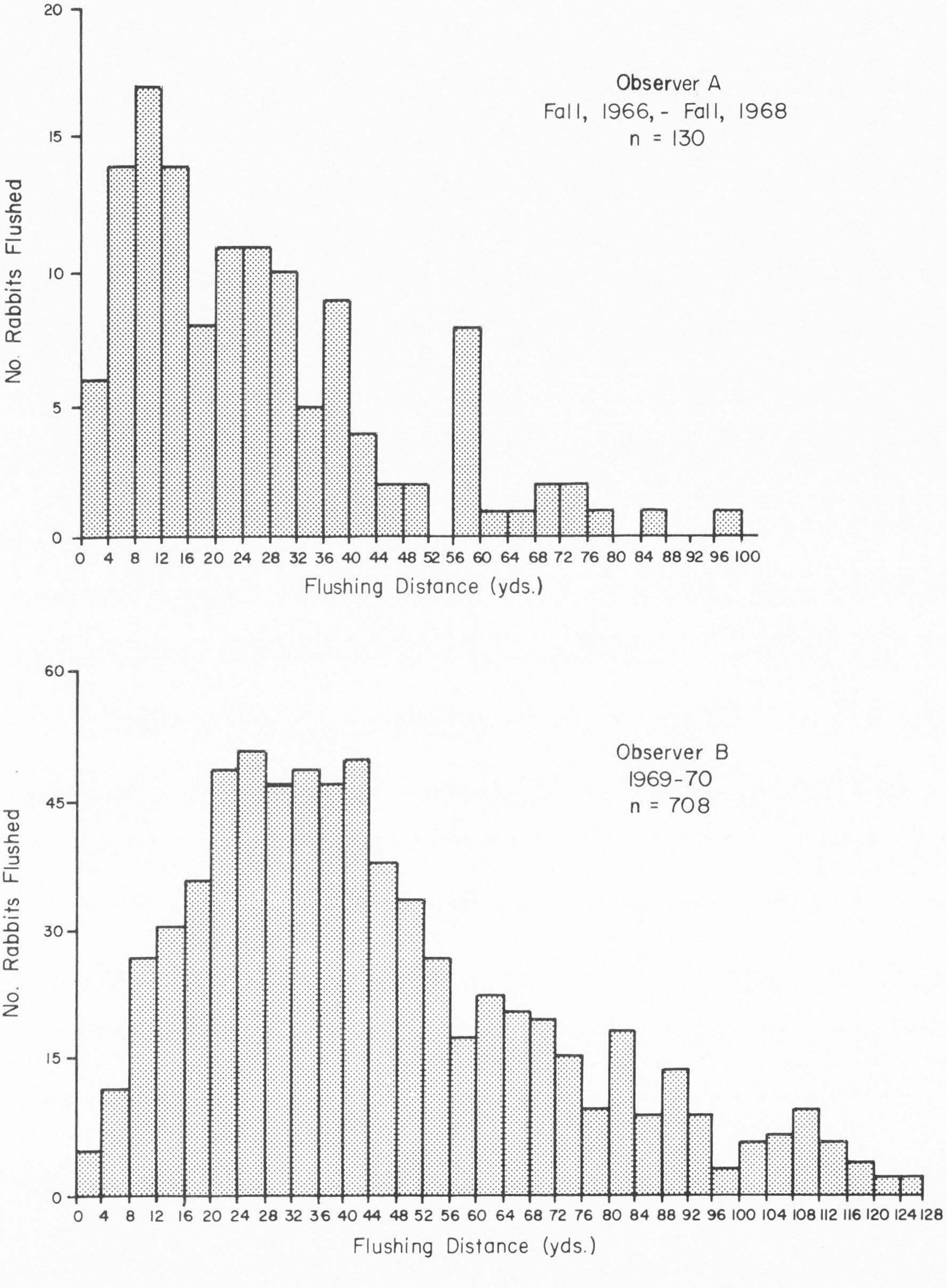


Figure 12. Observed distribution of flushing distances from transects walked in fall, 1966, to fall, 1968, and in 1969-70.

There are a number of possible explanations for the observed differences in the distributions of flushing distances and in the ratio of λ_1 to λ_2 between census periods covered by the two observers. In addition to variation between observers, these differences may have resulted from changes in rabbit behavior as a function of the observer's angle of approach. (A simple increase in flushing distance of all rabbits independent of the observer's angle of approach will not influence the ratio of λ_1 to λ_2.) Therefore, observer behavior and animal behavior are confounding factors. Because of the results shown in Figure 7, I think that observer bias had an important effect. On the other hand because of fall, 1970, census results, there is little question that the rabbit's behavior had changed, at least during that census period. It appears to me from the above discussion and from reviewing the observing habits of the two observers that, with the exception of the fall, 1970, census, a simple change in the angular distribution of observation time between observers is the most likely explanation to account for most of the observed differences.

To determine if the equation for $\hat{\lambda}$ must be modified to reflect these differences, I substituted Equation (6) and $\hat{P} = 2L/A\hat{\lambda}$ into Equation (7) to obtain $\hat{N} = (2n-1)A/2L\bar{r}$ where $\bar{r}$ is the mean flushing distance. As discussed above, under like conditions both n and $\bar{r}$ obtained by observer B are likely to be larger than those obtained by observer A. In the equation for $\hat{N}$, above, n and $\bar{r}$ are off-setting terms such that an increase in n might be compensated for by an increase in $\bar{r}$. $\hat{N}$ will not change in that case and there would be no net difference between observers. This result would seem to be a reasonable approximation to the data discussed above.

I have elected to use the Gates method with $\hat{\lambda}$ computed by Equation (6) for all census periods with the exception of fall, 1970, for two reasons: (1) A method based on flushing distances seems preferable to one based on lateral distances because of the potential error the latter incurs with a change in observer (Figure 7). (2) I chose the Gates method from among the flushing-distance alternatives because it apparently gives an unbiased estimate of absolute density under ideal conditions.

The three possible biases discussed above were accounted for in the following ways: (1) Bias resulting from a spring-to-fall change in distribution of flushing distances was automatically taken care of by the Σr term in Equation (6). (2) No correction was made for differences between observers because, as a first approximation, the biases produced in n and $\bar{r}$ were considered directly proportional producing no inter-observer bias in $\hat{N}$. (3) There was no indication of any appreciable double counting. Although the observed animals were not evenly distributed over the four transect legs, the observed distribution remained constant, and therefore no correction was required in the estimates of density.

1962-70 Rabbit Density in Curlew Valley

Relative measure

Following each census period, I computed a jackrabbit density value for each transect walked using Equation (7). To obtain a value for $\hat{P}$ for use in this euqation, the observer must arbitrarily pick a value for the area censused, A, and the length of the transect, L.

For this study I used a 1-square-mile area with L equal to 1 mile. This resulted in density estimates from Equation (7) having units of "rabbits per square mile." However, there were two factors which were not consistent with assumptions underlying Equation (7): (1) I found λ_1 not equal to λ_2; and (2) there were likely some unseen rabbits sneaking out ahead of the observer. I assumed these errors were constant within observers between census periods. Because of the errors I deleted the units, rabbits per square mile, and considered all estimates computed by Equation (7) as density indexes.

Index values from the transects were handled as individual samples from which a mean density index and standard error were calculated for each census period except fall, 1970, (Table 1). Standard errors were calculated from the error mean squares obtained from an analysis of variance of the samples from each period. In order to reduce the standard error, I classed transects into four habitat types: sage brush, greasewood, shadscale, and crested wheatgrass. I considered the classes as four treatments in the analysis.

The density index (Table 1) for fall, 1970, was derived from a direct comparison with transect results of fall, 1969. As shown in the first column of Table 1, 268 rabbits were observed on the transects in fall, 1970, compared with 192 in fall, 1969. This is an increase of 1.4 times. However, when Equation (7) was applied to the transect data, a mean density estimate of 114.0 was obtained, an estimate which is 8 percent below that of fall, 1969.

Apparently the problem resulted from a change in the rabbits' flushing behavior. (The same observer collected data in both years.) The distributions of flushing distances in fall, 1969, and fall, 1970,

Table 1. Mean density index, number of transects walked and number of rabbits observed. One standard error of the density index in parentheses.

Census Date	Number of Transects	Number of Rabbits Observed	Mean Density Index
Fall, 1962	78	29	40.0 (11.1)
Spring, 1963	78	19	13.9 (3.9)
Fall, 1963	78	66	60.6 (10.9)
Spring, 1964	78	26	26.3 (6.9)
Fall, 1964	78	49	42.4 (9.9)
Spring, 1965	78	30	17.9 (7.3)
Fall, 1965	72	28	33.4 (9.4)
Spring, 1966	72	15	11.7 (3.9)
Fall, 1966	72	20	23.7 (7.8)
Spring, 1967	72	9	7.4 (2.8)
Fall, 1967	72	12	21.2 (8.6)
Spring, 1968	72	15	9.2 (3.2)
Fall, 1968	72	81	64.8 (11.5)
Spring, 1969	72	75	43.1 (9.9)
Fall, 1969	72	192	123.2 (18.9)
Spring, 1970	70	173	67.0 (9.6)
Fall, 1970	70	268	185 (28.3)
Spring, 71			
Fall,			

were different at the 1 percent probability level (Kolmogorov-Smirnov test). The mean flushing distance in fall, 1969, was 40.6 yards compared with 57.0 yards in fall, 1970. With the observed change in flushing distance, one might expect a similar increase in the distribution of lateral distances. This increase did not occur (Figure 13); in fact, λ_1 in fall, 1970, was probably slightly larger than λ_1 in fall, 1969. These results indicate that if a rabbit were destined to flush, it would have flushed sooner, on the average, in fall, 1970. But, the small difference in the distributions of lateral distance between the two census periods implies that a rabbit that would not have flushed in fall, 1969, still would not have flushed in fall, 1970.

If rabbits were flushing sooner, one would expect flushing angles on the average to be smaller. This proved to be the case; average flushing angles were 27.1° and 19.2° in fall, 1969, and fall, 1970, respectively.

One can see by inspection of Equation (7) that an increase in flushing distance (λ_2 decreases) with no subsequent increase in lateral distance will result in a disproportionately low density estimate as compared with other census periods. Therefore, I based the estimate of fall, 1970, density on two other factors: (1) Using the Kelker (1945) census method, I found an increase in fall, 1970, density over fall, 1969, of 1.6 times. (2) Gates (1969) showed that density estimates are directly related to the product of $n\lambda_1$. As I have shown above (Table 1 and Figure 13), n in fall, 1970, was 1.4 times that in fall, 1969; and λ_1 in fall, 1970, was larger if anything than in fall, 1969. The fall, 1970, density was therefore estimated to be 1.5 times (the mean of 1 and 2 above) the fall, 1969, density; i.e., $1.5 \times 123.2 = 185$.

Absolute densities

Since density indexes (Table 1) for the study area presumably

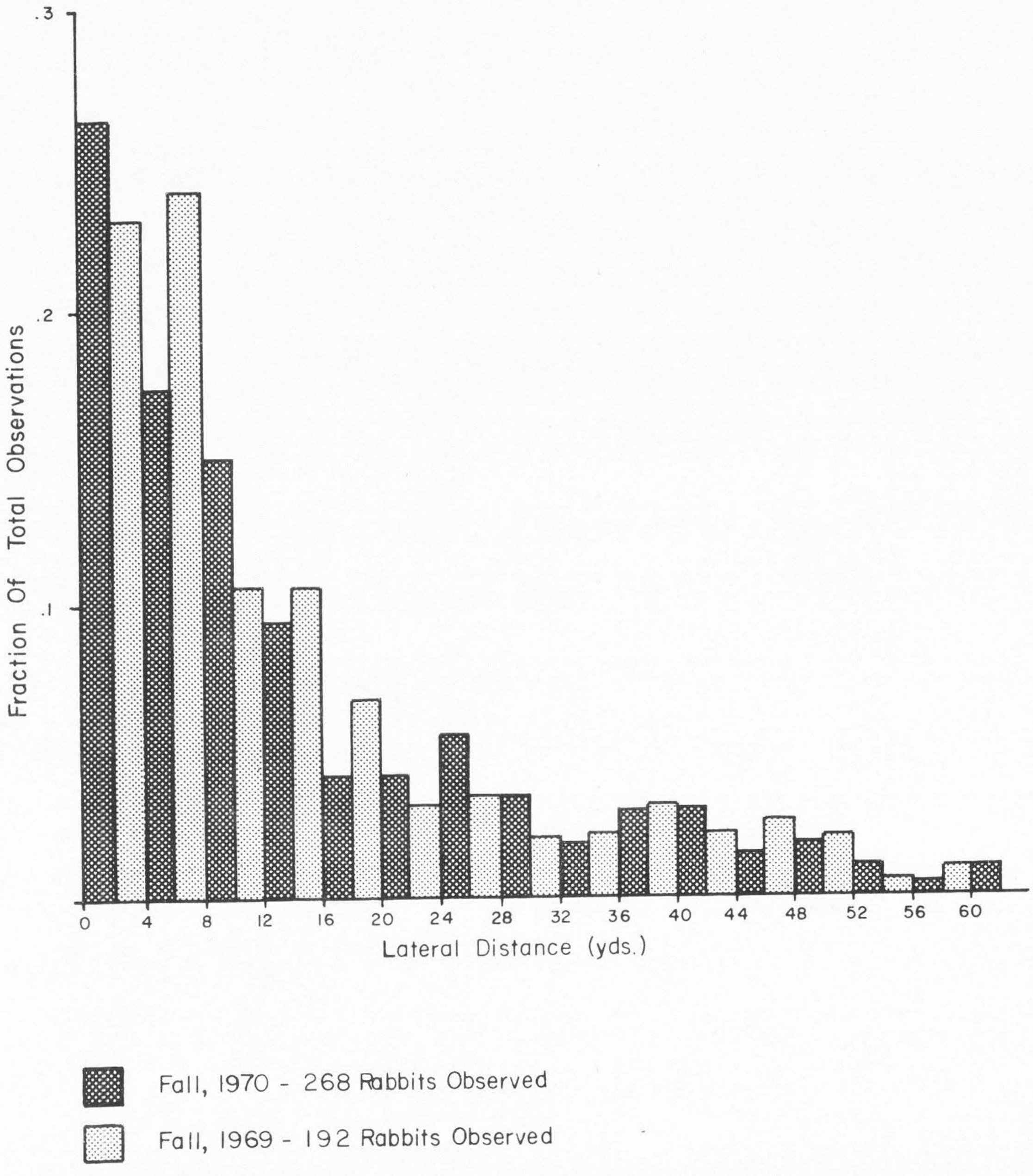


Figure 13. Relative distribution of observed lateral distances from transects walked in fall, 1969, and fall, 1970.

bore some relationship to absolute numbers, indexes could be converted to estimates of absolute density if this relationship were known. An estimate of the relationship between density indexes and absolute numbers can be obtained from a plot (Figure 14) of transect results and drive counts from the drive-count area (Table 2, Column A and B).

Because only four transects were walked in the drive-count area, the wide scatter of points in Figure 14 is likely due, in part at least, to sampling error. As a first approximation I assumed that a constant relationship existed between the indexes and absolute counts. If a regression line is to represent a constant relationship, it must be a straight line and pass through the origin. Therefore, I imposed these constraints in calculating the regression line in Figure 14.

The regression line has a slope of 0.7. One means of obtaining rough estimates of absolute density over the study area is to assume that the relationship between transects and actual numbers over the study area is the same as that observed for the drive-count area. Hence, my best estimate of the conversion or "weighting" factor by which the transect data over the study area should be multiplied to convert to estimates of absolute density, rabbits/square mile, (Table 2, Column D) is then 1.43 (1/0.7). Vegetation and other environmental factors in parts of the valley differed from those on the drive-count area. Hence, the density estimates are approximations of unknown precision.

As mentioned, the mean flushing distance during the fall, 1970, census period was markedly larger than that previously observed. With an increase in flushing distance one might expect a higher percentage of flushed rabbits to go unobserved as they sneak out ahead of the

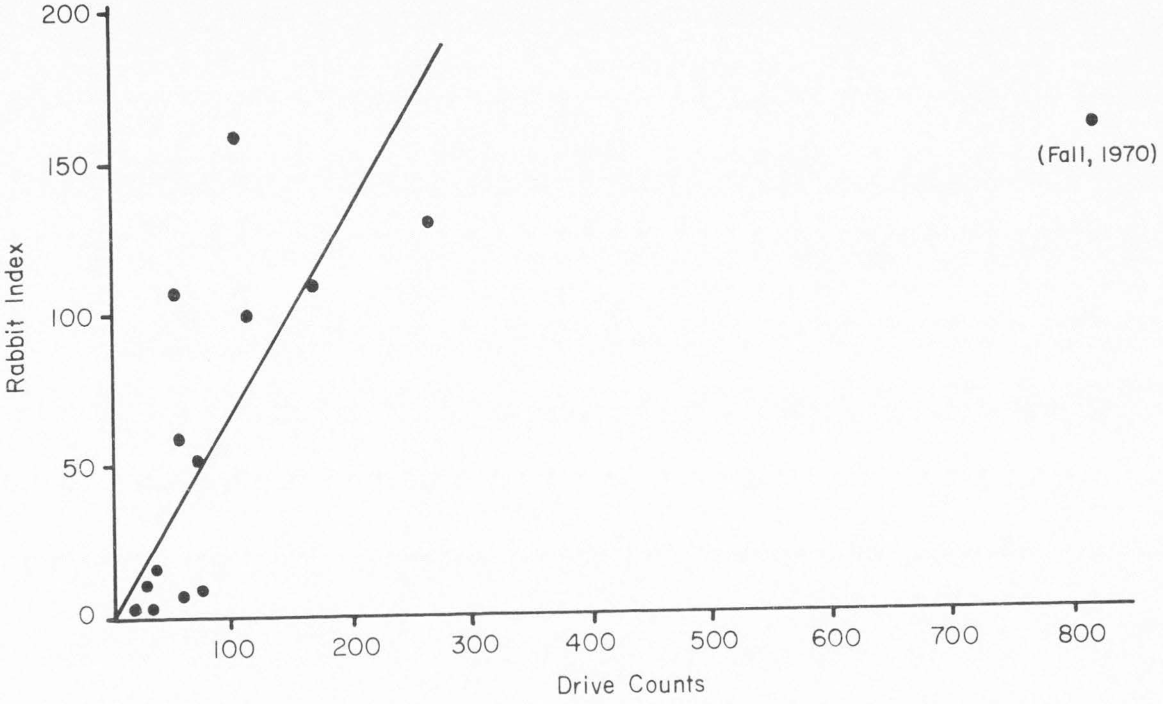


Figure 14. Linear regression (constrained to pass through the origin) of mean rabbit index from the four drive-count-area transects on drive counts from drive-count area (fall, 1970 data not included).

Table 2. Drive-counts, density index from drive-count-area transects and study-area transects, and absolute density estimates for the study area

Year	(A) Drive Count	(B) Density Index 4 Drive-count area Transects	(C) Density Index All Transects	(D) Absolute Density (rabbits/mile^2) (Cx1/0.7)
Spr., 1963	36	14.7	13.9	19.9
Fall, 1963	114	106.0	60.6	86.6
Spr., 1964	53	66.6	26.3	37.6
Fall, 1964	84	162.0	42.5	60.7
Spr., 1965	63	54.0	17.9	25.6
Fall, 1965	20	0.0	33.4	47.7
Spr., 1966	36	0.0	11.7	16.7
Fall, 1966	73	11.6	23.7	33.9
Spr., 1967	30	13.8	7.4	10.6
Fall, 1967	51	117.3	21.2	30.3
Spr., 1968	54	7.6	9.2	13.2
Fall, 1968	167	120.4	64.8	92.6
Spr., 1969	254	127.6	43.2	61.7
Fall, 1969	a		123.2	176.0
Spr., 1970	a		67.0	96.0
Fall, 1970	816	160.0	185.0	264.0

[a] A drive-count was not made during census period.

observer at some distance. This would bias transect results relative to other years and produce a deviation from the trend of previous years consistent with the observed deviation of the fall, 1970, point (Figure 14). On the other hand, the observed deviation in trend might be due simply to sampling error.

Since I do not know the cause of the fall, 1970, deviation and since I have only one point to support the possibility that a real change in trend occurred, I have not included the fall, 1970, point in the calculation of the regression line. If a real change in the relationship between transect results and absolute density did occur, fall, 1970, transect results may underestimate density relative to previous years.

Since precision of the weighting factor calculated above is likely poor, I used index values (Table 2, Column C) rather than absolute density estimates in calculating seasonal and annual rates of population change and in calculating reproductive and mortality rates in order not to give any implication that the absolute density estimates are precise to a known degree.

