THE ECOLOGY OF THE BLACK-TAILED JACKRABBIT (*Lepus californicus melanotis*, Mearns) IN SOUTHWESTERN KANSAS

by

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INTRODUCTION AND REVIEW OF LITERATURE

Many mammal populations are subject to extreme fluctuations in numbers over a period of years. In some instances, particularly noticeable in the more northerly residing species, these fluctuations appear to recur at definite time intervals and the levels of population abundance are therefore said to be cyclic. In general, mammal populations in the southern part of the United States do not show such pronounced fluctuations and do not seem to be cyclic in nature.

A classic illustration of what apparently were well defined population cycles was found in a study of trapping records of the snowshoe hare (*Lepus americanus*) by MacLulich (1937). The trapping records showed that this animal had minor peaks of abundance every third year and major peaks every nine to ten years. The causes for the fluctuations of the snowshoe hare, and other mammals whose populations appear to be cyclic, have been the philosophical subjects of many publications since the early part of this century. To date no one has been able to state a reason for these cycles to the complete satisfaction of all workers concerned. A comparatively recent development in mammal population research occurred in 1951 when Cole postulated the theory that cycles were in reality only random oscillations of populations and that many mammalian cycles were only artifacts of handling populations data. Thus the principal objective of mammalian population studies today rests in an undecided status. Most researchers agree that the populations of some mammals are definitely cyclic. However, serious doubts exist in the minds of many workers about the validity of population cycles occurring in all mammals for which they have been previously recorded.

Kansas, with its mid-continental position, apparently is in a transition zone where some mammals seemingly exhibit cyclic tendencies while others do not.

An animal which, although capable of increasing in numbers tremendously at certain times, apparently lies in an undetermined position in reference to population cycles is the Black-tailed Jackrabbit (Lepus californicus melanotis, Mearns). This jackrabbit is distributed throughout Kansas but is generally uncommon east of the flint hills region (Black, 1938). In Kansas, Hall (1955) stated: ". . . the numbers of the Black-tailed Jack Rabbits would increase year after year for several years and then in a period of only a few months or less the animals would die off. Contrary to popular belief, the length of the period of increase was not always the same; it varied from a few to many years". On the other hand, Cahalane (1947) stated: "In most regions jack rabbit populations fluctuate in cycles that average seven years in length but may vary between five and ten".

Whether cyclic in this state or not, it has become evident that jackrabbit populations are capable of assuming outbreak proportions from causes not readily understood. It has also become evident that the effects of these large jackrabbit populations exert an important economic influence upon the landowners of the region where they occur.

During the winters of 1954-'55 and 1955-'56, reports of heavy crop damage by jackrabbits in the western half of Kansas assumed proportions unequaled since the drought and accompanying jackrabbit increase of the 1930's. Since only a small amount of data were collected about this species during that population increase, it seemed an opportune time to attempt a thorough study of the causes and effects of jackrabbit population increases in the western half of the state.

In July of 1956, the author initiated a study of the ecology of the jackrabbit in southwestern Kansas. Field work on the project ended in June, 1957. The principle purpose of this study was to obtain information about the population dynamics of the animal. A cursory review of the literature revealed that even basic ecological factors, such as the jackrabbits' reproductive cycle, were unknown for the central region of the United States. It seemed unlikely that data collected for other subspecies in parts of the country climatically different from this area could be applied to populations work in this state. Consequently, this project has been directed along the lines of a basic ecological study in hopes that the data obtained could be utilized in an attempt to understand the basic causes underlying jackrabbit population fluctuations in southwestern Kansas. An attempt was made to relate drought conditions with certain aspects of the study because, in the past, jackrabbit population increases of consequence have apparently occurred only during drought periods. The increase to a large jackrabbit population only during a drought period would seemingly indicate that this species is not cyclic in southwestern Kansas.

Throughout the recorded history of the western United States several authors have commented on the amount of crop damage and the large numbers characteristic of population increases. Population fluctuations for this species have been recorded or mentioned by Bailey (1931) in New Mexico, Taylor (1948) in Texas, and Kelson (1951) and Durrant (1952) working in Utah. Hall (1946) stated that populations of the black-tail fluctuate markedly in Nevada but that the fluctuations are not consistent over a wide area. Woodbury (1955) charted an annual cycle of L. c. deserticola suggesting that a periodic difference in juvenile mortality would cause a secular cycle similar to that shown by the snowshoe hare, providing that the black-tail was cyclic in that locality.