Fall absolute density estimates (Table 2, Column D) ranged from 30 rabbits per square mile in 1967 to 264 per square mile in 1970. The range of values is, in general, low compared with other jackrabbit densities reported in the literature. Vorhies and Taylor (1933) estimated 320 jackrabbits per square mile in southern Arizona. Wooster (1939) and Tiemeier (1956) estimated 190 and 250 per square mile respectively in Kansas. Lechleitner (1958) reported about 700 rabbits per square mile in California.

Natality Rate

General considerations

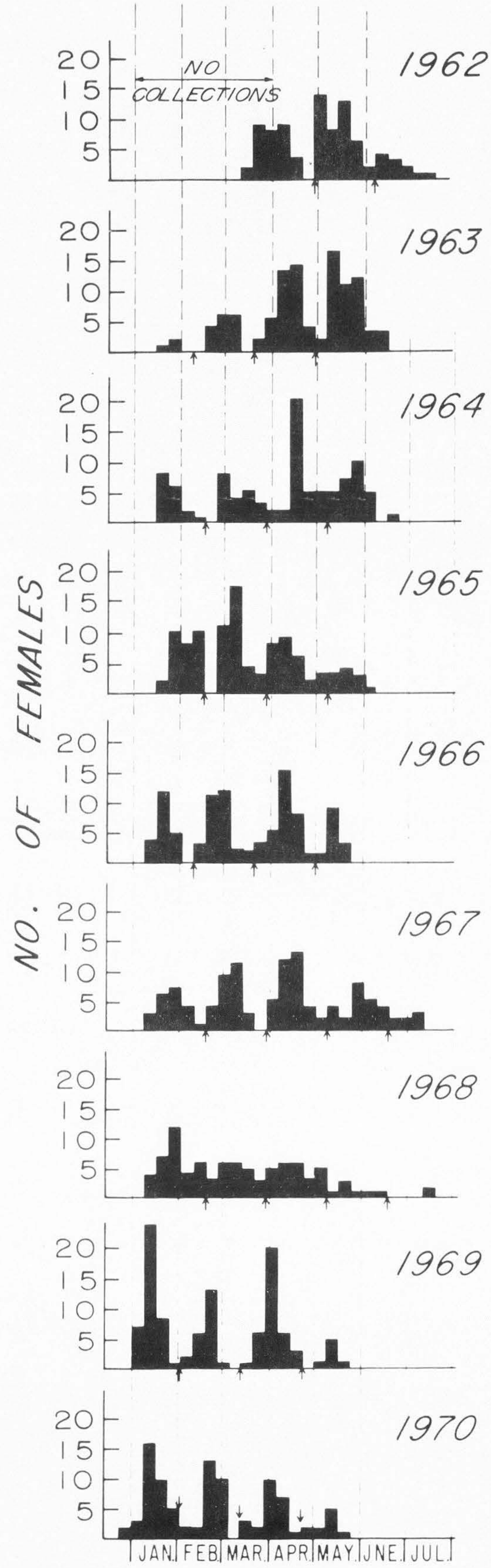
The level of sophistication and precision in a demographic study or a predictive model for jackrabbits will be enhanced by identifying and measuring the variability in as many facets of the animals' demography as possible. Since the rate at which a female ovulates and the subsequent implantation and fetal survival rates may be influenced by somewhat different factors, these rates may vary independently to some degree. Hence, I chose to analyze separately ovulation rates as shown by corpus-luteum counts and number of young carried to parturition by pregnant females.

Demographers have recognized some degree of option in applying the term "natality" to the several stages of the reproductive process. This option merits particular consideration when reproductive events in mammals and birds are compared. For my purposes here, I elected to apply the term to the number of eggs ovulated. I assumed, as is commonly done, that all such eggs were fertilized, so that the ovulation rate and the number of zygotes carried by recently bred females were equivalent.

Conception

Conception periods. Conception dates for all visibly pregnant adult females were plotted on a histogram at 8-day intervals (Figure 15). In five of the nine years represented (1963, 1966, 1967, 1969, and 1970) the distributions show a distinct four-mode pattern indicating synchronous breeding. In two of the nine (1964 and 1965) some tendency toward synchrony, with apparently four peaks, seems reasonably evident in the curves. Only in 1968 does there appear to be little or no synchrony. Collections did not begin until April in 1962; hence the pattern for the entire season cannot be evaluated.

In the most clearly synchronous years, the peaks were approximately 40 days apart. The mean gestation period in captive


NO. OF FEMALES
1962
NO COLLECTIONS
1963
1964
1965
1966
1967
1968
1969
1970
20
15
10
5
JAN.
FEB.
MAR.
APR.
MAY.
JNE.
JUL.

black-tailed jackrabbits reported by Haskell and Reynolds (1947) was 43 days.

I interpreted these results as indicating a relatively well synchronized initiation of breeding at the beginning of each breeding season in Curlew Valley, with each successive conception immediately following parturition of the previous litter. Lechleitner (1959) reported postpartum estrus with subsequent conception in the black-tailed jackrabbit. Synchronized conception has been found in other hare populations by Newson (1964), Bookhout (1965), Dodd (1965), and Meslow and Keith (1968) for the showshoe hare (_Lepus americanus_) and by James and Seabloom (1969) for the white-tailed jackrabbit (_Lepus townsendii_).

Four conception periods occurred each year, with a tendency toward a fifth in some years (1967, 1968, and possibly 1962). Accordingly, for purposes of estimating total natality, I subdivided the breeding seasons of the five, clearly synchronous years into four or five conception periods (separated by arrows in Figure 15). In 1964, 1965, and 1968, when the synchrony was not so pronounced and peaks not easily separated, I arbitrarily subdivided the seasons into 40-day periods which coincided as clearly as I could determine with what evidence of synchrony existed.

Conception rates. I defined the conception rate as the percentage of females conceiving in any given conception period. In order to calculate the rates for each conception period, I determined the percentage of females that had conceived, using all females collected on dates appropriate for indicating conception, or the absence thereof, during any given conception period. Data collected in 1969, a highly synchronous breeding year, can be used to demonstrate these calculations.

In the first 1969 collection, made in late January, 25 of 28 females were visibly pregnant; three had not conceived. The February collection, made during the peak of the second conception period, contained 35 females of which 14 were still in the late stages of pregnancy with the first litter. Of 14 recently postpartum females, 9 had new corpora lutea but no visible fetuses indicating that they were in the first 7 days postconception. Seven females were visibly pregnant with litters conceived during the second conception period.

Two females in the February collection had relatively small, nonparous uteri without striations, and no corpora lutea. These two females--6 percent of the February collection--either did not breed during the first conception period or had lost their litters *in toto* early in pregnancy. The former is the more likely since no corpora albicantia were found. Accordingly, I estimated a 94-percent conception rate for the first conception period in 1969. Although 10 percent of the January collection had not conceived, first-litter conception was still possible for these females, and hence an estimate of 94 percent is preferable to one of 90 percent.

All 15 females in the March collection were visibly pregnant with litters conceived during the second conception period. I accordingly infered a conception rate for the second conception period of 100 percent.

In the late April collection, 36 of 37 females were visibly pregnant with litters conceived during the third conception period.

The other female was postpartum but had recently conceived, also in the third conception period. I inferred a 100-percent conception rate for this period.

The next collection was made on June 4. Of the 25 females collected, 17 had apparently stopped breeding. Their uteri and ovaries were small with no visible corpora. Two females (8 percent) were classed as being pseudo-pregnant, a condition often following loss of entire litters. The remaining six females (24 percent) were visibly pregnant with litters conceived during the fourth conception period. A subsequent collection was made on June 17. Of the 19 adult females collected, two were in late stages of pregnancy, three were recently postpartum; the combined five constituted 26 percent of the sample. Since any pseudo-pregnancies from earlier in the month would no longer be evident in this latter collection, I based my calculation on the June 4 females and concluded that 32 percent (8 + 24) conceived in the fourth conception period. The 26 percent for the later collection is in accord with the June 4 collection under the assumption that the difference is due to absence of a small fraction of pseudo-pregnant females no longer detectable.

In this manner, I calculated 1969 conception rates of 94, 100, 100, and 32 percent for the four conception periods. Since females were dying during the breeding season, it does not follow that the total adult female population alive at the beginning of the breeding season conceived at the above four rates.

Conception rates were calculated for all conception periods for all years in the same manner as shown for 1969 (Table 3). The fact that synchrony was poor in some years--actually indiscernable only in

Table 3. Yearly mean percentage of females conceiving, number of females sampled, and 95 percent confidence intervals for each litter conceived, and mean number of litters conceived per female surviving the breeding season

	Litter Number															
	1			2			3			4			5			
Year	No.	%	95% Conf. Interval	No.	%	95% Conf. Interval	No.	%	95% Conf. Interval	No.	%	95% Conf. Interval	No.	%	95% Conf. Interval	Mean No. Litters per ♀[a]
1962	No collections			No collections			36	100	89-100	34	100	89-100	22	32	14-55	Incomplete Data
1963	24	13	3-33	21	95	75-100	37	100	89-100	47	70	55-82	12	0	-----	2.8
1964	22	100	83-100	21	100	83-100	30	100	88-100	30	100	88-100	18	0	-----	4.0
1965	25	100	85-100	36	100	89-100	24	100	85-100	30	50	31-69	15	0	-----	3.5
1966	21	100	83-100	24	100	85-100	26	100	85-100	38	37	22-54	12	0	-----	3.4
1967	25	100	85-100	28	100	86-100	25	100	85-100	27	100	86-100	17	29	10-57	4.3
1968	26	100	85-100	23	100	84-100	28	100	86-100	8	100	67-100	5	40	5-85	4.4
1969	35	94	80-99	15	100	78-100	36	100	89-100	25	32	14-54	17	0	-----	3.3
1970	27	96	80-100	29	100	86-100	26	100	85-100	18	45	22-70	10	0	-----	3.4
Unweighted Means		88	81-93[b]	--	99	97-100[b]	--	100	99-100[b]	--	70	63-75[b]	--	11	6-19[b]	3.6

[a] Σ% ♀♀ Conceiving/100.

[b] Based on all females, 1962-1970.

1968--did not seriously influence the calculations, in my opinion. Lack of synchrony during a breeding season apparently does not indicate poor breeding success since my estimates for the number of ova produced per female surviving the breeding season (see Table 5 below) was largest in 1968. This large estimate is probably not an artifact of the poor synchrony since most of the juveniles calculated to have been born were actually found, from the fall census, to exist (see below).

Two influences could conceivably upset synchrony: (1) time lapses between parturition and subsequent conception that varied between individuals; and (2) intra-uterine loss of total litters which placed some individuals out of phase. The first of these seems unlikely to me. With the exception of rabbits at the end of the season, and one in the second conception period of 1963, no females were collected after the first conception period which were not pregnant or very recently postpartum. If the reproductive pattern in the jackrabbit is the same as in the European rabbit (Brambell, 1944), there is a 12-hour period between copulation and ovulation which might account for the few rabbits observed which were recently postpartum but not yet pregnant. There does not appear to be any time lapse between litters once the season is well underway.

The second alternative seems more probable. The data indicate some prenatal loss of first and last litters. The events following loss of the first litter appear to me to parallel those described for the European rabbit by Brambell (1944) and for the domestic rabbit by Hughes and Myers (1966). If the European rabbit aborts in the first week or so of pregnancy, the animal will go into a state of pseudo-pregnancy for about one-half the normal gestation period, then it breeds again. Domestic rabbits bred by sterile bucks also wait for about one-half the normal gestation period before they breed again.

In either event, the rabbits will be about 2-3 weeks out of phase with the synchronous portion of the population. The important point for my calculation of conception rates, however, is that I have used arbitrary conception periods of 40 days, or approximately 6 weeks. Hence, a female can lose synchrony but still conceive a viable litter within each conception period. Therefore, asynchronous breeding likely does not seriously impair the calculation of conception rates.

Two final points bear mention in this section. The first relates to loss of first litters, as may occur in the years of low synchrony, and its effect on the total number of conceptions of which a female is capable. Except for 1963, any variation in breeding intensity seems to have taken place at the end of the season. The potential number of litters a female can produce might depend on the period of time between early conception in the first period and some terminal date in May or early June when breeding in the population ceases. A female which began early and remained on a 40-day cycle thereafter might reach the time for conceiving the fourth litter in advance of such a terminal date. A female which conceived early, lost her first litter, and conceived a first litter again some 3 weeks later might then arrive at the date in her cycle for the fourth litter some time beyond the terminal data. She might then not conceive for a fourth time. Success of the first litter, then, could conceivably influence the total number of conceptions experienced by a female surviving the breeding season.

This is speculative, but it seems worthy of note at this point because it bears on the question of the maximum possible reproductive rate for the species is this locale, and the influences which reduce that maximum. Seemingly, the only alternative hypothesis to the one outlined is that a female somehow has the potential for producing four litters in a season, almost irrespective of the success of the first attempt.

The second point deals with the decline in number of females in Table 3 at the end of the season, and in some cases throughout the season. The decline is due to an increasing number of juveniles which dilute the samples.

Ovulation rates

I defined the ovulation rate as the mean number of ova shed *per ovulating female* in any given conception period. I calculated mean ovulation rates (Table 4) by: (1) grouping all visibly pregnant females into their respective conception periods; and (2) determining the mean number of corpora lutea in the ovaries of females in each group.

Except for the majority of rabbits in 1963 and two in 1969 which probably did not conceive for the first litter, ovulation rates for the four or five conception periods probably closely approximate the mean number of ova shed by rabbits producing their first, second, third, fourth, and fifth litters respectively. This interpretation may be somewhat in error during those years when synchrony was poor. For example, some first-litter rabbits may have ovulated during the second conception period or third-litter rabbits may have ovulated during the second period.

Table 4. Mean number of eggs ovulated, ovulating females sampled, and standard errors of the mean for each litter conceived during the year as shown by corpus luteum counts

	Litter Number														
	1			2			3			4			5		
Year	No.	Mean No. Ova	St'd. Error	No.	Mean No. Ova	St'd. Error	No.	Mean No. Ova	St'd. Error	No.	Mean No. Ova	St'd. Error	No.	Mean No. Ova	St'd. Error
1962	No collections			No collections			31	6.8	0.2	43	5.5	0.3	11	4.7	0.7
1963	3	1.0	0.0	16	5.0	0.3	38	6.3	0.2	47	6.2	0.2	0	---	---
1964	17	2.7	0.4	20	5.3	0.3	34	6.5	0.2	28	5.7	0.5	0	---	---
1965	30	2.0	0.1	35	4.4	0.2	28	5.3	0.2	11	3.8	0.3	0	---	---
1966	21	1.6	0.1	30	4.3	0.2	32	5.8	0.2	13	3.9	0.4	0	---	---
1967	21	1.7	0.2	27	5.3	0.3	36	6.8	0.2	23	5.0	0.3	7	3.7	0.4
1968	33	1.8	0.2	23	5.8	0.3	25	6.7	0.3	7	4.9	0.3	2	2.5	0.5
1969	40	1.6	0.1	22	5.6	0.2	36	7.1	0.2	8	4.5	0.4	0	---	---
1970	36	1.8	0.1	27	5.2	0.2	23	5.9	0.2	10	3.9	0.4	0	---	---
71		1.8			3.9			5.3			4.3			-	
Unweighted Means		1.9	0.1^a	--	5.1	0.1^a	--	6.4	0.1^a	--	4.9	0.1^a	--	3.6	0.3^a

[a] Based on the pooled variances of the standard errors above.

72 2.0 4.6 4.6 – –

Ovulation rates on a per-litter basis have not previously been reported for the black-tailed jackrabbit. Pontrelli (1966) presented ovulation rates on a monthly basis, however, which show the same seasonal trend as my data; i.e., relatively low rates at the beginning of the season, higher in the middle of the season, then lower again toward the end of the season. This same trend can be deduced from Lechleitner's (1959) data, though he does not specifically state the ovulation rates observed. In both the above studies ovulation rates ranged from about one at the beginning of the season to a maximum of about four, then decreased again to about two at the end of the season. These compare with the rates I observed (Table 4) which ranged on the average from 1.9 for the first litter to a maximum of 6.4 for the third, then decreased to 4.9 for years when four littering periods were observed and 3.6 for years in which a fifth litter was attempted. These rates are not strictly comparable, however, since the rates I observed were based on a littering period and not on a monthly basis.

Total time-specific, adult natality

Mean number of ova produced per adult female in the population (Table 5) was calculated for each conception period by multiplying the ovulation rate for each period (Table 4) by the respective proportion of females conceiving (Table 3). Annual production of ova per female surviving the breeding season was then estimated for each year by summing the production over the four or five conception periods for that year (Table 5). The mean annual production over the 8 years for which I have complete data was 16.6 ova per surviving female.

Table 5. Mean number of eggs ovulated per female in the population for each litter, and total number ovulated per female surviving the breeding season

	Litter Number										Total Ova per ♀ per year[b]	
	1		2		3		4		5			
Year	Mean Ova/ [a]	St'd. Error	Mean Ova/ [a]	St'd. Error	Mean Ova/ [a]	St'd. Error	Mean Ova/ [a]	St'd. Error	Mean Ova/ [a]	St'd. Error	No. Ova	St'd. Error
1962	No collection		No collection		6.8	0.2	5.5	0.3	1.5	0.5	Data not complete	
1963	0.1	0.1	4.8	0.4	6.3	0.2	4.4	0.4	0.0	---	15.6	0.6
1964	2.7	0.4	5.3	0.3	6.5	0.2	5.7	0.5	0.0	---	20.2	0.7
1965	2.0	0.1	4.4	0.2	5.3	0.2	2.1	0.4	0.0	---	13.8	0.5
1966	1.6	0.1	4.3	0.2	5.8	0.2	1.4	0.4	0.0	---	13.1	0.5
1967	1.7	0.2	5.3	0.3	6.8	0.2	5.0	0.3	1.1	0.4	19.9	0.6
1968	1.8	0.2	5.8	0.3	6.7	0.3	4.9	0.3	1.0	0.6	20.2	0.8
1969	1.5	0.1	5.6	0.2	7.1	0.2	1.4	0.5	0.0	---	15.6	0.6
1970	1.7	0.1	5.2	0.2	5.9	0.2	1.8	0.5	0.0	---	14.6	0.6
71	1.8		3.9		5.3		2.4		-			
Unweighted Means	1.6	0.1[c]	5.1	0.1[c]	6.4	0.1[c]	3.6	0.1[c]	0.4	0.1[c]	16.6	0.2[c]

---

[a] Mean number of ova (Table 4) multiplied by percentage of females conceiving (Table 3).

[b] Sum of mean number of ova per female over all litters.

[c] Based on the pooled variances of the standard errors above.

72 2.0 4.6 1.5 — —

Breeding by juvenile females

Breeding by juvenile females was observed in every year of the study except 1965 and 1969. Dates on which all pregnant juveniles in my collections conceived are presented in a histogram at 8-day intervals (Figure 16). Eye-lens weights and body weights of pregnant juveniles indicated, with the exception of one rabbit in 1967, that juveniles which conceived during the year of their birth were themselves conceived in the first adult conception period of the year. The one exception was conceived during the second conception period.

Since only first-litter juveniles bred (with the exception mentioned), juvenile conception rates were based on first-litter juveniles only. I defined juvenile conception rate as the percentage of first-litter juvenile females surviving to the end of the juvenile breeding season, that bred during the year of their birth. Ideally, this rate could be estimated from a single collection taken at the end of the breeding season by dividing the number of maternal, first-litter juveniles (as determined by the presence of corpora albicantia or uterine striations) by the total number of first-litter, juvenile females in the collection. However, by the end of the breeding season, usually July, I could not separate first-litter juveniles from the much more numerous second-litter juveniles with any degree of reliability because of the eye-lens aging technique used prior to 1969 (previously discussed).

I, therefore, made my estimates of juvenile conception rates from the June collections. There were some second-litter juveniles in the June collections, but they were usually much smaller during this month than first-litter juveniles and could be quite accurately

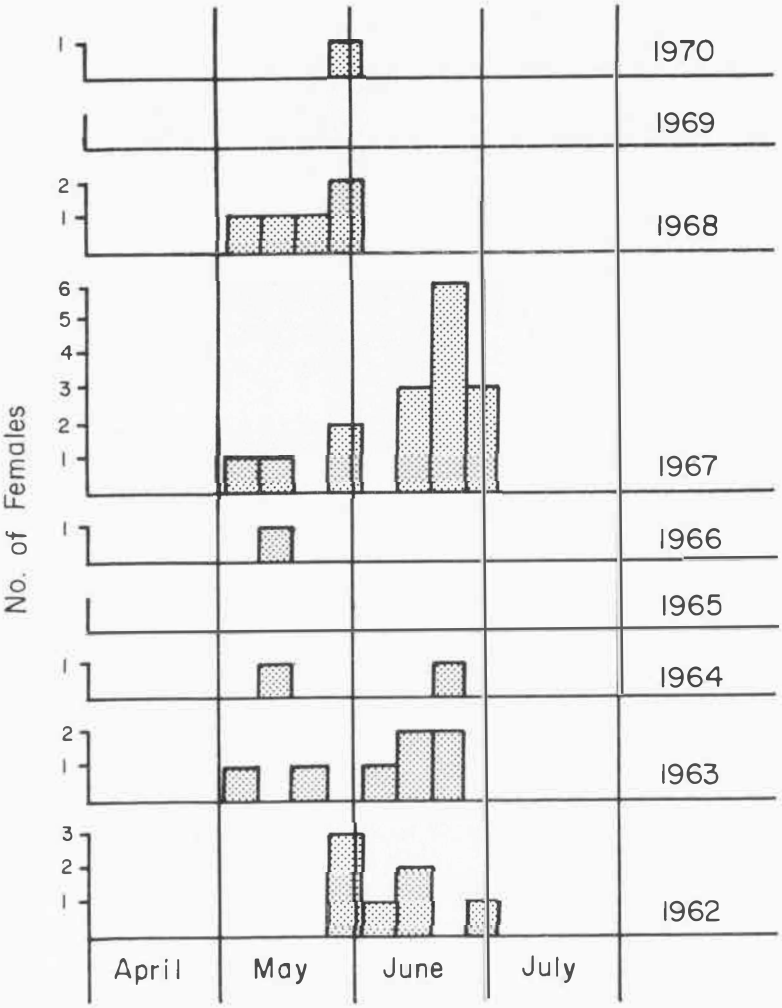


Figure 16. Conception dates of all visibly pregnant juveniles in the monthly collections presented in a histogram at 8-day intervals.

separated on the basis of body weight. In most years relatively few juveniles appeared in the May collections; apparently most juveniles born in the first litter were still too young and secretive to be subject to the collecting technique. But, by June there was probably little age bias in the collections as far as first-litter juveniles were concerned.

My procedure for estimating the juvenile conception rates (Table 6) was to sum the number of pregnant and postpartum juveniles in the June collection, divide by the total number of first-litter juvenile females and multiply by 100. One problem with this procedure is that some females (one in 1962, two in 1963, one in 1964, and one in 1967) did not conceive until after the June collection. This will result in a slight under-estimation of juvenile conception rates during these years.

Juvenile ovulation rates (Table 7) were estimated for each month in which visibly pregnant juveniles were observed in the collection. Monthly ovulation rates were the mean number of ova ovulated by juveniles in that month's collection which had become visibly pregnant after the previous month's collection. I used this restriction so that I could compare juvenile ovulation rates with rates of fetal production by the same juveniles.

Breeding by juveniles has not previously been reported for other jackrabbit populations. Only one instance of juvenile breeding has been shown for the snowshoe hare (Keith and Meslow, 1967). However, Flux (1967) reported that as high as 70 percent of the European hare (Lepus europaeus) juveniles which were above the "minimum breeding weight" in New Zealand were pregnant in the year of their birth.

Table 6. Total number, number of pregnant and postpartum, and conception rate of first-litter, juvenile females in the June collections

Year	No. of Females[a] (A)	Sum of Pregnant and Postpartum (B)	Conception Rate (B/A)x100
1962	13	6	46
1963	11	4	36
1964	4	1	25
1965		No Juvenile Breeding	0
1966	10	1	10
1967	19	10	53
1968	8	5	63
1969		No Juvenile Breeding	0
1970	11	1	9
Mean			27

[a] Number of first-litter, juvenile females in the June collection.

Age and Sex Structure

Age structure

One common characteristic of a population with changing density is a varying age ratio. The way the age ratio changes with respect to density lends information on the mechanisms involved in density change. In this study I used age ratios directly in estimating recruitment and mortality rates (discussed in subsequent sections), two factors which act jointly to determine density.

Table 7. Observed number of pregnant juveniles and mean number of ova ovulated for May, June, and July from 1962-70

Year and Month	No. Pregnant[a]	Mean No. Ova
1962		
June	5	3.2
July	1	1.0
1963		
June	3	4.3
July	2	4.0
1964		
June	1	6.0
July	1	3.0
1965	No juvenile breeding	
1966		
May	2	1.0
1967		
May	2	4.5
June	9	4.1
July	1	3.0
1968		
June	5	2.8
1969	No juvenile breeding	
1970		
June	1	5.0
Pooled Mean		3.6

[a] Number of visibly pregnant juveniles collected that became visibly pregnant after the previous collection.

As previously mentioned, by definition, all animals in the population became adults on January 1. Therefore, I estimated the age ratio each month utilizing the rabbit collections from March, the month when juveniles first began to appear in the collections, through

October (Table 8). Age ratios were not estimated for collections after October since in most years the aging technique, as discussed, was not sufficiently refined to separate adults and juveniles accurately.

Juveniles usually began to appear in the collections at about 2 months of age. The percentage of juveniles in the collections began to increase rapidly in May-June of each year and reached a peak in September when all juveniles of the year were apparently subject to the collecting procedure.

In no year was there a significant difference between the percentage of juveniles in the September and October collections. However, in all years except 1965 the observed percentage of juveniles in the October collection was somewhat lower than in September (Table 8). This may indicate a slightly higher rate of juvenile mortality over adult mortality at this time of year or a change in age-specific bias in the collections between September and October.

Sex structure

Adult sex ratio. Adult sex ratios (Table 9) were estimated each month from the rabbit collections. Weighted means calculated for each month from pooled data for the 9 years of the study indicated that from January-March the sex ratio was not significantly different from a 50:50 ratio. However, in each month in the April-October period (with the exception of September) males made up significantly less than 50 percent of the sample (Table 9) at the 5 percent probability level or lower (χ^2 test). In September males were significantly fewer at the 10 percent level.

Table 8. Percent juveniles in the monthly collections. Ninety-five percent confidence limits are shown in parentheses and sample size in brackets

Month	1962	1963	1964	1965	1966	1967	1968	1969	1970
March	No collection	0 (0-8) [44]	0 (0-8) [44]	2 (0-9) [55]	0 (0-8) [46]	0 (0-8) [50]	4 (1-14) [50]	0 (0-8) [47]	2 (0-9) [52]
April	2 (0-9) [56]	3 (1-12) [59]	0 (0-8) [47]	4 (1-14) [52]	7 (2-18) [46]	0 (0-8) [50]	13 (5-26) [60]	0 (0-8) [50]	13 (5-26) [52]
May	15 (7-28) [65]	4 (1-14) [52]	2 (0-9) [50]	18 (8-32) [66]	27 (18-37) [88]	23 (12-38) [60]	43 (33-53) [82]	48 (38-58) [120]	63 (53-73) [95]
June	57 (47-65) [115]	43 (35-53) [123]	25 (14-40) [53]	57 (46-61) [111]	80 (70-87) [99]	48 (38-58) [84]	86 (77-92) [100]	50 (40-60) [110]	No collections
July	79 (71-86) [130]	80 (69-88) [85]	73 (63-82) [91]	82 (72-88) [147]	85 (76-91) [101]	76 (66-84) [114]	88 (79-93) [105]	72 (62-80) [123]	74 (64-82) [101]
August	82 (67-90) [62]	83 (74-90) [96]	94 (88-97) [97]	80 (70-87) [139]	83 (74-90) [101]	81 (71-88) [98]	89 (81-94) [104]	78 (68-86) [128]	73 (64-81) [148]

Table 8. Continued

Month	1962	1963	1964	1965	1966	1967	1968	1969	1970	71	72
September	94 (88-98) [95]	94 (88-98) [97]	93 (87-97) [104]	85 (76-91) [104]	87 (77-92) [100]	90 (82-95) [102]	89 (81-94) [100]	87 (77-92) [112]	73 (63-82) [98]	60	55
October	86 (74-94) [64]	92 (85-96) [105]	91 (78-97) [46]	87 (77-92) [96]	84 (75-90) [100]	87 (77-92) [99]	85 (76-91) [100]	86 (77-92) [96]	71 (60-80) [91]		

Table 9. Percent males in the monthly collections of adults and number of adults sampled (in parentheses)

Month	1962	1963	1964	1965	1966	1967	1968	1969	1970	Weighted Mean	Unwt'd. Mean
January	No collection	55 (55)	70 (56)	57 (53)	43 (46)	63 (49)	50 (52)	45 (51)	50 (52)	54 (414)	54
February	No collection	45 (44)	54 (48)	52 (52)	53 (45)	51 (51)	47 (49)	36 (55)	47 (51)	48 (395)	48
March	No collection	52 (44)	52 (44)	33 (54)	48 (46)	44 (50)	52 (48)	68 (47)	43 (51)	49 (384)	49
April	35 (55)	35 (57)	36 (47)	42 (50)	40 (43)	46 (50)	56 (52)	26 (50)	42 (45)	40*** (449)	40
May	38 (55)	30 (50)	47 (49)	56 (54)	41 (64)	46 (46)	40 (47)	60 (63)	49 (35)	45* (463)	45
June	18 (49)	33 (70)	25 (40)	38 (48)	35 (20)	39 (44)	43 (14)	65 (55)	No collection	37*** (340)	37
July	19 (27)	29 (17)	28 (25)	42 (26)	20 (15)	37 (27)	62 (13)	51 (35)	62 (26)	39*** (211)	39
August	36 (11)	25 (16)	17 (6)	32 (28)	47 (17)	47 (19)	64 (11)	43 (28)	52 (29)	42* (165)	40

Table 9. Continued

Month	1962	1963	1964	1965	1966	1967	1968	1969	1970	Weighted Mean	Unwt'd. Mean
September	33	33	29	33	54	20	27	57	54	42	38
	(6)	(6)	(7)	(15)	(13)	(10)	(11)	(14)	(26)	(108)	
October	22	38	25	50	44	77	20	23	39	39**	38
	(9)	(8)	(4)	(12)	(16)	(13)	(15)	(13)	(26)	(116)	

*Significantly different from a 50:50 ratio at the 5 percent level.
**Significant at the 1 percent level.
***Significant at the 0.5 percent level.

These results could occur through a real difference in sex ratio or through a sex-specific bias in the collections. If it were a real difference, a loss of at least 34 percent of the males would be required to produce the observed drop in the percentage males in the collections. This loss would have to be rapid since in 1 month, from March-April, the observed percentage of males in the collections dropped from 49 percent to 40 percent, a loss of 31 percent of the males. I think this rate of male mortality is highly unlikely (Stoddart, 1970).

Sex-specific biases in the collections were likely. Rabbits that were in the open, moving and feeding at night were most prone to my collecting procedure. Rabbits that were resting in heavy brush were usually not seen. Pontrelli (1966) found that during the breeding season, females moved to and from feeding areas more than males and stated that this was probably the reason he found it easier to collect females at night. Since I found female body weights increased and male body weights decreased during the breeding season (see Appendix B) and since females were producing fetuses and nursing young at this time of year, females probably spent more time feeding and were thus more likely to be collected. This does not explain why the females continued to dominate the collections from August-October after the breeding season.

In December, 1969, and December, 1970, using the more refined aging technique (previously mentioned), I was able to separate accurately adults and juveniles in the collections. Also in January, February, and March of 1970 I could still separate the previous year's juveniles from the previous year's adults. Adults during these 5 months should still have been predominantly females if the male-to-female ratio observed in the April-October period was real and not due to collecting bias. However, two-thirds of the 53 adults collected in these 5 months were males.

From the data discussed above I concluded that the observed sex ratios among adults in my collections deviated from the expected 50:50 ratio through biases in the collecting procedure and that the true ratio in the adult population was approximately 50:50.

Preparturition and postpartum juvenile sex ratio. During this study 1,019 fetuses were sexed; 50.7 percent were males. This indicates an even sex ratio among preparturition juveniles during the 9-year period. Also, in no 1 year was the sex ratio significantly different from the expected 50:50 ratio.

The sex ratio of postpartum juveniles (Table 10) was estimated from the monthly rabbit collections from March, when juveniles first began to appear in the collections, through December. Since in most years I was unable to separate juveniles from adults accurately in December, the December percentages in Table 10 are for the whole population. However, juveniles probably comprised 70-90 percent of these samples as estimated from the age composition in the October collections (Table 8).

Unweighted means from the pooled data over 9 years of study indicated a significantly higher percentage of juvenile males in August ($P<0.05$) and a significantly higher percentage of juvenile females in September ($P<0.05$) than expected from a 50:50 ratio (Table 10). I cannot explain these observed differences which occurred in consecutive months. I suspect, again, that the differences were

Table 10. Percent males in the monthly collections of juveniles and number of juveniles sampled (in parentheses)

Month	1962	1963	1964	1965	1966	1967	1968	1969	1970	Weighted Mean	Unwt'd. Mean
March	No collection	-- (0)	-- (0)	0 (1)	-- (0)	-- (0)	100 (2)	-- (0)	100 (1)	75 (4)	67
April	100 (1)	0 (2)	-- (0)	100 (2)	67 (3)	-- (0)	50 (8)	-- (0)	43 (7)	52 (23)	60
May	50 (1)	100 (2)	0 (1)	42 (12)	46 (24)	57 (14)	54 (35)	46 (57)	43 (60)	47 (215)	49
June	52 (66)	58 (53)	38 (13)	60 (63)	54 (79)	40 (40)	48 (86)	53 (55)	No collection	52 (456)	50
July	48 (103)	49 (68)	48 (66)	49 (121)	50 (86)	51 (87)	37 (92)	42 (88)	59 (75)	48 (786)	48
August	49 (51)	61 (80)	62 (91)	50 (111)	55 (84)	52 (79)	49 (93)	60 (100)	53 (72)	55* (761)	55
September	48 (89)	49 (91)	43 (97)	44 (89)	55 (87)	37 (92)	53 (89)	46 (98)	41 (71)	46* (803)	46

Table 10. Continued

Month	1962	1963	1964	1965	1966	1967	1968	1969	1970	Weighted Mean	Unwt'd. Mean
October	35 (55)	43 (97)	48 (42)	46 (84)	49 (84)	45 (86)	54 (85)	55 (83)	50 (64)	48 (680)	47
December[a]	48 (58)	49 (61)	No collection	47 (47)	49 (51)	36 (50)	43 (100)	55 (53)	49 (43)	47 (463)	47

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*Significantly different from a 50:50 ratio at the 5 percent level.

[a] Percent males for the whole population.

not real. Of the 4,190 juveniles collected, 50.9 percent were females. This was not significantly different from a 50:50 ratio (χ^2 = 1.4).

Mortality Rates

Fall-spring mortality of total population

I calculated the October-March mortality rates of the total population each year (Table 11) by dividing the spring density index by the preceding fall index (Table 1), subtracting the quotient from 1, and multiplying by 100 (cf. Gross, 1967). As previously shown (Table 8), the population age structure was essentially constant by October of each year; the estimated mortality rates therefore applied to both juveniles and adults. October-March mortality rates varied from 33 percent in 1968-69 to 69 percent in 1966-67. The unweighted mean for the eight spring-fall periods was 56 percent.

Spring-fall mortality of adults

March-October mortality rate of the adult population for each year was estimated (Table 12) by dividing the fall adult density index by the spring population density index (Table 1), subtracting the quotient from 1, and multiplying by 100 (cf. Gross, 1967). The fall adult index was obtained by multiplying the fall population index by the unweighted, mean percentage of adults in the September and October collections (Table 8). The range in over-summer adult mortality rates was 9-87 percent.

The above demographically measured mortality rates for 1968 and 1969 were consistent with those measured telemetrically over the same

Table 11. October-March mortality rates of total population; standard error in parentheses

Year	Density Index (Table 1)		Percent Oct.-March Mortality (1-B/A) x 100
	October (A)	March (B)	
1962-63	40.0	13.9	65 (12)
1963-64	60.6	26.3	57 (8)
1964-65	42.4	17.9	58 (20)
1965-66	33.4	11.7	65 (15)
1966-67	23.7	7.4	69 (16)
1967-68	21.2	9.2	56[a] (23)
1968-69	64.8	43.1	33[a] (19)
1969-70	123.2	67.0	46 (11)
70-71			30
71-72			46
Unweighted Mean			56
72-73			72

[a] These values vary somewhat from those previously reported (Stoddart, 1970) because of changes in density estimates. In the 1970 report, the Gates' (1969) census method was applied to the transect data pooled rather than to the individual transect data.

periods (cf. Stoddart, 1970).

Postpartum mortality

Postpartum mortality is an estimate of the percentage of postpartum juveniles (from all littering periods pooled) that die before fall census. I calculated it each year (Table 13) by dividing the fall juvenile index by the estimated index of postpartum juveniles produced from all litters pooled, subtracting the quotient from 1, and multiplying by 100 (cf. Gross, 1967). Estimates of the indexes

Table 12. March-October mortality rates of adult population; standard errors in parentheses

Year	Adult Density Index March (Table 1) (A)	October[a] (B)	Percent March-Oct. Mortality (1-B/A) x 100
1963	13.9	4.2	70 (12)
1964	26.3	3.4	87 (6)
1965	17.9	4.7	74 (14)
1966	11.7	3.5	70 (14)
1967	7.4	2.6	65 (20)
1968	9.2	8.5	9[b] (38)
1969	43.1	17.3	60[b] (12)
1970	67.0	52.0	23 (13)
71			50
72			67
Unweighted Mean			57

[a] October density index (Table 1) multiplied by unweighted mean percentage of adults in September and October collections (Table 8).

[b] These values vary somewhat from those previously reported (Stoddart, 1970) because of changes in density estimates. In the 1970 report the Gates' (1969) census method was applied to the transect data pooled rather than to the individual transect data.

of postpartum juveniles and fall juveniles are derived in a following section on recruitment. Postpartum mortality rates varied from 22-69 percent with an unweighted mean of 58 percent.

Preparturition mortality

Loss of ova in litters surviving to term. Preparturition loss of ova in litters that survived to term was estimated for litters conceived in each of the four or five conception periods of each

Table 13. Mortality rate of juveniles from parturition to fall census; standard error in parentheses

Year	Postpartum Juvenile Index (Table 18, Column H) (A)	Fall Juvenile Index (Table 19) (B)	Percent Mortality (1-B/A) x 100
1963	71.8	56.4	22 (17)
1964	126.2	39.0	69 (8)
1965	94.2	28.7	69 (10)
1966	60.7	20.1	67 (12)
1967	56.6	18.7	67 (14)
1968	91.6	56.4	38 (13)
1969	274.5	104.9	61 (8)
1970	414.0	133.0	68 (9)
71			85
72			88
Unweighted Mean			58

year. Estimates were based on differences in number of corpora lutea and number of live fetuses observed in litters 20 days old or older. Brambell (1944) showed that intrauterine mortality was virtually complete in the wild rabbit, Oryctolagus cuniculus, by mid-term. On the basis of his work I assumed that all intrauterine mortality in jackrabbits had occurred by day 20 in litters that survived to term.