Various aspects of jackrabbit biology have attracted some scientific study. Palmer (1897) made an early attempt at recording the taxonomic distribution of the jackrabbits. He discussed the breeding habits as known at that time, crop damage and methods of controlling the animals. Of interest, are the records of numbers killed in some of the "rabbit drives" during a population outbreak of the late nineteenth century in California. In one instance, 8,000 people driving the animals from 60 square miles killed an estimated 20,000 jackrabbits.

Burnett and McCampbell (1926) discussed the reproduction, habits, crop damage and controls of L. c. melanotis. As in the preceding publication, much of the material on the natural history of the animal was based on unsubstantiated opinions.

Seton (1929) wrote of many personal observations of the Black-tailed Jackrabbit but was forced to rely on assumptions based on the biology of the European Rabbit (Oryctolagus cuniculus)because of a lack of information on the jackrabbit. Some of these assumptions have proven valid; others were erroneously made. A few of his observations were made in Kansas and included statements about the home range and population densities of the species.

Vorhies and Taylor (1933), working with L. californicus ssp. and L. alleni alleni, studied the reproduction, habits, food, populations and the effect of the animals upon rangeland. An important outgrowth of this study was the concept of the jackrabbit as an "animal weed". In this, and later publications (Taylor, et al, 1935; Vorhies, 1936) the concept was developed that, rather than as popularly believed, the jackrabbit is an effect rather than a cause of rangeland depletion. They found that overgrazing on an area, unless severe, was usually accompanied by an increase of jackrabbits on that area and suggested that possibly this was due to the secondary successions being more suitable habitats than the climax. Additional evidence that these animals prefer moderately grazed rangeland is found in Phillips (1936) and Taylor and Lay (1944).

Haskell and Reynolds (1947) working in Arizona with pen-raised L. c. eremicus, studied the behavior, growth and developmental food requirements of juveniles and recorded findings on the reproductive cycle.

Lechleitner (1955) working with L. c. californicus, calculated the reproductive cycle, including percentages of prenatal mortality. He also extended the aging techniques formerly applied to cottontails (Sylvilagus sp.) to this species and worked on the home range, mortality and estimated the population of certain areas of the Gray Lodge Waterfowl Area in California. This is the most complete study of jackrabbit ecology to date but as will be shown later, many of the data were not applicable in Kansas.

Only a few workers have conducted population studies on the jackrabbit in this state. Carter (1939), using data obtained from questionnaires sent to early settlers, traced the increase in abundance of this jackrabbit and many other mammals found in Kansas back to 1860. When settlers first came to western Kansas, the black-tail was rare or absent in much of the state, but increased steadily in range and abundance until about 1920. Carter stated that the jackrabbit population in western Kansas was relatively stable for a period of years and then erupted in 1934. Wooster (1935, 1939) showed a relationship between the drought conditions of the 1930's and an increase in jackrabbits in western Kansas; conversely, the jackrabbits were fewer in numbers in wet years. Brown (1947) recorded the change in distribution in this state of the White-tailed Jackrabbit (Lepus townsendii campanius) and the black-tail. The White-tailed Jackrabbit formerly ranged extensively in Kansas but has since undergone a reduction in range until it is now found only in the northwestern counties of the state. An increase in the amount of cultivation is the reason given by Brown for the reduction in white-tail range while this same practice has been beneficial to L. c. melanotis.

MATERIALS AND METHODS

Because of the many-aspected scope of the project and in an effort to maintain clarity in this paper, details of methods and materials used for each phase of the study will be presented in the section where they are applicable.

Studies conducted on the ecology of L. c. melanotis may be briefly categorized as follows: (1) collecting an unspecified number of animals each month for laboratory examination; (2) making field observations which consisted of obtaining population trends for certain areas, recording data pertinent to these trends such as mortality and variation in the abundance of natural food, estimating crop damage and observing the animals for their movements, habits and basic behavior patterns; and (3) examining county records and questioning various persons about certain aspects of the jackrabbit population.

A total of 88 field days was spent in Kearny, Finney, Haskell and Grant Counties obtaining information relative to the outbreak of the jackrabbit population which was occurring in that area. The majority of this time was spent in the vicinity of the Arkansas River and the sand-hills lying to the south of the river in east-central Kearny County. During the summer of 1956, field work was conducted for 49 days in this sand-hill region for the purpose of obtaining fundamental ecological data on the jackrabbit and setting up routines to be followed throughout the rest of the study period. The remaining field days were spent in monthly trips to collect material for the reproductive and population density studies.

The primary study area was located approximately six miles southeast of Lakin in Kearny County. This area was chosen after conversations with residents indicated the presence of a dense jackrabbit population and heavy crop damage. The study area was assumed to be representative of the general region where heavy crop damage had been reported.