Preparturition mortality in litters that survive can occur either before or after implantation of the embryos in the uterus. Both pre- and postimplantation mortality rates were estimated (Table 14). Preimplantation loss was calculated by comparing the

Table 14. Percent ova lost before implantation, percent fetuses lost by resorption, and total percent preparturition loss, 1962-70

Year	Litter	No. Litters	No. Corpora Lutea	No. Implanted Embryos	No. Live Fetuses	% Lost Before Implantation	% Resorb. After Implantation	Total % Loss of Ova
1962	3	19	129	116	115	10	1	11
	4	31	163	146	140	10	4	14
	5	8	39	34	34	13	0	13
Mean						11	2	13
1963	1	2	2	2	2	0	0	0
	2	5	26	24	24	8	0	8
	3	17	107	90	89	16	1	17
	4	20	117	109	102	7	6	13
Mean						8	2	10
1964	1	11	28	23	23	18	0	18
	2	13	68	58	56	15	3	18
	3	15	97	91	82	6	10	15
	4	8	39	31	27	21	13	31
Mean						15	7	21
1965	1	16	31	27	25	13	7	19
	2	12	62	58	54	6	7	13
	3	13	72	72	67	0	7	7
	4	6	24	21	21	13	0	13
Mean						8	5	13
1966	1	12	20	19	19	5	0	5
	2	22	95	94	92	1	2	3

Table 14. Continued

Year	Litter	No. Litters	No. Corpora Lutea	No. Implanted Embryos	No. Live Fetuses	% Lost Before Implantation	% Resorb. After Implantation	Total % Loss of Ova
	3	20	116	116	115	0	1	1
	4	0	---	---	---	---	---	---
Mean						2	1	3
1967	1	16	24	24	23	0	4	4
	2	17	89	89	89	0	0	0
	3	16	110	109	109	1	0	1
	4	15	68	68	68	0	0	0
	5	2	8	8	7	0	1	1
Mean						0	1	1
1968	1	26	48	48	48	0	0	0
	2	16	89	85	84	4	1	6
	3	12	80	75	75	6	0	6
	4	6	28	25	25	11	0	11
	5	2	5	5	5	0	0	0
Mean						4	0	5
1969	1	19	36	32	31	11	3	14
	2	15	86	82	80	5	2	7
	3	25	179	169	161	6	5	10
	4	8	36	30	30	17	0	17
Mean						10	3	12

Table 14. Continued

Year	Litter	No. Litters	No. Corpora Lutea	No. Implanted Embryos	No. Live Fetuses	% Lost Before Implantation	% Resorb. After Implantation	Total % Loss of Ova
1970	1	24	44	34	34	23	0	23
	2	21	108	102	100	6	2	7
	3	18	105	99	97	6	2	8
	4	8	29	29	29	0	0	0
Mean						9	1	10
Unweighted Mean						8	3	10

number of corpora lutea with the number of fetuses both alive or resorbing in litters 20 days old or older. Postimplantation loss was determined by comparing the number of fetuses both alive and resorbing with the number of live fetuses. Resorbing fetuses were classes as such only if a lump with resorbing material was found in the uterus.

Fetuses dying early in the gestation period may have resorbed completely, leaving no lumps, and thus been erroneously classed as preimplantation loss. Brambell (1948) found that implantation sites of resorbed fetuses, although sometimes difficult to find, remained visible throughtout gestation. No estimates have been reported, however, as to the length of time visible lumps remain after death of a fetus, so the extent of this error is not known.

The relationship of initial litter size; i.e., number of ova ovulated, to percentage preparturition loss was also investigated. All data from pregnant females with litters 20 days old or older were pooled for each of the first four conception periods. The fifth conception period was not investigated because of small sample size. The percentage of litters showing some loss (Figure 17) increased significantly with increasing initial litter size in litters conceived in conception periods 2, 3, and 4. The rate of increase in period 4 was about double that in periods 2 and 3 and was significantly different from them at the 1 percent level. The percentage of ova lost also increased significantly with initial litter size in periods 3 and 4. The rate of increase was 3.5 times greater in period 4 than in period 3; they were significantly different at the 0.5 percent level.

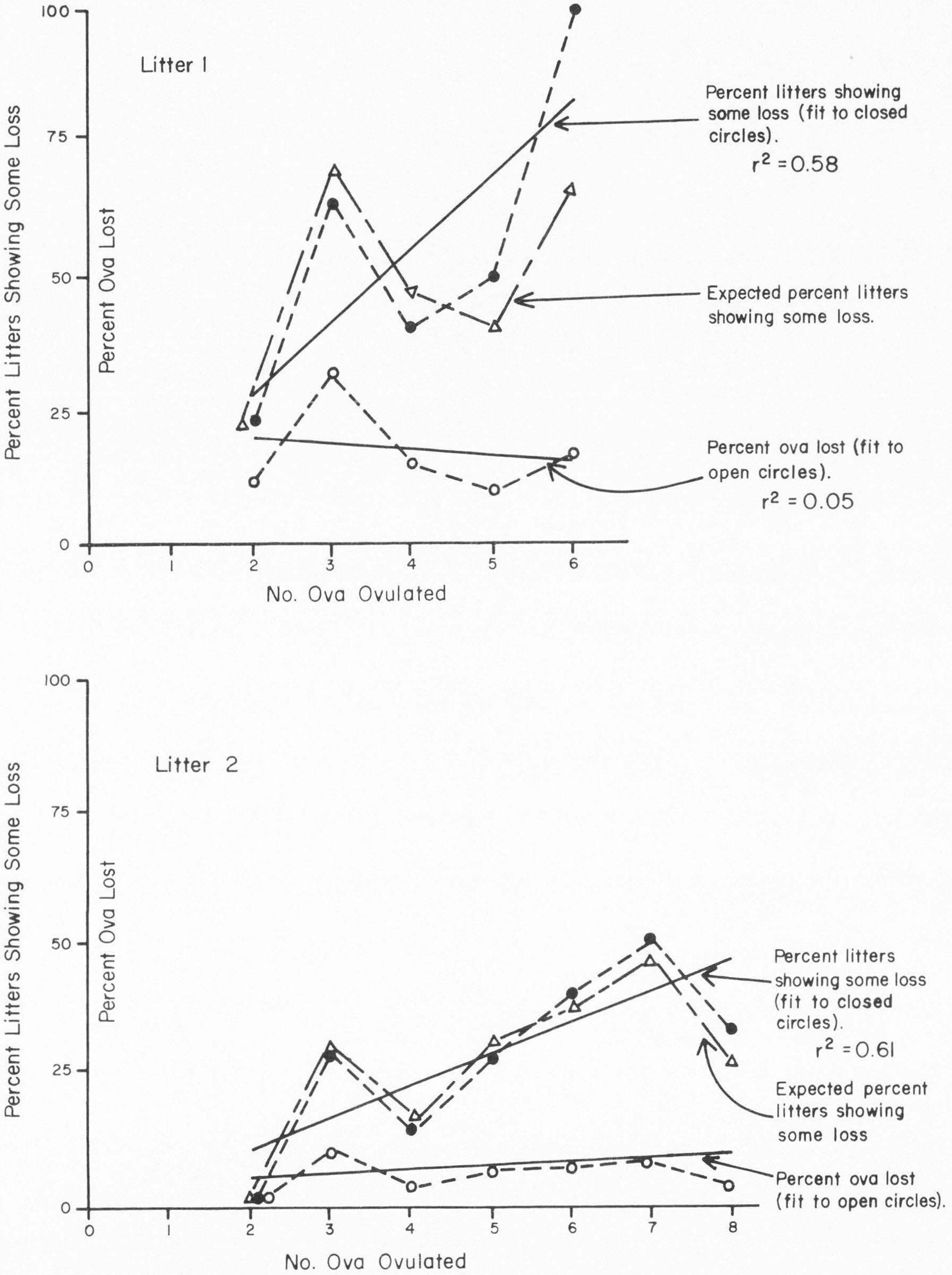

Figure 17. Regression of observed and expected percent litters showing some preparturition loss and percent ova lost on initial litter size.

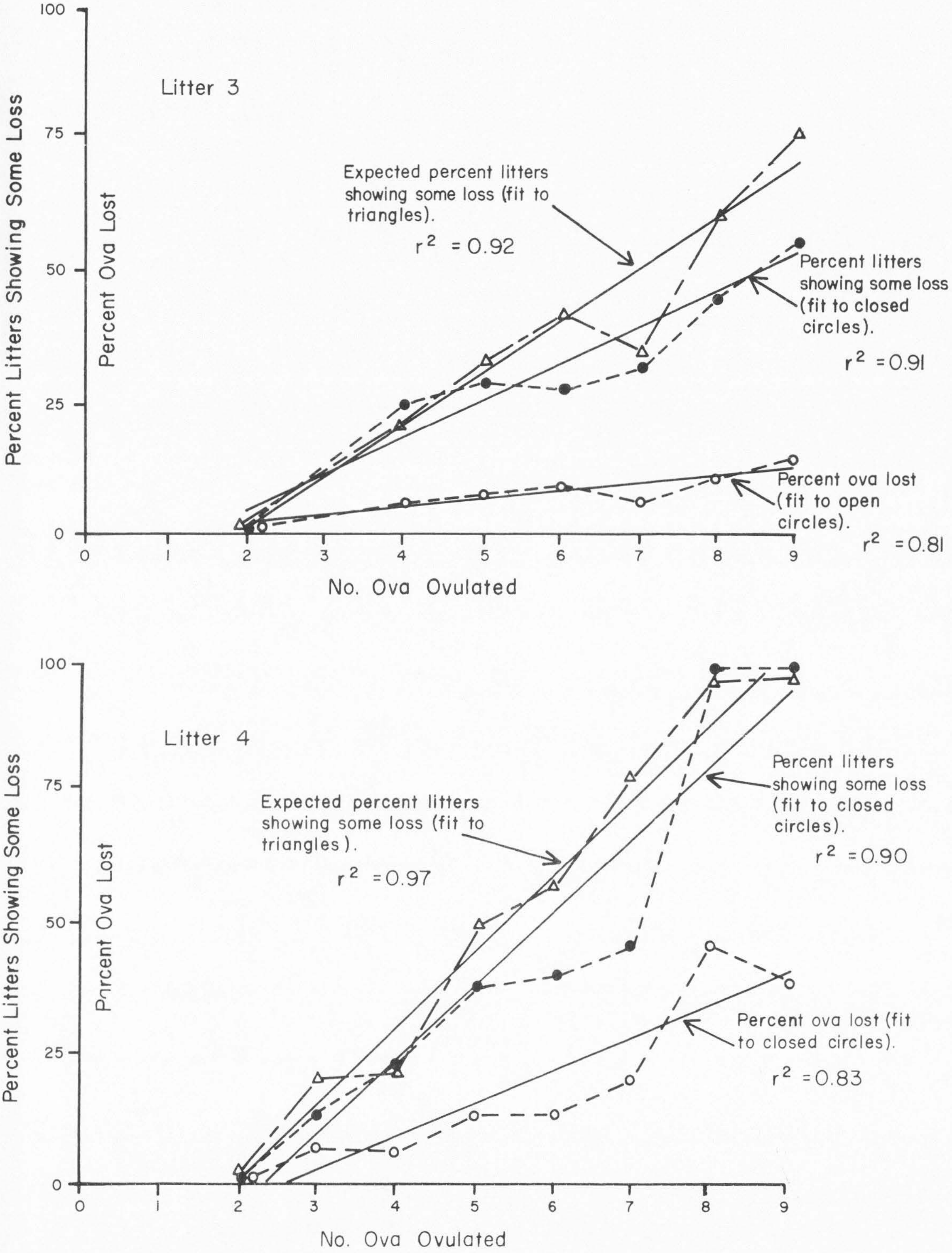

Figure 17. Continued.

If it is assumed that mortality of individual ova is random, the expected percentage of litters showing some loss as a function of initial litter size (triangles in Figure 17) can be calculated from the observed percentages of ova lost for each initial litter size (cf. Brambell, 1948). For example, if 10 percent of the ova from litters with an initial size of three were lost, then the probability that any individual litter would show no loss would be 0.9 x 0.9 x 0.9 = 0.73 (the probability that each ova will survive multiplied together). Therefore, the probability that a litter would show some loss is 0.27 (1.0 - 0.73). The expected percentage of litters with initial size of 3 showing loss is then 27 percent.

The slopes of the regression lines (not shown in Figure 17) for the expected percentages of litters showing loss from conception periods 1 and 2 are not significantly different from the slopes (Figure 17) of the observed percentage of litters showing loss. This suggests that the loss of ova from these conception periods is random. The slopes of the regression lines for the expected and observed percentages of litters showing loss (Figure 17), however, are different in conception periods 3 and 4 at the 89 and 75 percent levels respectively. Apparently, mortality tends to be somewhat concentrated in some litters from these conception periods.

My unweighted mean, preimplantation and postimplantation mortality rate estimates of 8 percent and 3 percent respectively (Table 8) for litters which survived are comparable to those reported for the jackrabbit by other authors. Lechleitner (1959) and Pontrelli (1966) reported preimplantation mortality rates in California of 6.7 and 8.9 percent and postimplantation rates of 6.2 and 4.6 percent respectively. Tiemeier (1965) estimated pre- and postimplantation mortality rates in Kansas to be 9.4 and 5.1 respectively.

Preparturition loss of litters in toto. I found evidence of intrauterine loss of total litters only in litters conceived in the first and last conception periods of the breeding seasons. In February, 1970, two animals (7 percent of the collection) were collected which had recently conceived for the second time during the breeding season as shown by corpora lutea and corpora albicantia in the ovaries. Both uteri were still small indicating neither animal had carried a litter to term. Apparently both animals had become pregnant, lost their entire litters, and become pregnant again. In 1969 two animals, 25 percent of the females in the collection which had conceived during the fourth period, were in the process of resorbing all their fetuses. Of the females conceiving during the fourth period in 1966, 57 percent should still have been pregnant at the time of the June collection. No pregnant females were collected in June, however, indicating at least 57 percent of those pregnant lost the fourth litter in toto.

Apparently total loss of litters from conception periods 2 and 3 was rare. No pseudo-pregnant females or females carrying litters in which all fetuses, or even a majority of fetuses, were in the process of resorption were found from these periods.

Brambell (1944 and 1948) made a strong case against treating lightly the loss of litters in toto when estimating total prenatal mortality in mammalian populations. He demonstrated that if the total loss of litters is neglected a gross underestimation of prenatal mortality might occur. His case was championed by a number of authors studying hare populations--Lechleitner (1959), Watson (1957), Poole (1960), Newson (1964), and Flux (1967)--all of whom found loss of total litters in the range of 20-60 percent using Brambell's methods for estimating the loss.

Brambell (1948) suggested two methods which are commonly used for estimating loss of litters _in toto_. One method is based on a comparison of the percentage of litters showing some resorptive loss of fetuses at two stages in the gestation period. Brambell's findings indicate that if a litter is lost _in toto_ the loss usually occurs just before mid-term. The contention is that the litters lost _in toto_ are those that had previously incurred some loss. Therefore, the comparison of the percentages of litters showing some loss is made between litters that are about mid-term in age and those that are past mid-term.

For example, Newson (1964) found 26.7 percent of the litters that were about mid-term to have resorbing fetuses. But, only 5.0 percent of the litters older than mid-term showed resorptive loss. Since her findings indicated that resorption sites remain detectable throughout the gestation period, she attributed the changing percentage of litters showing some resorptive loss to the complete loss of 20 percent of the litters.

Other authors (Raczynski, 1964, and Pontrelli, 1966) think that early resorption sites disappear or at least are not readily found in the later stages of gestation and therefore they would expect results such as those of Newson's on the basis of this disappearance.

The second method for calculating loss of litters _in toto_ involves a comparison of the frequency of litters in the collections which are less than mid-term in age with those that are older than mid-term. Using this procedure with their jackrabbit collections, Lechleitner (1959) and Tiemeier (1965) found 39.4 and 11 percent more pregnancies in the first half of gestation than in the last half, respectively. These percentages are their estimates of the rate of litter loss _in toto_ sometime before mid-term.

This second method has shortcomings: (1) If breeding is synchronized, the age of the collected litters will be determined by the data on which collections were made relative to the breeding cycle. (2) Collections might be biased by secretive behavior of near-term females as suspected by Pontrelli (1966).

Neither of the above methods for estimating the rate of total litter loss is compatible with my data. First, as mentioned above, I made no attempt to count implantation sites in the uteri. Resorptions were recorded as such only when some residual material was still present.

I am not convinced that an implantation-site count is feasible with any degree of accuracy, particularly in the later litters of the breeding season when scars from earlier pregnancies might still be found. Second, breeding was synchronized, thus the ages of collected litters were biased. As mentioned above, in the later years of the study I intentionally selected collecting dates so as to bias collections toward older litters.

If there were extensive loss of litters _in toto_ near mid-term, I would expect to find some litters in my collections in which all fetuses were in the process of resorbing. However, this did not occur except in the isolated cases already mentioned. If fetal loss were progressive; i.e., if more and more of the fetuses in litters that were destined to be lost *in toto* started to resorb as time went on, I would expect to find a greater difference between the regression lines (Figure 17) of the observed and expected percentage of litters showing loss. (There was no significant difference in the first and second litters.)

I conclude then that *some* total loss might go undetected if: (1) all fetuses in litters that are to be lost entirely die within a short time period; i.e., the loss is not progressive; (2) total resorption is rapid; and (3) time lapse between death of all fetuses and subsequent conception is short. Extensive loss of this type would result in loss of breeding synchrony. This was not observed in most years of the study.

Effects of a moderate amount of total-litter loss on the ultimate production of juveniles would probably not be great since a female which loses a litter would likely still have time to conceive a viable litter in each of the conception periods, as previously discussed. Some effect on juvenile production would occur, however, if some individual females habitually lost litters *in toto.*

Data collected by some investigators of hare populations apparently indicate, as do mine, that loss of litters *in toto* is not extensive. Pontrelli (1966) estimated, on the basis of litters actually observed in the process of total resorption, that 4.4 percent of the litters were lost completely.

Meslow and Keith (1968) stated that intrauterine mortality in their snowshoe hare study was consistently low. They found by palpation during 20-day periods between conception peaks that 96 percent of the females were pregnant for the first and second litters and 89 percent for the third litter. I think that if these percentages of females had palpable fetuses during the 20-day periods, there is little chance for significant loss of litters *in toto*.

James and Seabloom (1969) found 7 percent of the female white-tailed jackrabbits they collected to be either non-pregnant between conception peaks of the population or pregnant but out of phase with the population. They considered the 7 percent to represent the percentage of females which had lost litters *in toto.*

Recruitment

I use recruitment here as a general term referring to the juveniles actually produced or present in the population at some specified time from birth (ovulation)-December 31 of the year in which they were born. Recruitment at three stages in the juvenile life history will be presented: (1) number of ova produced per January 1 female (realized natality), (2) index to number of post-partum juveniles produced (normally termed "born"), and (3) index to number of juveniles at the time of fall census.

Realized natality

Realized natality is a measure of the mean number of ova produced during the ensuing breeding season per female alive January 1. Since all January 1 females do not survive the breeding season, the mean is corrected for breeding-season mortality of females. The mean number of ova produced (Table 15, totals in Column E) is the sum of the mean number of ova produced during the four or five conception periods each year. Mean number of ova produced during each conception period per female alive January 1 (Column E) was determined by (1) multiplying the mean number of ova ovulated per breeding female (Column C) by the percentage of females ovulating

(Table 3) and (2) multiplying the product (Table 15, Column D) by the fraction of January 1 females surviving (Column A). The fractions in Column A are the survival rates (percentage of females surviving) from January 1 to the time of the conception peak in each conception period.

Survival rates in Table 15, Column A were calculated using monthly survival rates (Table 16). First, for each conception period, the appropriate monthly survival rates (Table 16) were multiplied together to obtain the survival rate of January 1 females to the end of the month immediately preceding the conception peak and the end of the month in which the conception peak occurred (as determined from Figure 15). Then, the percentage of January 1 females alive at the time of each conception peak was estimated by interpolating (assuming a constant mortality rate) between these month-end survival rates to the date of peak conception.

Monthly mortality rates (Table 16) were calculated using the equation $M = 1 - (1 - n)^2$ where M represents the mortality rate for the March-October or October-March period, m is the monthly mortality rate, and n is the number of months in the March-October or October-March period.

The mean number of ova shown in Table 15, Column C is not always consistent with the mean number of ova shown in Table 4. Only those litters 20 days old or older were used for calculating the means in Table 15. I did this so that the mean number of ova ovulated could be compared with average litter sizes which were calculated from litters 20 days old or older (see below).

Table 15. Percent of the January 1 female population alive and percent ovulating in each conception period of each year. Mean number of ova per ovulating female, per female in the population, and per female alive on January 1

Year	Conception Period	(A) Percent of Jan. 1 Female Pop.	(B) Percent Ovulating (Table 3)	(C) Mean Number of Ova	(D) Mean Ova/Female BxC	(E) Mean Ova/Jan. 1 Female AxO
1963	1	81	13	1.0	.1	.1
	2	66	95	5.2	4.9	3.3
	3	49	100	6.3	6.3	3.1
	4	39	70	5.9	4.1	1.7
Totals				18.4	15.4	8.2
1964	1	84	100	2.5	2.5	2.1
	2	66	100	5.2	5.2	3.4
	3	49	100	6.5	6.5	3.2
	4	33	100	4.9	4.9	1.6
Totals				19.1	19.1	10.3
1965	1	80	100	1.9	1.9	1.5
	2	66	100	5.2	5.2	3.4
	3	54	100	5.5	5.5	3.0
	4	43	50	4.0	2.0	0.9
Totals				16.6	14.6	8.8
1966	1	85	100	1.7	1.7	1.4
	2	66	100	4.3	4.3	2.8
	3	51	100	5.8	5.8	3.0
	4	41	37	3.8	1.4	0.6
Totals				15.6	13.2	7.8
1967	1	80	100	1.5	1.5	1.2
	2	59	100	5.2	5.2	3.1
	3	45	100	6.9	6.9	3.1
	4	37	100	4.5	4.5	1.7
	5	30	29	4.0	1.2	0.4
Totals				22.1	19.3	9.5
1968	1	85	100	1.8	1.8	1.5
	2	69	100	5.6	5.6	3.9
	3	60	100	6.7	6.7	4.0
	4	60	100	4.7	4.7	2.8
	5	59	40	2.5	1.0	0.6
Totals				21.3	19.8	12.8

Table 15. Continued

Year	Conception Period	(A) Percent of Jan. 1 Female Pop.	(B) Percent Ovulating (Table 3)	(C) Mean Number of Ova	(D) Mean Ova/Female BxC	(E) Mean Ova/Jan. 1 Female Ax0
1969	1	96	94	1.9	1.8	1.7
	2	88	100	5.7	5.7	5.0
	3	76	100	7.2	7.2	5.5
	4	64	32	4.5	1.4	0.9
Totals				19.3	16.1	13.1
1970	1	94	96	1.8	1.7	1.6
	2	78	100	5.1	5.1	4.0
	3	67	100	5.8	5.8	3.9
	4	64	45	3.6	1.6	1.0
Totals				16.3	14.2	10.5

Postpartum juveniles

The index to number of postpartum juveniles added each year to the population; i.e., born, in usual usage, was calculated by summing the indexes to postpartum juveniles produced by adult females and those produced by juvenile females.

Production by adult females. I estimated adult-female production of postpartum juveniles each breeding season (1) in terms of postpartum juveniles per female alive January 1; and (2) in terms of an index to total postpartum juveniles. These two production estimates (Table 17, totals in Columns F and G) are the sums of the production estimates for the four or five littering periods of each year.

The number of postpartum juveniles produced per January 1 female during any littering period (Table 17, Column F) is the number of fetuses per female in the population (Column E) multiplied by the

Table 16. Jackrabbit mortality and survival rates for two life-history stages by years, 1962-70

	Total Population for Period Oct.-Mar.			Adult Population for Period Mar.-Oct.		
Year	Percent Oct.-Mar. Mortality (Table 11)	Percent Monthly Mortality (A)	Percent Monthly Survival (1-A)	Percent Mar.-Oct. Mortality (Table 12)	Percent Monthly Mortality (B)	Percent Monthly Survival (1-B)
1962-63	65	19	81			
1963				70	16	84
1963-64	57	16	84			
1964				87	25	75
1964-65	58	16	84			
1965				74	18	82
1965-66	65	19	81			
1966				70	16	84
1966-67	69	21	79			
1967				65	14	86
1967-68	56	15	85			
1968				9	1	99
1968-69	33	8	92			
1969				60	12	88
1969-70	46	12	88			
1970				23	4	96

percentage of January 1 females alive at the time of the littering peak for that period (Column A). Since gestation is approximately 40 days, a littering peak is assumed to come 40 days after the respective conception peak for each period. The percentage of January 1 females is calculated from the monthly mortality rates (Table 16) in the same manner as discussed above. Number of fetuses per female is the mean litter size (Column D) multiplied by the percentage of females

Table 17. Female population index, percentage of January 1 female population alive, percentage littering, mean litter size, mean number of fetuses per female, postpartum juveniles per female alive January 1, and index to total postpartum juveniles in each littering period of each year

Year	Jan. 1 and Litter	(A) Percent of Jan. 1 Female Pop.	(B) Female Index	(C) Percent Littering	(D) Mean Litter Size	(E) Fetuses per Female (CxD)	(F) Postpartum Juv./Jan. 1 Female (AxE)	(G) Postpartum Juvenile Index (BxE)
	Jan. 1	100	13.1					
1963	1	66	8.6	13	1.0	.1	.1	1.0
	2	49	6.3	95	4.8	4.6	2.2	28.3
	3	39	5.0	100	5.2	5.2	2.0	25.5
	4	30	4.0	70	5.1	3.6	1.1	14.6
Totals					16.1	13.5	5.4	69.4
	Jan. 1	100	21.4					
1964	1	66	14.3	100	2.1	2.1	1.4	30.0
	2	49	9.5	100	4.3	4.3	2.1	40.9
	3	33	6.5	100	5.5	5.5	1.8	35.7
	4	23	4.6	100	3.4	3.4	0.8	18.4
Totals					15.3	15.3	6.1	125.0
	Jan. 1	100	15.0					
1965	1	66	9.7	100	1.6	1.6	1.1	15.5
	2	54	8.1	100	4.5	4.5	2.4	36.5
	3	43	6.6	100	5.2	5.2	2.2	34.3
	4	33	4.5	50	3.5	1.8	0.6	7.9
Totals					14.8	13.1	6.3	94.2

Table 17. Continued

Year	Jan. 1 and Litter	(A) Percent of Jan. 1 Female Pop.	(B) Female Index	(C) Percent Littering	(D) Mean Litter Size	(E) Fetuses per Female (CxD)	(F) Postpartum Juv./Jan. 1 Female (AxE)	(G) Postpartum Juvenile Index (BxE)
	Jan. 1	100	10.8					
1966	1	66	7.1	100	1.6	1.6	1.1	10.9
	2	51	5.4	100	4.2	4.2	2.1	22.7
	3	41	4.3	100	5.8	5.8	2.4	24.9
	4	33	3.4	16	3.8	0.6	0.2	2.1
Totals					15.4	12.2	5.8	60.6
	Jan. 1	100	7.3					
1967	1	59	4.2	100	1.4	1.4	0.8	5.7
	2	45	3.3	100	5.2	5.2	2.3	17.1
	3	37	2.7	100	6.8	6.8	2.5	18.4
	4	30	2.1	100	4.5	4.5	1.4	9.4
	5	25	1.8	29	3.5	1.0	0.3	1.8
Totals					21.4	18.9	7.3	52.4
	Jan. 1	100	7.6					
1968	1	69	5.2	100	1.8	1.8	1.2	9.4
	2	60	4.6	100	5.3	5.3	3.2	24.4
	3	60	4.5	100	6.3	6.3	3.7	28.4
	4	59	4.4	100	4.2	4.2	2.5	18.5
	5	58	4.3	40	2.5	1.0	0.6	4.3
Totals					20.1	18.6	11.2	85.0

Table 17. Continued

Year	Jan. 1 and Litter	(A) Percent of Jan. 1 Female Pop.	(B) Female Index	(C) Percent Littering	(D) Mean Litter Size	(E) Fetuses per Female (CxD)	(F) Postpartum Juv./Jan. 1 Female (AxE)	(G) Postpartum Juvenile Index (BxE)
	Jan. 1	100	27.1					
1969	1	88	23.7	94	1.6	1.5	1.3	34.9
	2	76	21.3	100	5.3	5.3	4.0	112.9
	3	64	17.6	100	6.4	6.4	4.1	112.6
	4	56	15.5	24	3.8	0.9	0.5	14.1
Totals					17.1	14.1	9.9	274.5
	Jan. 1	100	47.2					
1970	1	78	36.9	93	1.4	1.3	1.0	48.0
	2	67	32.0	100	4.8	4.8	3.2	154.0
	3	64	30.5	100	5.4	5.4	3.5	165.0
	4	61	29.0	45	3.6	1.6	1.0	47.0
Totals					15.2	13.1	8.7	414.0
Unweighted Mean						14.9		
1971						1.3		
						3.3		
						4.9		
						1.8		
						11.3		
1972						1.7		
						4.3		
						1.5		
						7.5		

littering. Mean litter size is determined from litters 20 days old or older since intrauterine mortality is assumed to be complete by this time. The percentages of females littering are the same as the percentages of females ovulating (Table 3) except for the fourth period in 1966 and 1969 and the first period in 1970 when some loss of total litters was observed (discussed previously under total litter mortality).

An index to the number of postpartum juveniles recruited was determined by multiplying the number of fetuses per female (Table 17, Column E) by the index to female density at the time of the littering peak for each littering period. Female density indexes were calculated by multiplying the January 1 female index by the percentages of January 1 females alive (Column A). I calculated the January 1 female density indexes (Column B) from the fall density indexes (Table 1) and the October-March monthly mortality rates (Table 16, Column A). I assumed a 50:50 sex ratio.

Recruitment of postpartum juveniles, as I have defined it, has not been measured for other jackrabbit populations. Other authors have presented estimates for the number of fetuses produced per surviving female, however. My estimates for the number of juveniles produced per surviving female ranged from 12.2 in 1966 to 18.9 in 1967 (Table 17, Column E). The unweighted mean number of juveniles produced per surviving female for 1963-70 was 14.9 and is the largest reported for the jackrabbit. Vorhies and Taylor (1933) estimated a value of 8. Lechleitner (1959) and Pontrelli (1966) reported values of 9.8 and 7.9 respectively in California. In Kansas and Idaho, Tiemeier (1965) and French *et al*. (1965) obtained estimates of 13.1 and 11.8 respectively.

Production by juvenile females. An index to production of post-partum juveniles by juvenile females (Table 18, totals in Column F) was calculated by summing production over the months in which pregnant juveniles were observed. Production per month (Column F) was determined by multiplying the pregnant juvenile index (Column E) by the average litter size (Column B). The pregnant juvenile index for each month was estimated by dividing the number of pregnant juveniles in the monthly collection (Column A) by the number of adult females in the collection (Column C) and multiplying the quotient by the adult female index at the mean parturition date of the pregnant juveniles (Column D). The adult female index was calculated in the same manner as mentioned above in the section on adult female production.

Only juveniles which became visibly pregnant following the previous month's collection were included in the number of pregnant females collected (Column A). In this way production estimates of a population of pregnant juveniles whose pregnancies may extend between two collecting periods will not be calculated and added twice to the total production.

Fall juvenile index. The juvenile index at time of fall census (Table 19) was calculated by multiplying the fall density index (Table 1) by the unweighted percentage of juveniles in the September and October collections (Table 8).

Table 18. Monthly average litter size of pregnant juveniles from 1963-70. Index to realized production of postpartum juveniles by juvenile females and total realized production by juvenile and adult females from 1963-70

No/sq mile

Year and Month	No. Preg. Juveniles Collected[1] (A)	Average Litter Size (B)	No. Adult Females Collected (C)	Adult Female Index (D)	Preg. Juv. Index ($\frac{A}{C}$ x D) (E)	Index to Recruitment by Juv. (ExB) (F)	Index to Recruitment by Adult (Table 17) (G)	Index to Total Recruitment (F+G) (H)
1963								
June	3	2.4	47	4.1	0.26	0.6		
July	2	3.0	12	3.5	0.58	1.8		
Total						2.4	69.4	71.8
1964								
June	1	3.0	30	5.3	0.18	0.5		
July	1	3.0	18	4.0	0.22	0.7		
Total						1.2	125.0	126.2
1965	No Juvenile Breeding							
1966								
May	1	1.0	38	3.6	0.10	0.1		
Total						0.1	60.6	60.7
1967								
May	2	4.5	25	2.5	0.20	0.9		
June	9	4.1	27	2.1	0.70	2.9		
July	1	3.0	17	1.9	0.11	0.3		
Total						4.1	52.4	56.5

Table 18. Continued

Year and Month	No. Preg. Juveniles Collected[1] (A)	Average Litter Size (B)	No. Adult Females Collected (C)	Adult Female Index (D)	Preg. Juv. Index $(\frac{A}{C} \times D)$ (E)	Index to Recruitment by Juv. (ExB) (F)	Index to Recruitment by Adult (Table 17) (G)	Index to Total Recruitment (F+G) (H)
1968								
June	5	2.4	8	4.4	2.75	6.6		
Total						6.6	85.0	91.6
1969	No Juvenile Breeding							
Total						0.0	274.5	274.5
1970								
June	1	3.0	18	29.0	1.60	3.8		
Total						3.8	414.0	417.8
71							645.0	645.0
72							292.0	292.0

Table 19. Fall juvenile density index for the study area from 1963-70

Year	(A) Fall Population Index[a] (Table 1)	(B) Percent Juv. In Fall[b] (Table 8)	(C) Fall Juvenile Index[a] (AxB)
1963	60.6 (10.9)	93 (88-96)	56.4 (10.2)
1964	42.4 (9.9)	92 (87-95)	39.0 (9.1)
1965	33.4 (9.4)	86 (80-91)	28.7 (8.1)
1966	23.7 (7.8)	85 (79-90)	20.1 (6.7)
1967	21.2 (8.6)	88 (82-93)	18.7 (7.6)
1968	64.8 (11.5)	87 (81-92)	56.4 (10.0)
1969	123.2 (18.9)	86 (80-91)	105.9 (16.3)
1970	185.0 (28.3)	72 (65-77)	133.0 (23.2)

[a] Standard error in parentheses.
[b] Ninety-five percent confidence interval in parentheses

Population Model

General considerations

With the arithmetic speed and memory storage afforded by the modern computer, broad in-depth mathematical models for simulation of biological systems are now practical (Watt, 1968). A simulation model usually evolves slowly through interaction and feedback between the experimental effort and the computer analysis. The model I constructed in this section is the first evolutionary phase toward such a model. Even this first phase of the model is not complete since I have only observed the jackrabbit population during the last years of population decline and first 3 years of population increase.

My initial equation (Stoddart, 1971) is patterned after the well-known spruce budworm model (cf. Morris, 1962); i.e., it is in the form of a series of survival rates representing each life-history state of the rabbit:

$$\frac{N_{t+1}}{N_t} = S_{pw} \left(\sum_{i=1}^{5} S_{a_i} F_i P_i S_{pre_i} S_{post_i} \right) + S_{pw} S_{as} \quad . \; . \; . \; (9)$$

where N_t = number of animals at the end of October

N_{t+1} = number of animals at the end of the following October

S_{pw} = survival rate of population from October-March

S_{as} = survival rate of adults from March-October

S_{ai} = survival rate of adults from March to each conception period (subscript i indicates the conception period)

F_i = mean number of ova ovulated per female at each conception period

P_i = proportion of adult females in adult population at each conception period

S_{pre_i} = preparturition survival rate of each litter

S_{post_i} = postpartum survival rate of each litter to October

I think that movement has not significantly affected density because of the large size of the study area and the relatively short distances over which rabbits generally move (less than 1 mile: Stoddart, unpublished data; Nelson, 1970; and Rusch, 1965). Therefore, it was not included in Equation (9).

Equation (9) is a mathematical identity. If the equation is to become a functional, predictive model, ideally each independent variable (those variables on the right hand side of the equation) would be described mathematically in terms of the environmental factors which affect it. These functional relationships would then act together to form the model. In practice where resources are limited, the most productive results are obtained from efforts concentrated on finding functional relationships for those variables which contribute most to variance in the dependent variable.

Rabbit model

I first attempted to determine which variables in Equation (9) should be explored; i.e., which ones accounted for most of the observed change in density from year to year. It was apparent that variation in the number of ova produced per surviving female, $\sum_{i=1}^{5} F_i$, was relatively small (Table 15). There was only a 50 percent difference between the low of 13.2 in 1966 and the high of 19.8 in 1968. Also, there was no constant relationship between the number of ova per surviving female and the rate of density change. For example, the population decreased in 1964 and 1967 (Table 1), years of highest ova production with the exception of 1968. In 1970, when ova production reached its lowest level with the exception of 1966, the population increased.

Changes in density are a function of both natality and mortality. One would, therefore, normally expect changes in density to reflect variations in natality rate unless the variations in natality rate were masked by relatively more extreme variations in mortality rate. This was the case in my study. For example, there was an 860 percent difference in summer adult mortality from the low of 9 percent in 1968 to the high of 87 percent in 1964. And, in contrast to natality rates, there was a close relationship between mortality rates and annual, October-October, rates of density change. Multiple regression analysis (Figure 18) indicated that about 85 percent of the variation in October-October density change was associated with changes in mortality rate of adults from October-October and juveniles from birth-October. The October-October mortality rates were calculated from the summer adult and winter population mortality rates (Tables 11 and 12) using the equation: $M = a + b - ab$. M is the October-October mortality rate and a and b are the summer and winter mortality rates.

Since variation in mortality was apparently responsible for much of the variation in annual rates of density change, I looked for functional relationships between density change and mortality factors. For this analysis I divided October-October density change into October-March change and March-October change. October-March change in density was plotted as a function of the independent variable, coyote/rabbit ratio (Figure 19). About 90 percent of the variation in October-March density change is associated with variation in the coyote/rabbit ratio.

The coyote/rabbit ratio was calculated for each October-March period by dividing the mean number of coyotes/square mile for the period by the mean number of rabbits/square mile for the period. Coyote density estimates were obtained by multiplying Clark's (1972) coyote indexes for the period 1963-70 by 2.67. I used the conversion factor, 2.67, so coyote density estimates would be within the range of coyote densities estimated for Curlew Valley (Clark, 1972).

Mean numbers of rabbits/square mile were calculated by: (1) plotting a continuous curve of rabbit density over each period;

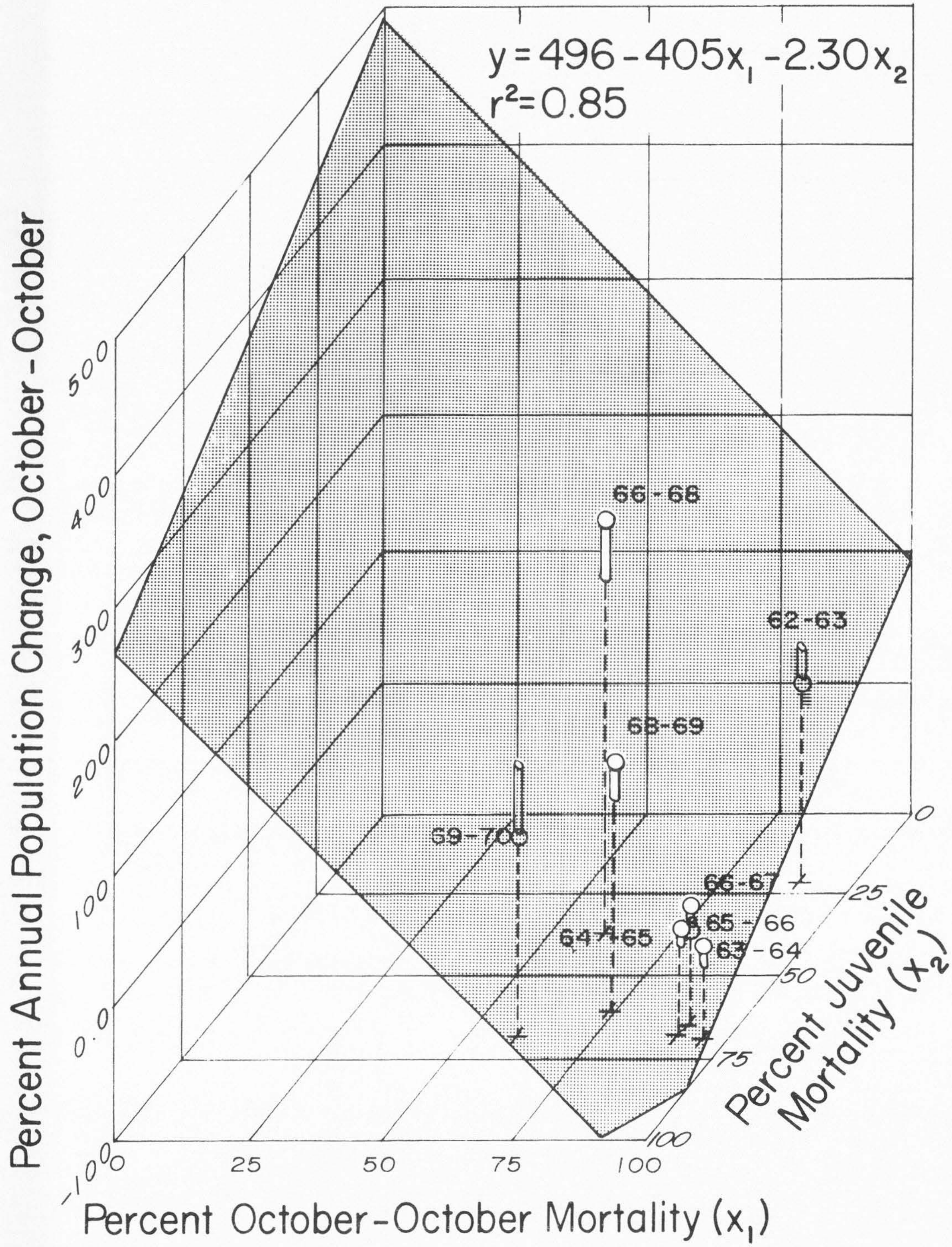

Figure 18. Multiple regression of percent annual population change, October-October, on percent annual mortality of adults and percent mortality of juveniles from parturition to fall census.