Monthly collections during the 12-month study period totaled 696 specimens. These animals were weighed, measured and examined in the field for abnormalities, obvious diseased conditions and reproductive status. The reproductive organs, and in some cases certain of the endocrine glands, were removed and brought back to Manhattan for laboratory examination.

The primary study area was censused six times and a companion area was censused twice during the one-year period. From these data it was hoped to determine any relationship existing between the changes in abundance of jackrabbits and the drought conditions present in the region.

The late afternoon and evening hours of all field days were spent collecting specimens, making movement or feeding counts or observing the animals' movements and habits from a series of observation points. Crop damage was estimated in order to relate the amount of damage to the field location, the effect of drought conditions on the natural food supply and the population density changes.

Throughout the study period many persons were questioned about their opinions on the population densities, amount of crop damage and the control methods being used in their locality. County records were investigated in an attempt to obtain information on the past fluctuations of the jackrabbit population.

HABITS

The Black-tailed Jackrabbit is essentially an animal of the more arid regions of the western United States. It is intimately associated with the short or mixed grass regions and with the true desert biome. Where cultivation has infringed upon these regions, excessive crop damage may result from the activities of these animals.

Jackrabbits spend the mid-day hours resting or dozing in their forms and activity is at a minimum during this period. Jackrabbit forms in this area, in general, are hollowed out areas varying from one to four inches in depth and otherwise are approximately the size of the animal. Forms are usually situated on the northeast or northwest side of sagebrush (Artemisia filifolia) or soapweed (Yucca glauca) plants to take advantage of the shade. Because of the large number of forms present in an area compared to the number of jackrabbits present, it was evident that the animals had more than one form which they regularly used. Jackrabbits sit in their forms facing outward, presumably in readiness to escape should the need arise.

Weather played a predominant role in jackrabbit activity and wind was by far the most important weather factor in limiting the amount of activity in a population of these hares. Hunting was done at night when the animals were normally active, and therefore hunting success was generally proportional to the amount of activity in the population. Wind velocities were recorded for each hunting trip as "strong", "moderate" or "absent". While as many as 40 animals were killed in a single hunt when the wind was at a minimum, five specimens was the maximum number collected during hunting trips when the wind was recorded as "strong". On two occasions, a strong wind which had been present during the afternoon and evening decreased in velocity between 12 P.M. and 2 A.M. and the effect on jackrabbit activity was readily noticeable. Only an occasional animal had been seen before the wind died down but after this occasion, feeding jackrabbits were in evidence in their usual large numbers. The effect of moonlight on jackrabbit activity is not known. The data collected in this regard are confusing and indicated that other factors were more important in regulating the amount of nocturnal movement.

Falling snow and fog limited the amount of nocturnal activity while rain and temperature seemed to have little effect upon the amount of movement. However, in a few instances jackrabbit activity was negligible for a period of a few hours following a sharp drop in temperature. As expected, blizzard conditions caused a cessation of all activities. During a three-day blizzard of exceptional intensity in March of 1957, jackrabbits were observed to crouch and permit the blowing snow to gradually cover them almost completely.

With the exception of the breeding season, the jackrabbit is not gregarious. Groups of animals, sometimes as large as 200 to 250 individuals, were seen during the winter months. These large groups were concentrations of feeding animals which were observed on winter wheat or milo fields. Smaller groups of two to five animals were noticed commonly only during the breeding season and the congregating by these animals was undoubtedly associated with the activities of that season.

Aggressiveness was uncommonly displayed by Black-tailed Jackrabbits in natural situations. Typically there were few interactions observed and usually two animals which were situated close to one another ignored each others' presence. Certain responses were noticed when interactions occurred and these observed responses took the form of head butting, biting, jumping one or two feet into the air, running in circles at high speed around another animal or simply an avoidance reaction. The acts of copulation and "boxing", as described by Vorhies and Taylor (1933), were never observed during the course of the study, and it was evident that these activities must generally occur only during the twilight or night hours. No evidence of territoriality was observed and it is improbable that territoriality occurs in this species with the possible exception of a female with young.