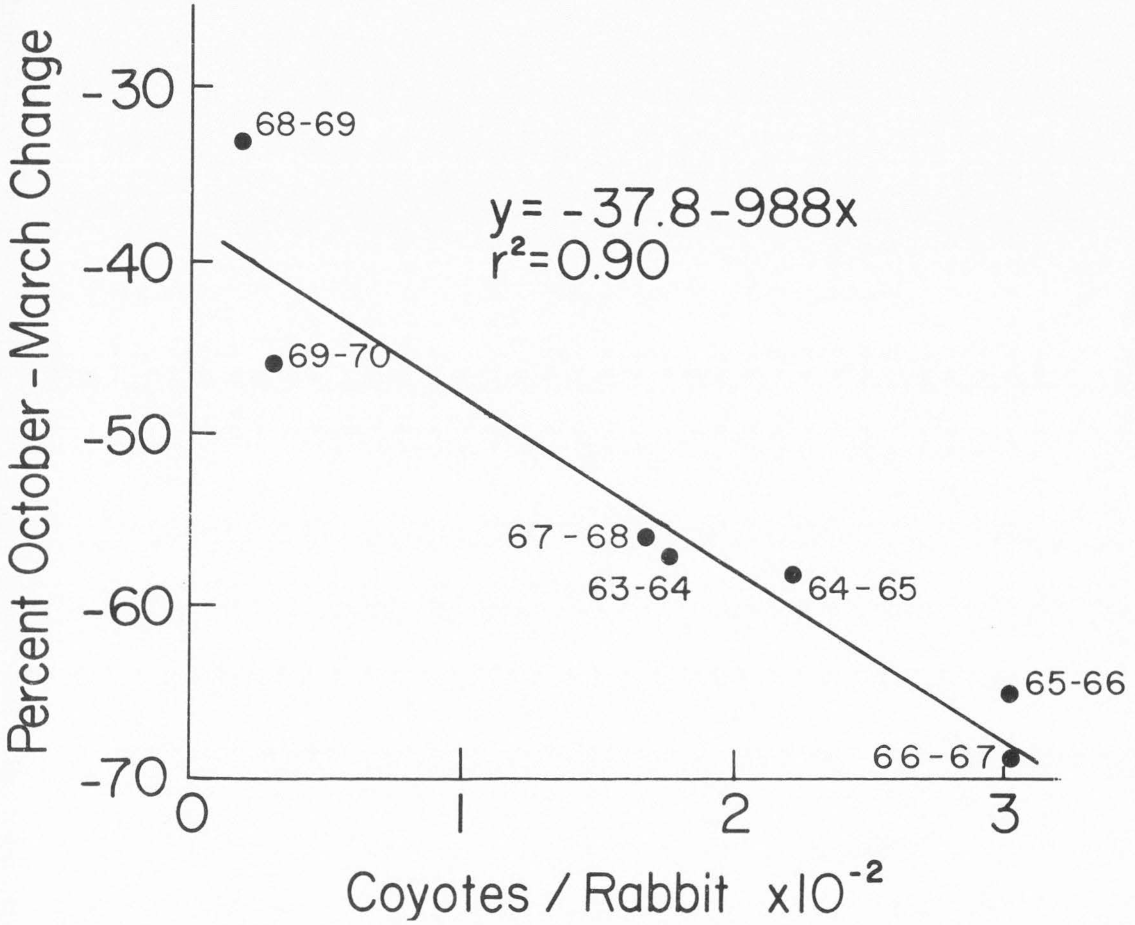

Figure 19. Linear regression of percent October-March change in density on the coyote/rabbit ratio over the study area.

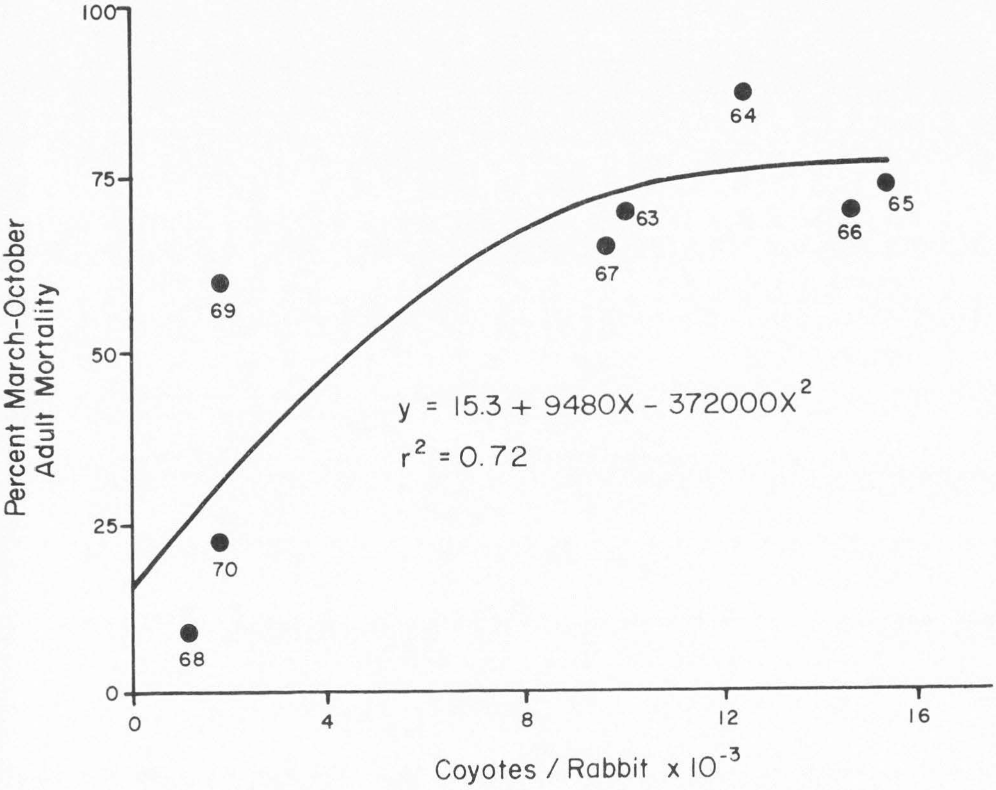

Figure 20. Curvilinear regression of percent March-October adult mortality on the coyote/rabbit ratio over the study area.

(2) integrating over the curves; and (3) dividing the integrals by the March-October time period. The continuous rabbit-density curves were obtained through utilization of absolute adult densities (Table 2), summer adult mortality rates (Table 12), number of fetuses per female (Table 17, Column E), and juvenile mortality rates (Table 13). Juveniles were arbitrarily considered part of the population at 40 days postpartum. I used absolute rabbit numbers rather than index values so that the coyote/rabbit ratios would represent the best estimate of the true ratio of coyotes to rabbits in the study area.

During the March-October period I divided the population into adults and juveniles and examined the two classes separately. March-October adult mortality was plotted, again, against the coyote/rabbit ratio (Figure 20). The second-order equation explains about 72 percent of the observed variation in adult mortality.

Finally, birth-October mortality (expressed in the model by a 10-day survival rate) of juveniles was plotted as a function of two independent variables: (1) coyote/rabbit ratio; and (2) mean rabbit density from March-October (Figure 21). This function explains 82 percent of the observed change in juvenile survival.

The 10-day survival rates were calculated by trial and error. I assumed juvenile survival rate each year to be constant from birth-October. A rate was selected so that when applied to the total juvenile population each 10 days, the juvenile population sustained a total mortality at the time of fall census equal to those values in Table 13.

Observed juvenile mortality in 1963 was 22 percent (Table 13).

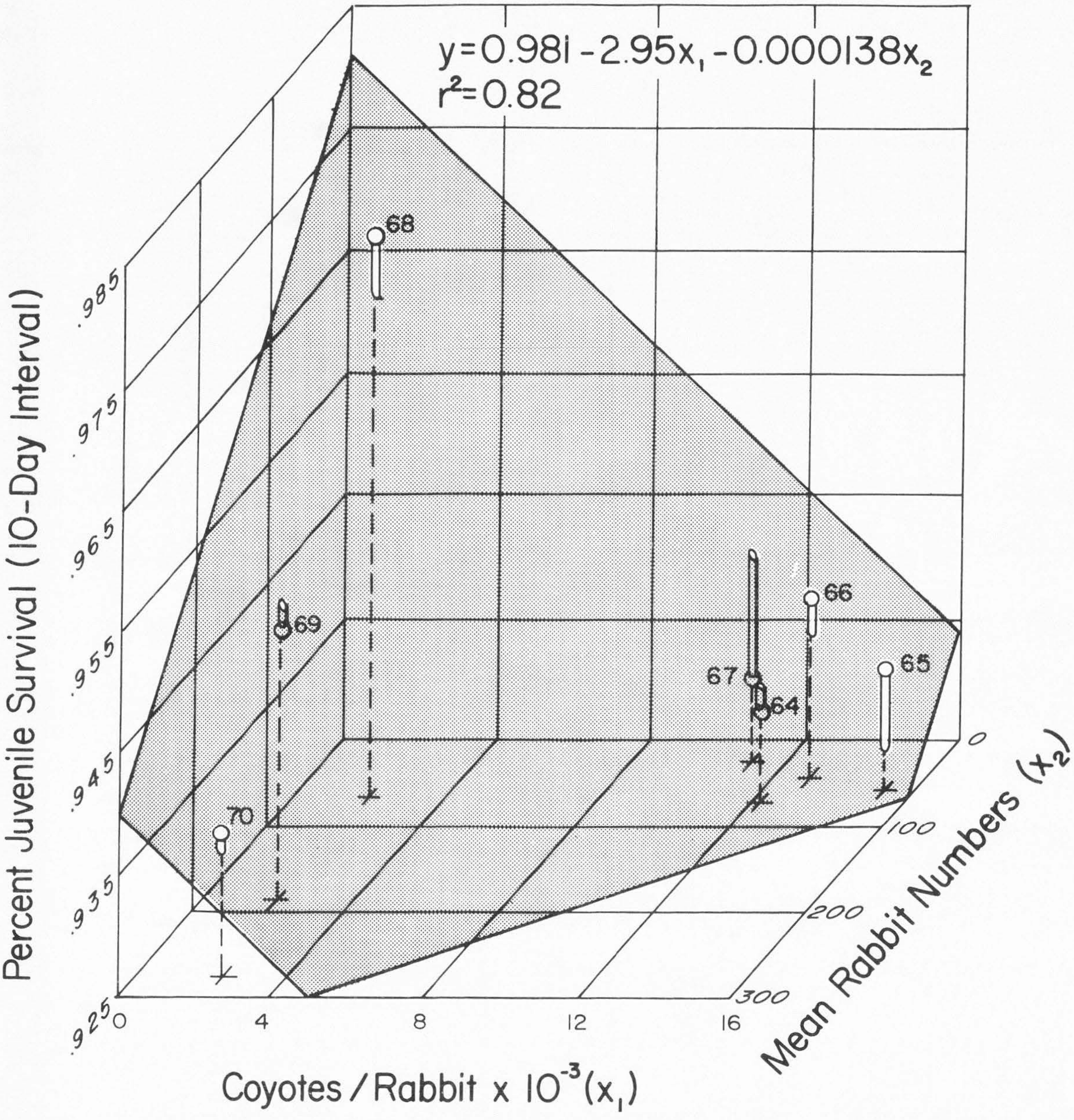

Figure 21. Multiple regression of percent juvenile survival (calculated as a 10-day survival rate) from parturition to fall census on the coyote/rabbit ratio and mean rabbit numbers/square mile during the period March-October. See text for calculation of 10-day survival rates.

This is the lowest value measured during the course of the study and is not consistent with my model of juvenile mortality in subsequent years. Becuase of this inconsistency and because it occurred during the early stages of the study, I suspect it may have resulted from error in the collecting and/or data-processing procedure. Hence, I did not use 1963 juvenile mortality data in Figure 21 or in subsequent figures which utilize juvenile mortality.

Rabbit density _per se_ will likely not affect juvenile mortality rate as indicated in Figure 21. Rather, rabbit density in this model represents one or more density-dependent mortality factors such as reduction in postnatal care by females, disease, or starvation of juveniles. At present, I do not know what mechanisms are involved, but I do know that observed juvenile mortality has been increasing with rabbit density independently of the coyote/rabbit ratio (Figure 21).

Since March-October adult mortality was well correlated with coyote/rabbit ratios and juvenile mortality was correlated with both coyote/rabbit ratios and rabbit density, I used these two independent variables (coyote/rabbit ratio and rabbit density) in a model to describe the observed March-October change in density (Figure 22). This model accounts for 97 percent of the observed changes in March-October density.

Equation (9) can be modified to accomodate directly the models in Figure 19 and 22. Since ${}^{N_{t+1}}/{}_{N_t} = \frac{N_{t+1}}{N_m} \times \frac{N_m}{N_t}$ where N_m equals the number of rabbits at the end of March and $S_{pw} = \frac{N_m}{N_t}$, $\frac{N_{t+1}}{N_m} = (Y + S_{as})$ where Y equals the contents of the brackets in Equation (9). But, since N_{t+1}/N_m equals some function of adult and juvenile survival rates (cf. Figure 18), Equation (9) is equivalent to:

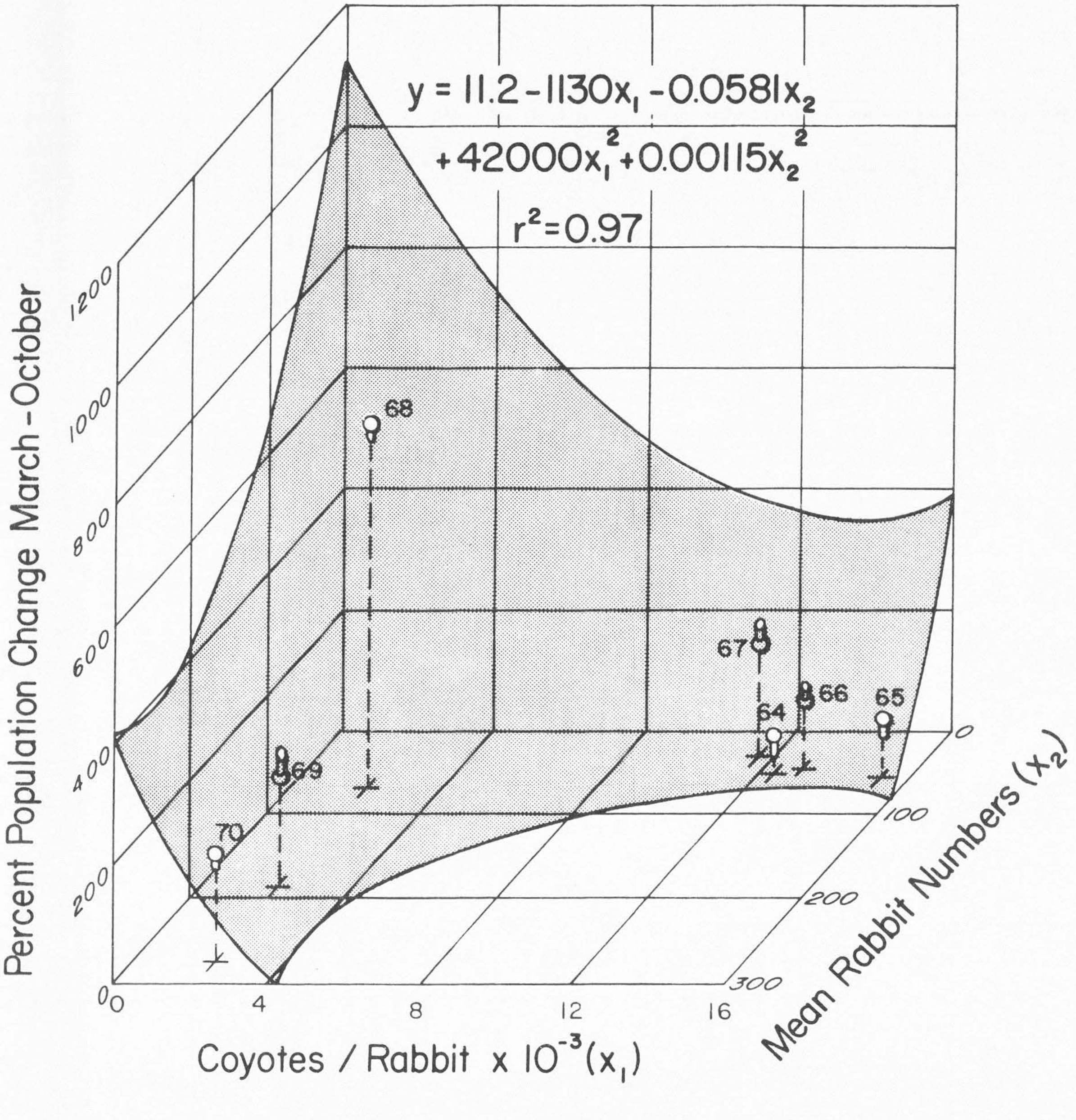

Figure 22. Multiple regression of percent population change from March-October on the coyote/rabbit ratio and mean number of rabbits/square mile during the March-October period.

$$N_{t+1}/N_t = S_{pw}\ f_1(S_{as}, S_{post}) \ldots\ldots\ldots\ldots \quad (10)$$

Equation (10) is a simplified version of Equation (9) where F_i, P_i, and S_{pre_i} have not been considered because of their relative constancy. Equation (10) can be written in the form:

$$N_{t+1} = N_t[1 + f(\text{coyote/rabbit})][1 + g(\text{coyote/rabbit, mean rabbit density})] \ldots\ldots\ldots\ldots \quad (11)$$

Estimates of the functions f and g are the models in Figures 19 and 22 respectively. When these two models are substituted for the functions in Equation (11), the best statistical estimate of N_{t+1} becomes:

$$N_{t+1} = N_t(1 - 37.8 - 988X_1)(1 + 11.2 - 1130X_2 - 0.0581X_3 + 42000X_2^2 + 0.00115X_3^2) \ldots\ldots\ldots\ldots \quad (12)$$

The density changes indicated by the model, Equation (12), can be compared with the observed data (Figure 23). This comparison or fitting of the model to the observed data is analogous to the fitting of any regression equation to observed data, except in this case the model is composed of two regression equations combined as indicated in Equation (11).

Variation in natality rates is not utilized directly in the model. It does, however, have an indirect effect since it influences the value of the coordinates, coyotes/rabbit and mean rabbit density, in Figures 19 and 22.

The data presented above suggest that when coyote/rabbit ratios are relatively high, coyotes are a major factor contributing to the mortality of adults and juvenile rabbits. There are other sources of evidence which suggest that coyotes, in fact, are responsible for

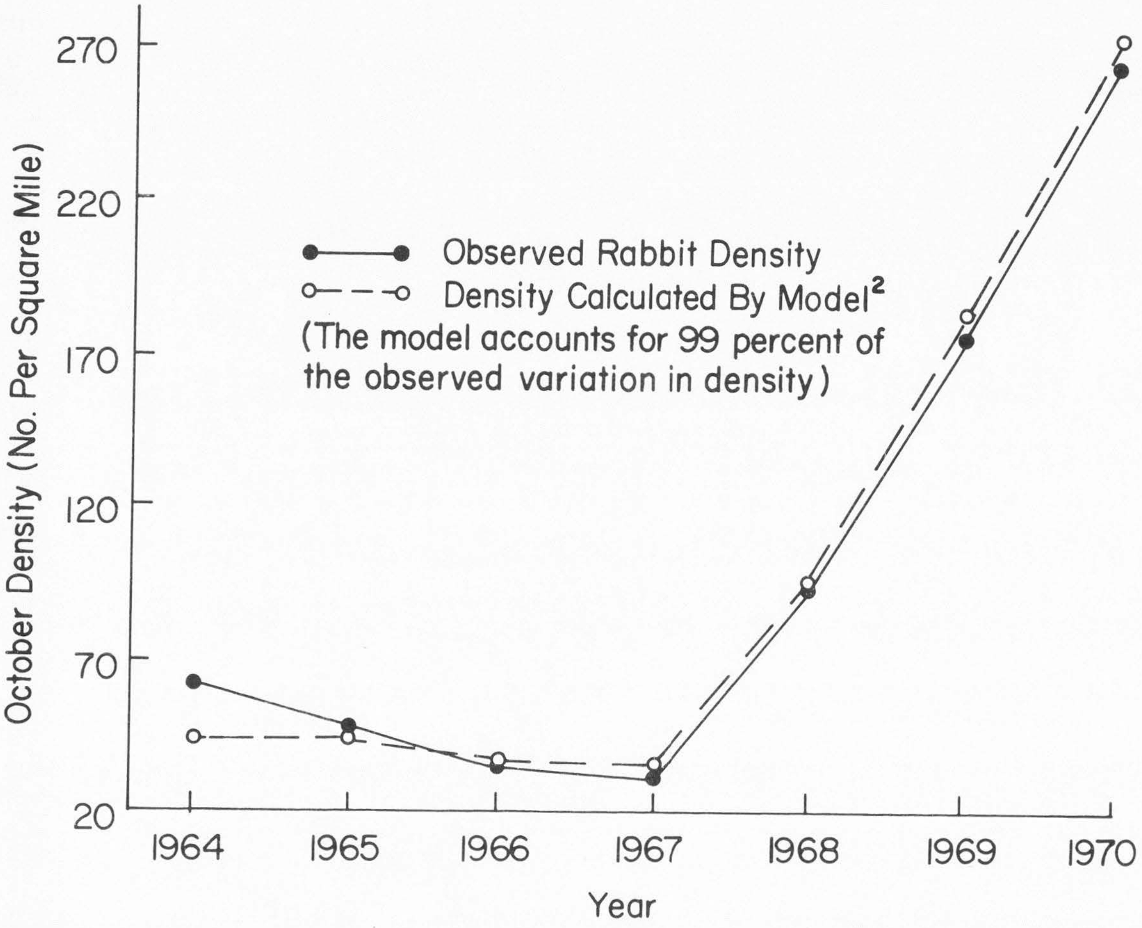

Figure 23. Plot of observed fall rabbit density over the study area and density estimated from the rabbit model from 1964-70.

considerable mortality in the rabbit population:

(1) I conducted a mortality study in 1968 and 1969 using radio telemetry to follow animals to their death and determine the causes of mortality. Mortality rates of the telemetered animals were consistent with those measured demographically. Therefore, I assumed that the mortality factors were also consistent with those operating on the rest of the population. Of those animals found dead about two-thirds were killed, in my opinion, by coyotes (Stoddart, 1970).

(2) Frank Clark estimated from food habits that a coyote killed on the average about 0.5-1.0 rabbit/day. The number of rabbits killed by coyotes can be estimated by multiplying this kill rate by the number of coyotes in the area. For most years this number corresponds well with estimates from the demographic studies of the total number of rabbits lost on the area (Wagner and Stoddart, 1972). The exceptions occurred in the summers of 1969 and 1970 when the loss of juveniles, as discussed above, was too great to be accounted for by mortality due to coyote predation.

The effect of this increased loss of juveniles in 1969 and 1970 is not immediately obvious from Figure 23 since there is almost a straightline increase in density from 1967-70. A plot of the log of the population density, however, shows the decreasing rate of growth from October-October (Figure 24, dashed line). The slope of the lines between census dates in Figure 24 are the instantaneous rates of population change.

Description and Summary of Population Change

The means by which mortality and natality rates have operated

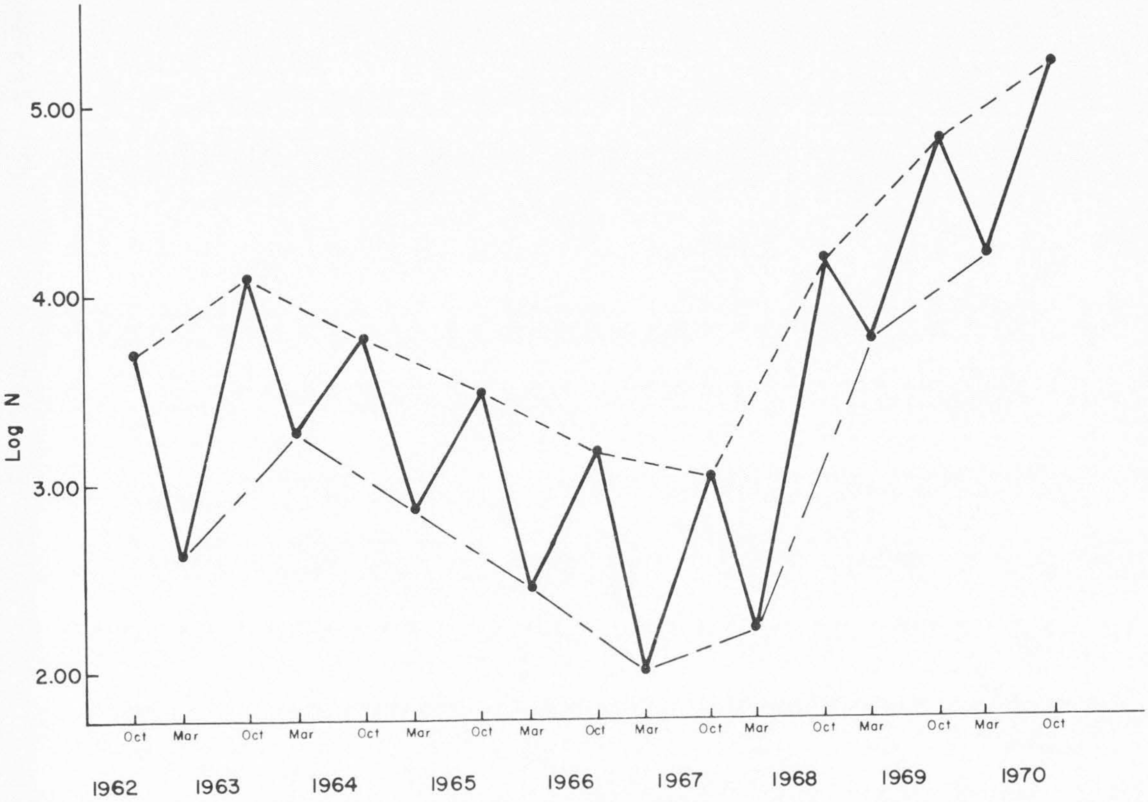

Figure 24. A plot of the log of rabbit density in March and October for nine years of the study, 1962-70. The slopes of the lines are the instantaneous rates of density change between census periods.

jointly to determine population density are summarized in Figure 25. The line connecting the open and closed circles (spring and fall indexes, respectively) indicates the observed change in density index between the consecutive spring and fall census periods. Changes between fall and spring are determined by October-March mortality rates of the total population (Figure 11). Spring-fall changes result from the combined effect of summer adult mortality rates (Figure 12) and, most importantly, the production rate of fall juveniles as measured per female alive January 1 (Table 20, Column D). (The relative rates of change from spring-fall and fall-spring are indicated graphically by the slope of the solid line in Figure 24.)

Table 20 shows the relative contribution of natality rate (Column A) and combined mortality rates to the production of fall juveniles by females alive January 1 (Column D). The number of fall juveniles per female alive January 1 was calculated by dividing the fall juvenile index (Table 19) by the January 1 female index.

Variations in Table 20, Column A are due to annual differences in total number of eggs ovulated (herein considered "birth") per female surviving the entire breeding season. The reduction in numbers from Column A to B is due to preparturition mortality of juveniles (Table 14). Further reduction from Column B to C results from mortality of adult females during the breeding season. (The breeding season essentially started January 1.) Numbers are further reduced to those in Column D through postpartum mortality of juveniles (Table 13). The percentage of potential fall juveniles actually realized, Column E, ranged from 35 percent in 1968 to only 10 percent in 1964.

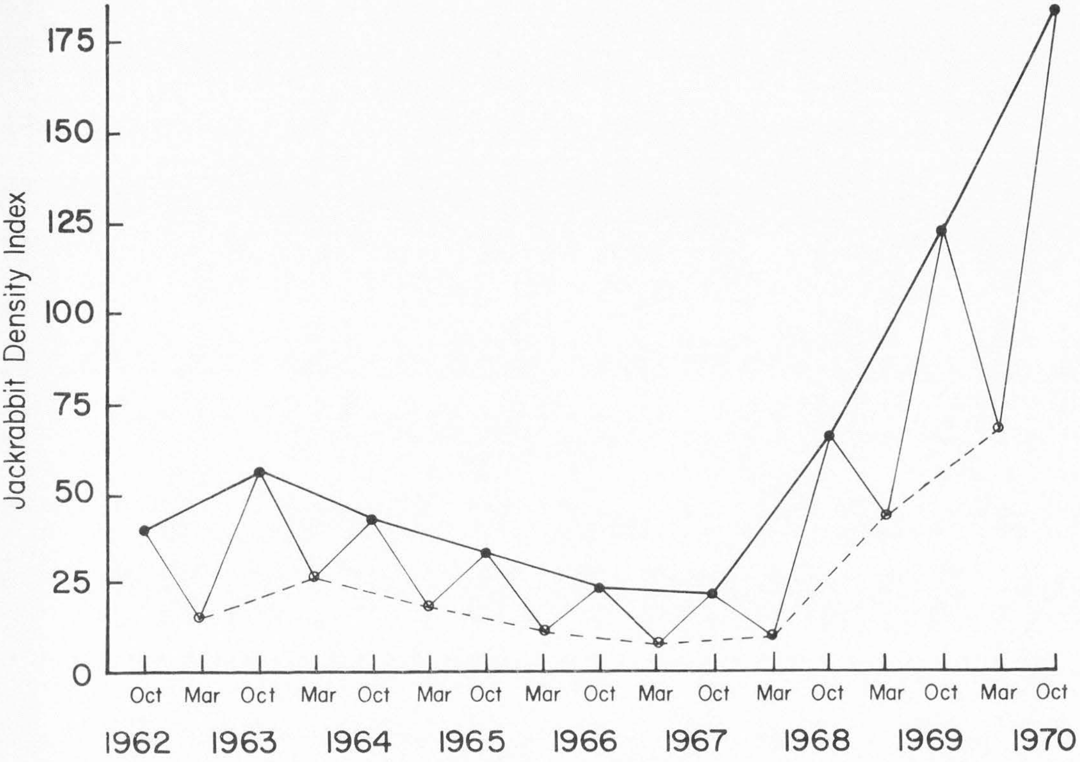

Figure 25. Plot of jackrabbit density index, estimated from results of 78 transects over the study area, from fall, 1962 to fall, 1970.

Table 20. Mean number of ova and fetuses produced per female surviving the breeding season, mean number of fetuses produced, and mean number of juveniles alive at fall census per female alive January 1, and percent of potential juveniles actually observed at time of fall census from 1963-70

Year	(A) Ova/female (Table 15)	(B) Fetuses/female (Table 16)	(C) Fetuses per Jan. 1 Female (Table 16)	(D) Observed Juv. in Fall per Jan. 1 Female	(E) Percent Potential Juv. Obser. (D/Ax100)
1963	15.4	13.5	5.4	4.1	27
1964	19.1	15.3	6.1	1.9	10
1965	14.6	13.1	6.3	2.1	14
1966	13.2	12.2	5.8	1.9	14
1967	19.3	18.9	7.3	2.4	12
1968	19.8	18.6	11.2	6.9	35
1969	16.1	14.1	9.9	3.9	24
1970	14.2	13.1	8.7	2.8	20

DISCUSSION

An understanding of the factors which determine mortality and natality rates is of fundamental importance to population studies, since these two parameters determine rates of population change and ultimately population density. Animal populations usually fluctuate about a long-term equilibrium density. It is generally agreed that the effects of some factors which influence mortality and natality rates must vary with density in order to maintain an equilibrium. The maintenance of equilibrium by these density-dependent factors is termed "population regulation" (cf. Wagner, 1969).

Because the effects of some factors on mortality and natality rates are subject to random change, population densities are forced away from equilibrium. Density-dependent influences are then either strengthened or relaxed to bring numbers back to equilibrium. There has been much debate by ecologists for many years over which specific factors regulate density (cf. Solomon, 1949). Some theories on population regulation may have application to hare populations. Thompson (1929) suggested an "over-flow" theory in which animals move from the most desirable habitats, where birth rate exceeds death rate, to less desirable habitats. Mortality rate in the less desirable habitats is high and thus these areas act as sinks for the more prime areas. Wynne-Edwards (1962) also described this type of dispersal activity as one form of social behavior which he thinks functions to limit density.

Pontrelli (1966) concluded that the population of jackrabbits at the Oakland Airport was regulated by juvenile migration from the area. The rate of migration increased with density. He implied that mortality rate of the migrating animals was high because of the inhospitable areas surrounding the airport. Juveniles were apparently restricted from food and resting areas by behavioral means and thus were forced to leave.

Christian and Davis (1957) suggest that there is an endocrine system response to increased stress due to social competition as density increases. Physiological changes resulting from changes in the level of various endocrines (cf. Selye, 1946) include reduced reproductive activity and increases susceptibility to some mortality factors.

Chitty (1967) and Myers and Krebs (1971) suggest that the frequency of various phenotypes and genotypes in the population may change with density. These changes in the population result in an adverse modification of the individual's environment. The outcome is increased mortality. Because of a feed-back system, mortality rates continue to increase and the density is depressed well below the equilibrium level. Krebs (1966) implied that observed decreases in natality in some declining populations of microtines may have been a result of these changes rather than a causative factor in population decline.

Green and Evans (1940) concluded from their 9-year study of snowshoe hare in Minnesota that there was no significant change in natality rate during a severe population decline. The decline was attributed to increased birth-February mortality in juveniles. They suggested the increased mortality was due to "shock disease" or hypoglycemic shock resulting from increased social stress. This condition results from adrenal insufficiency as Christian (1950) describes it and is one effect of endocrine-system involvement.

Chitty (1960 and 1967), in discussing Green and Evans' data noted that juvenile mortality became more severe with population decline. He did not believe the decline was due to shock disease, but instead, thought the data were consistent with his ideas of increased mortality due to a changing frequency of phenotypes and/or genotypes.

French, _et_ _al_. (1965) found prevalence of pregnancy and mean litter size to decrease with increased density in black-tailed jackrabbits in Idaho. They concluded that these two factors regulated density in a density-dependent fashion. Their results might be attributed to some type of physiological stress related to density.

In the present study, natality rate varied independently of density during years of population decline (Table 15). However, I found a continuous decrease in natality rate during the first 3 years of population increase. These results are supported by similar data of Meslow and Keith (1968) who studied the snowshoe hare population at Rochester, Alberta during 4 years of density decrease and 3 years of density increase.

I found that juvenile mortality remained high during years of population decline in Curlew Valley jackrabbits. This is consistant with results of Green and Evans, Newson and DeVos (1964) and Meslow and Keith. One can only speculate as to why juvenile mortality remained high in their studies even though densities were depressed. I am reasonably confident that high rates of juvenile mortality during population decline in my study resulted from coyote predation. As population density declined, the coyote/rabbit ratio remained relatively high. This resulted in a reduction of rabbit numbers to a level which was likely well below the equilibrium density.

Meslow and Keith found that increases in adult mortality during years of population decline were not as great as the increases in juvenile mortality. This is contrary to my findings. Adult mortality during declining years remained relatively high as did juvenile mortality (Table 11, 12, and 13). The high rates of adult mortality were, again, apparently a result of coyote predation.

During years of population increase, adult mortality decreased markedly and was, in general, consistent with values expected from the coyote/rabbit ratios (Figures 19 and 20). Changes in juvenile mortality during population increase were not as expected. There was a marked reduction in juvenile mortality during the first year of increase, but, in 1969 and 1970 mortality was much higher than could be accounted for by the coyote/rabbit ratio (Figure 21). As previously mentioned, I do not know what factor or factors are responsible for the observed increase in juvenile mortality.

The increased juvenile mortality with no concurrent increase in summer adult mortality in 1970 resulted in the lowest fall juvenile-to-adult ratio recorded during the study (Table 8). This is markedly different from the results of Meslow and Keith. They observed an increase in juvenile-to-adult ratio from 36 percent yearlings in spring when the population was decreasing to 90 percent yearlings during the third year of population increase.

During the years of rabbit population decline, the coyote population also declined. But, more importantly, coyote numbers declined at a faster rate than rabbit numbers (cf. Wagner and Stoddart, 1972). By 1967, the coyote/rabbit ratio was less than it had been during the previous four years. As a result, adult and juvenile mortality rates were also at a 4-year low (with the exception of juvenile mortality rate in 1963), and the rate of population decline was slowed. In 1968 the coyote/rabbit ratio was at the lowest level during the study. Both adult and juvenile mortality rates were markedly reduced from the previous year and the population density increased significantly (Table 1).

Meslow and Keith found that reduced natality rates during some years contributed substantially to population decline. They also noted that in addition to reduced mortality rates of both adults and juveniles, a sharp increase in natality helped to reverse the down trend. Green and Evans thought, however, that a reduction in juvenile mortality from 92 percent one year to 9 percent the next year was solely responsible for the reversal in density trend in their population.

Since rate of density change is a function of both mortality and natality rates, variation in natality in my study certainly had some effect on density change. The relative effects of natality and mortality on the number of juveniles produced each year are quite evident in Table 20. Apparently variation in natality was of little consequence to the general population trend.

Because variation in natality rate had little effect on population trend, I did not include natality as an independent variable in the jackrabbit model. As Watt, (1968) stated, only those independent variables which make an important contribution to the variance in the dependent variable under study are included in a model. In the future, however, as rabbit density continues to increase and/or starts to decline, natality may become relatively more variable and therefore assume greater importance. Similarly, new mortality factors, such as disease, may take on an important role. Consequently, the model will need to be revised if it is to continue to accurately describe density change.

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APPENDIXES

Appendix A

Testis Weights

Monthly mean testis weights for all years are plotted in Figure 26. The weights are superimposed on the unweighted pooled, 9-year means for each month as a reference for comparison between years. Chronology of testis weight change varied between years. The variation was apparently related to variation in rates and dates of conception. There were 5 years (1963, 1965, 1966, 1969, 1970) when the fourth-litter conception rate was not 100 percent (Table 3). These were the same 5 years (with the questionalbe exception of 1963) that testis weights decreased earliest at the end of the breeding season. The early first-litter conception dates in 1969 and 1970 (Figure 15) were likewise consistent with marked, early increase in testis weights for these years.

Meslow and Keith (1968) also found a low rate of fourth-litter conception with early decline of testis weight. They suggested that termination of the breeding season is contingent on the loss of male potency. I suspect, however, that factors which bring about the end of the breeding season are affecting both females and males.

Each year of my study testis weights began to drop rapidly about the same time that fourth litters were being conceived. As pointed out by Meslow and Keith, the females have no comparable organ by which their breeding status can be determined. However, I estimated that 57 percent of the females which had conceived during the fourth littering period in 1966 (previously discussed) lost their litters

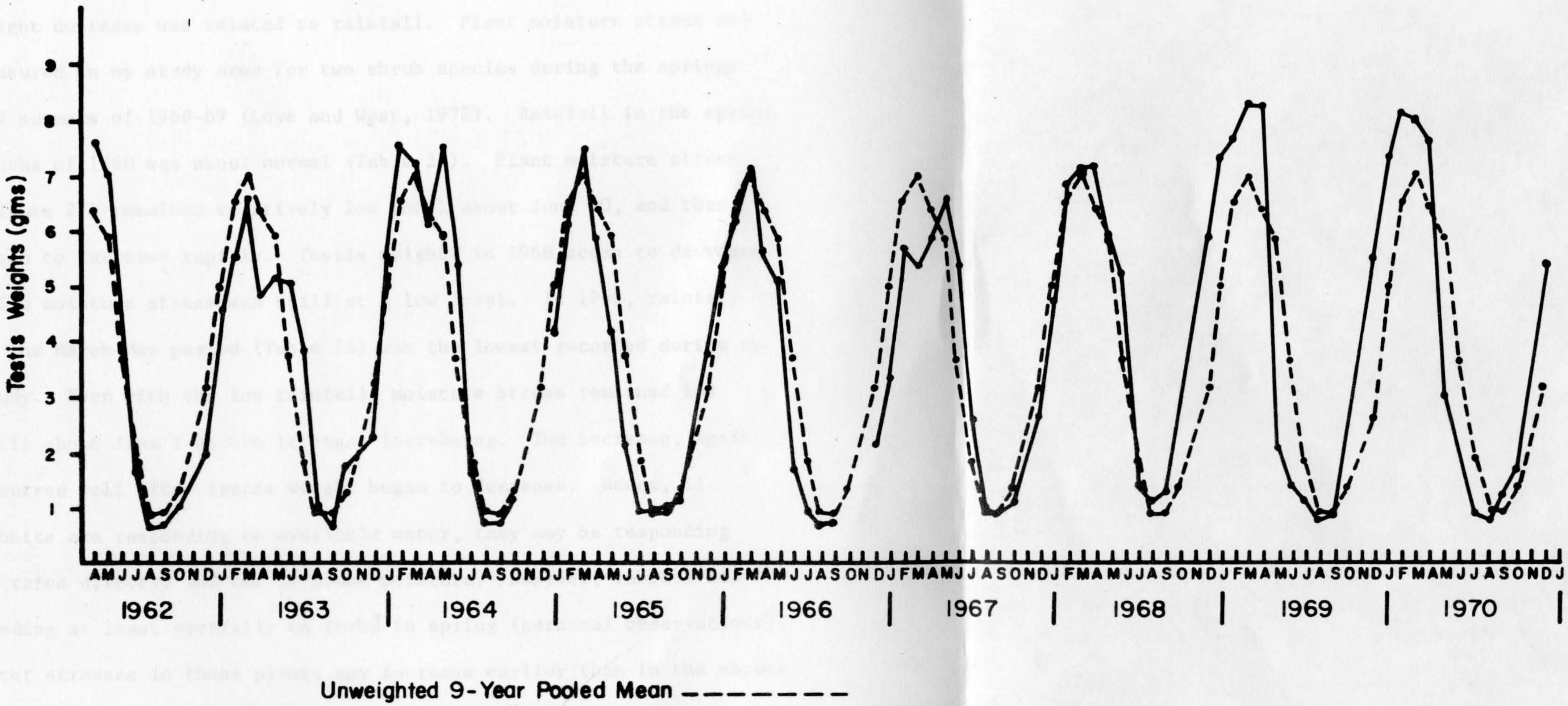

Figure 26. Unweighted 9-year pooled mean testis weights for each month and mean monthly testis weights from 1962-70.

in toto. Apparently the reproductive season of these females had come to a close about the same time as the reproductive season for the males. I suspect that loss of part of the fourth or fifth litters occurred in other years at the same time testis weights were decreasing, but because of the particular dates on which collections were made the evidence has not been conclusive.

I have some evidence that variation between years in testis-weight decrease was related to rainfall. Plant moisture stress was measured in my study area for two shrub species during the springs and summers of 1968-69 (Love and West, 1972). Rainfall in the spring months of 1968 was about normal (Table 21). Plant moisture stress (Figure 27) remained relatively low until about June 20, and then began to increase rapidly. Testis weights in 1968 began to decrease while moisture stress was still at a low level. In 1969, rainfall in the March-May period (Table 21) was the lowest recorded during my study. Even with the low rainfall, moisture stress remained low until about June 1 before it began increasing. The increase, again, occurred well after testis weight began to decrease. Hence, if rabbits are responding to available water, they may be responding to rains directly and not to plant moisture. However, rabbits are feeding at least partially on forbs in spring (personal observations). Water stresses in these plants may increase earlier than in the shrubs measured.

The 3 years with highest measured April-May rainfall, 1963, 1964, and 1967 (Table 21), were also the years when testis weights decreased latest in the season. However, 1967 was the only one of these years in which a fifth litter was produced. Without knowing

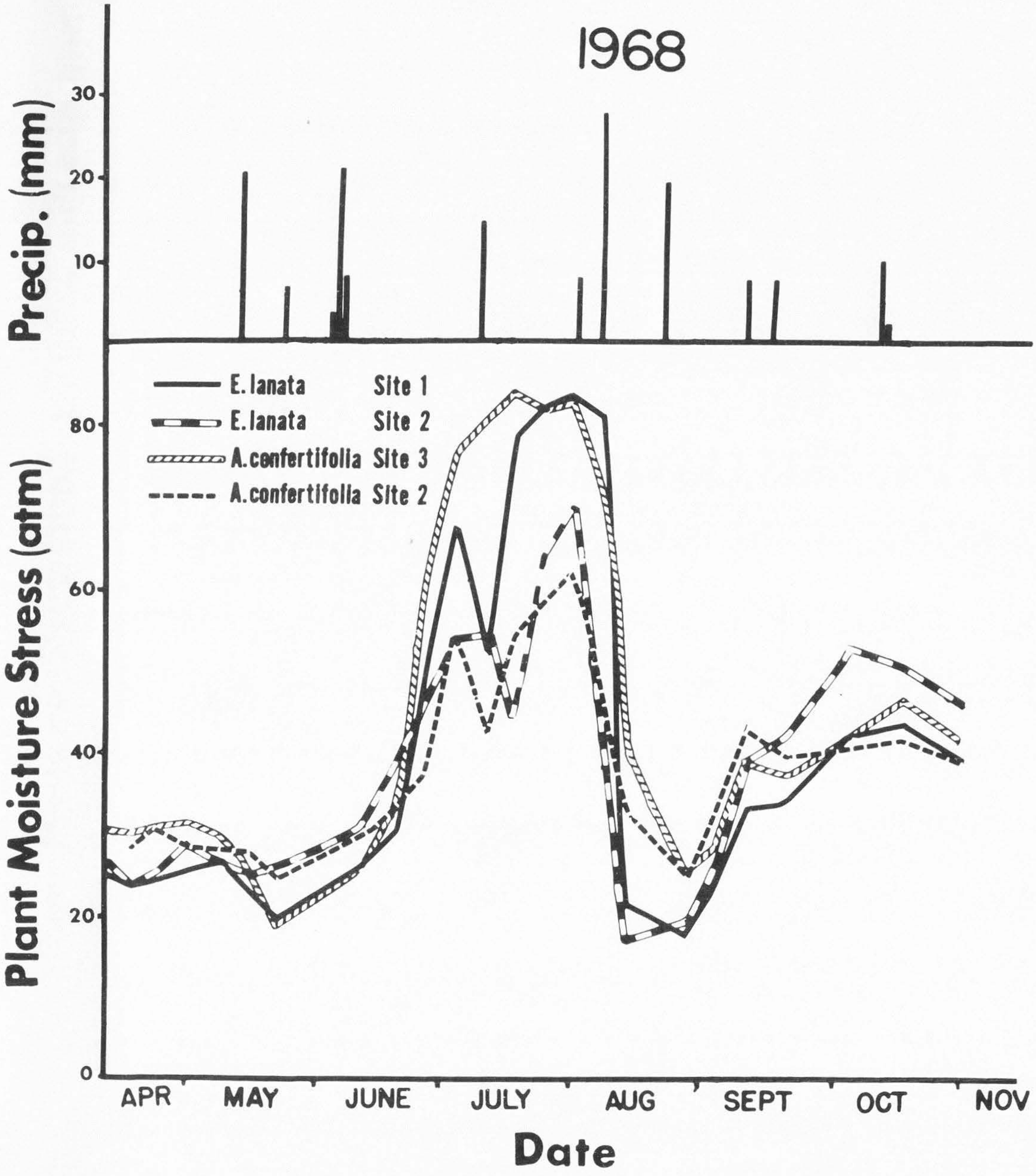

Figure 27. Trends of mean plant moisture stress for the 1968 and 1969 growing seasons with concomitant precipitation events; figure taken from Love and West, 1972.

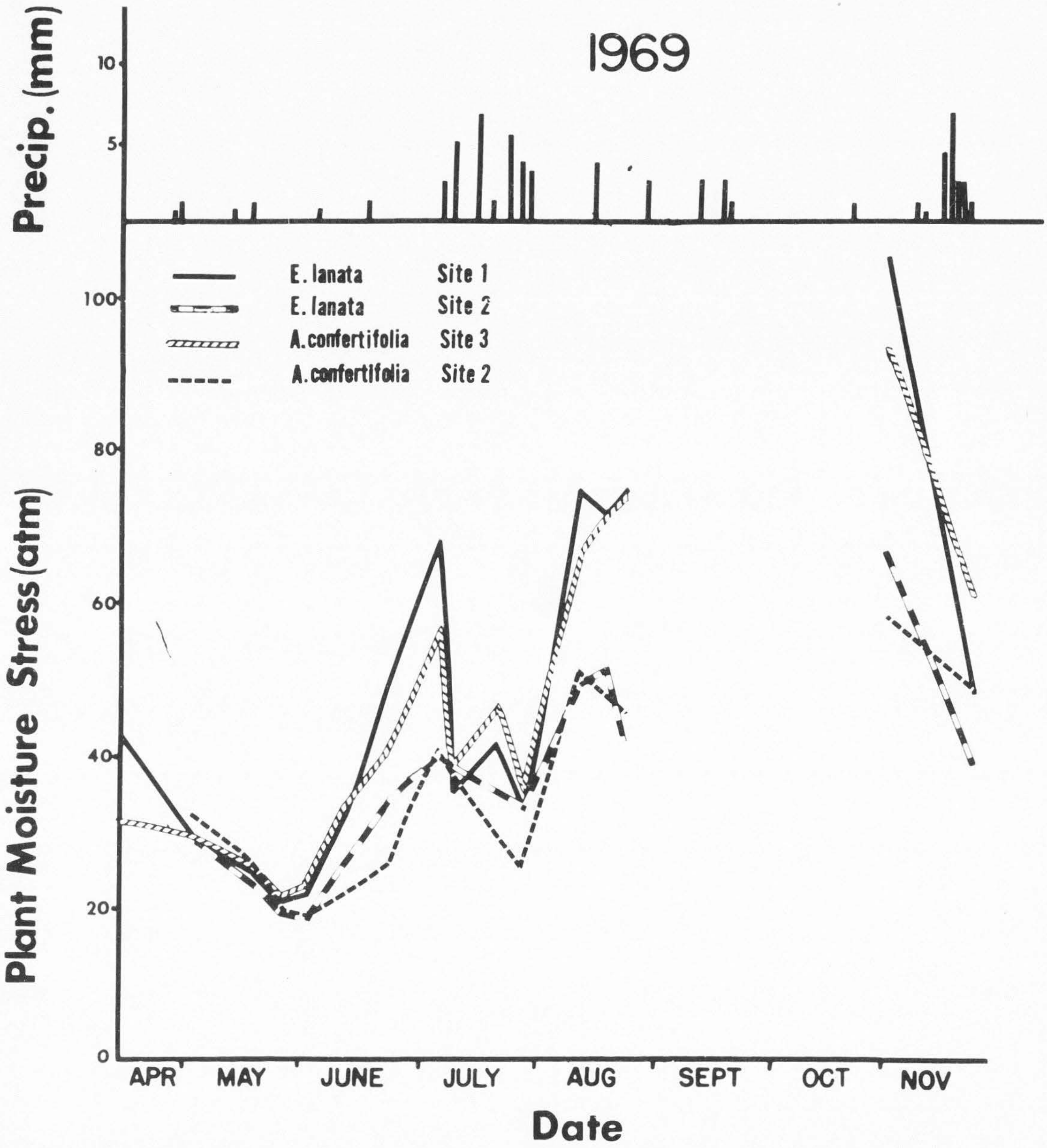

Figure 27. Continued.

specifically what rabbits are eating or the effect of particular rainfall events on plant moisture stress, it is difficult to determine what effect, if any, rainfall has on rabbit breeding chronology.

In 1970, spring precipitation rate was comparable to that in 1968. There is marked difference in the testis weights, however. If variation between years in testis weights is a result of extrinsic factors only, it is hard to reconcile the relatively extreme variation in 1969 and 1970 as compared with other years. In these two consecutive years the curves increased and decreased earlier than in any other years during the study.

French _et_ _al_. (1965) found the length of breeding season (as determined from dates of first and last observation of pregnant females during the breeding season) for jackrabbits in Idaho to decrease with rabbit density. They concluded that neither the length nor total production of young is greatly altered by weather. They did not weigh testes, however, so it is not known how testis weights may have varied with length of breeding season or density.

Pontrelli (1966) found no variation between years in testis weights, but did find that the start and end of the breeding season varied between years. He concluded that the variation resulted from changes in female behavior which was a function of variation between years in rainfall pattern.

Appendix B

Adult Body Weights

No differences were observed between the 9-year pooled monthly mean body weights and mean monthly weights for consecutive months

Table 21. Monthly precipitation rates (inches) for February-June, 1962-70[a]

Year	February	March	April	May	June
1962	1.06	0.40	0.42	1.68	0.44
1963	0.32	0.68	2.15	1.60	2.48
1964	0.19	0.77	1.38	4.00	1.59
1965	0.40	0.54	1.20	0.77	1.30
1966	0.44	0.28	0.11	0.92	0.61
1967	0.39	1.33	1.36	1.02	4.39
1968	0.99	0.66	0.41	1.36	1.60
1969	1.45	0.07	0.31	0.09	1.39
1970	0.20	0.43	0.43	0.95	1.58
Mean	0.61	0.57	0.86	1.32	1.71

[a] Precipitation data collected by Range Science Department, Utah State University.

over extended periods of time with the possible exception of summer 1969 when male weights were relatively high (Figure 28). Both male and female (exclusive of fetuses and uteri) 9-year monthly mean body weights varied significantly between months. Also a definite sexual difference existed in the seasonal chronology of weight change (Figure 28). Female weights increased from a low in January to a peak in May-June, decreased to a low in August, increased slightly again in September and October, and then decreased to the August level. Male weights decreased from a high in January to a low in April, increased through July to near the January level, then, like

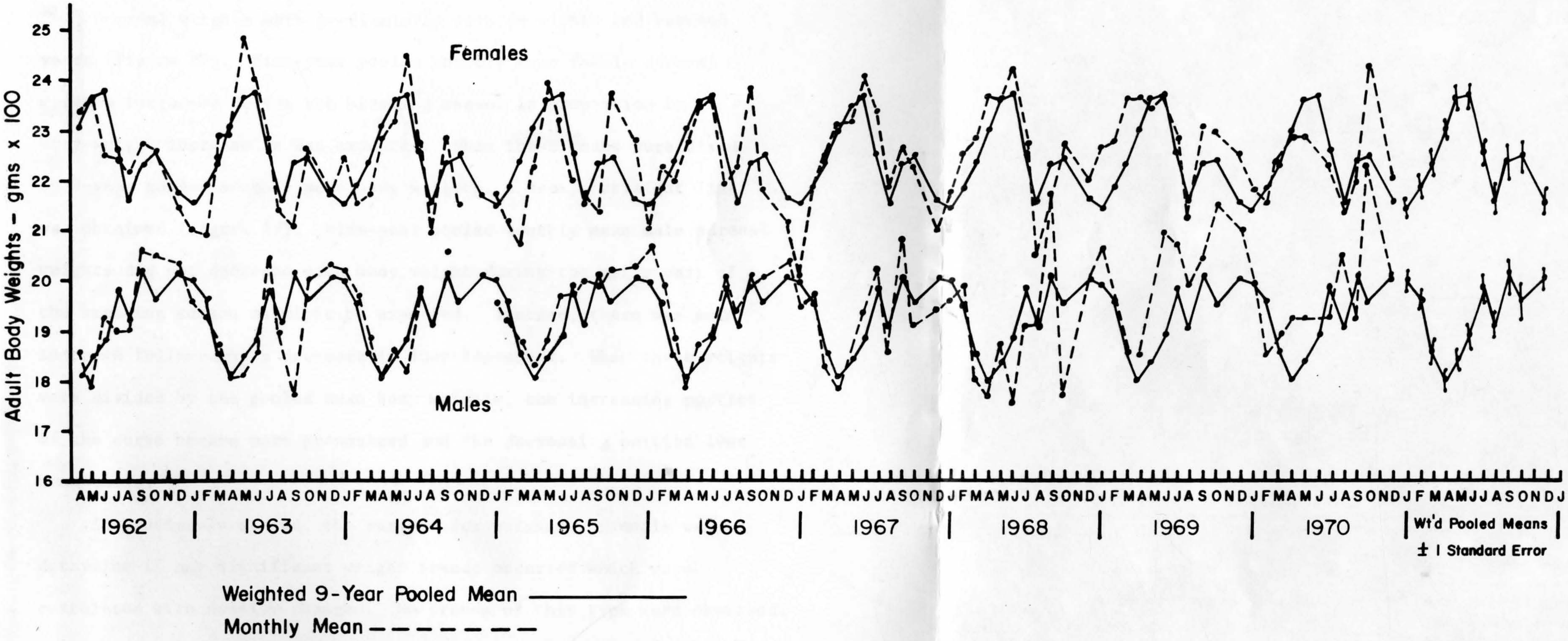

Figure 28. Weighted 9-year pooled mean adult body weight for each month and mean monthly adult body weight from 1962-70.

the female weights, decreased in August. From August there was an increase back to the January level. Body weights measured by Tiemeier (1965) showed very similar trends.

Appendix C

Adrenal Weights

Adrenal weights were particularly erratic within and between years (Figure 29). Nine-year pooled monthly mean female adrenal weights increased during the breeding season in proportion to body-weight increase as was expected. When these means were divided by 9-year pooled monthly mean body weights, a nearly straight line was obtained (Figure 29). Nine-year pooled monthly mean male adrenal weights did not decrease with body weight during the early part of the breeding season as might be expected. Instead, there was some increase followed by a decrease in June-September. When these weights were divided by the pooled mean body weights, the increasing portion of the curve became more pronounced and the decreasing portion less pronounced.

As previously stated, the purpose for weighing adrenals was to determine if any significant weight trends occurred which were correlated with density changes. No trends of this type were observed.

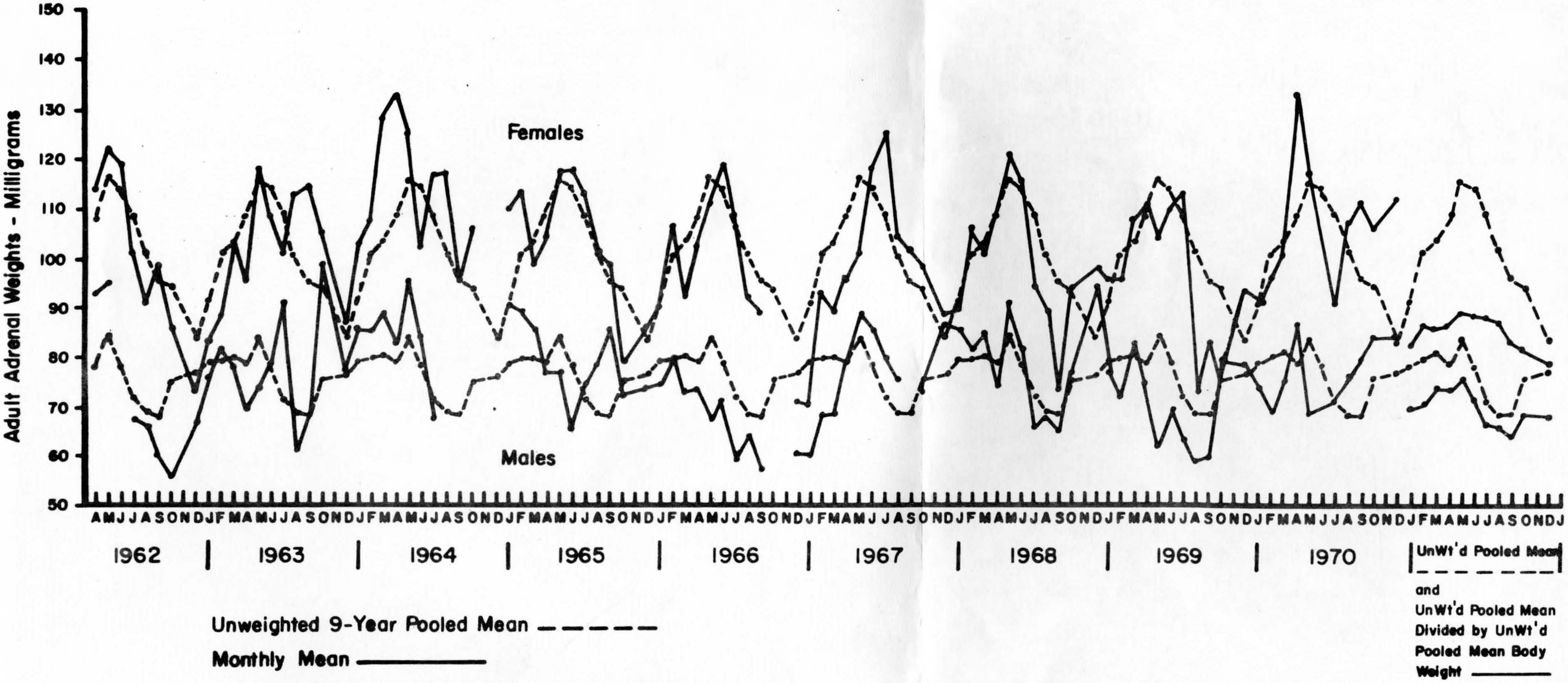

Figure 29. Unweighted 9-year pooled adult mean adrenal weight for each month and monthly adult adrenal weight from 1962-70.