The most often observed behavior pattern was the chase. Observed chases varied in intensity from one instance of a clear-cut courting chase to much less intense chases which lasted less than three seconds. Many cases of these short pursuits were observed and almost all were the result of the same interesting sequence of events. This behavior pattern was initiated when two individuals would cease their normal activities and turn to face each other. One would then either attempt to butt heads with, or run in a tight circle around the other jackrabbit. The second jackrabbit would then chase the first individual for a few feet, often attempting to bite the pursued on the flanks. As if by mutual consent, this action would cease after a short duration and both animals would resume their original activities. The action usually was not repeated. In the author's opinion there are two possible explanations for this often observed action. The first is that one animal was a non-receptive female and was repulsing a male. However, most lagomorphs are receptive during a large portion of the breeding season, even at certain times during pregnancy. The second explanation is that this action is merely a form of play between two jackrabbits and that the pattern is not related to the breeding season. Because of the early sunset and time limitations, it could not be learned if this pattern was exhibited in the non-breeding season as well as the breeding season. Either or possibly both, depending upon the intensity of the interaction, could be a valid explanation for this behavior pattern. Other instances of animals running after one another appeared to be the result of a flushed jackrabbit frightening other animals in his flight and causing them to follow him away from the source of danger.

The habit of dusting by jackrabbits is an interesting activity and was observed commonly from one observation point located by a sandy trail in the sand-hills. Hares were observed to dig shallow forms in the loose sand or loess and roll over and over in them. The animals were heavily infested with ectoparasites, and through the binoculars they were seen to scratch at the ticks in their ears. It seems reasonable to assume that the dusting activity is an attempt to dislodge the ectoparasites.

Vorhies and Taylor (1933) show pictures of what they describe as a "jack-rabbit defecatorium" where jackrabbits dusted and defecated. Concentrations of pellets were common in the sand-hills (Plate I, Fig. 2)[1]. These concentrations were not defecatoriums but merely low spots into which water had carried pellets from the surrounding areas. No evidence was found in this study to support the idea that some jackrabbits defecate, at least a part of the time, in a definite area.

The natural food of the jackrabbit seems to be predominantly grasses and the smaller forbs. However, during periods of food shortage, they were observed to eat almost any green vegetation available. The water requirements are evidently slight and probably consist of the water obtained from green vegetation. During periods of food abundance, jackrabbits were commonly found in the center of extensive pasture areas where there was no free water available for as great a distance as seven miles.

SIZE AND AGE DISTRIBUTION

The size of an animal, either weight, length or a size index obtained by relating length to weight, has been used by workers as a criterion for aging mammals. Weight and total length, which was measured from the tip of the nose to the last tail vertebra, were recorded for all adult (Table 1) and juvenile jackrabbits collected. Excessive variation within the age classes prevented the use of these criteria as an aid in aging the animals.

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[1] All Plates are in the Appendix.

Table 1. Total length and weight of 205 adult males and 191 adult females.

Measurement	Mean	Range
Total Length		
Male	533 mm	477 - 594 mm
Female	551 mm	499 - 611 mm
Weight		
Male	91 oz	67 - 115 oz
Female	102 oz	70 - 135 oz

In computing weight averages, pregnant and non-pregnant females were grouped into one category. The range in weight of pregnant females with healthy litters was from 81 ounces to 133 ounces. The definite sexual dimorphism in weights of adults is not the result of including pregnant females in the averages. This difference in weight was evident during the non-breeding as well as the breeding season.

The standard mammal measurements of ear from notch to tip, hind foot and tail from base to tip of last vertebra were recorded for the initial 100 animals collected during the study period. The mean measurements in millimeters for 26 adult males and 19 adult females were as follows: males, tail 73, ear 107 and hind foot 126; and females, tail 79, ear 106 and hind foot 126. As was found in total length and weight, there was much variation present in the measurements of ear, tail and hind foot. Sexual dimorphism was not evident in these standard measurements with the exception of the length of the tail.

Measurements of the young at the time of birth were obtained indirectly by measuring animals taken by caesarean section. Five jackrabbits of two litters, taken by the author and another worker, which lived for a sufficiently long time to be considered at or near full term had the following mean measurements in millimeters: total length 158; tail 21; ear 29; and hind foot 44.

The degree of closure of the epiphyses and diaphyses of long bones has been used for aging lagomorphs. Among others, Thomsen and Mortensen (1946), Hale (1949) and Petrides (1951) used this method for aging the cottontail rabbit (Sylvilagus floridanus). Lechleitner (1955) used the degree of epiphyseal closure and formation of the bony trabeculae for aging L. c. californicus and was able to determine the monthly age distribution of this jackrabbit using three age classes. The left humeri, unless too badly fractured by shooting, were collected from all jackrabbits killed between November, 1956 and June, 1957.

Young of the year can be successfully aged by the degree of closure of the epiphysis and diaphysis only until all traces of this closure are gone in members of the earliest born litters. After that time, animals born in the first litters cannot be separated from adults. It became apparent when examining the humeri collected in November and December of 1956 that this aging method was of limited value in these months. A few differences were noticeable when comparing the age of animals as determined by the epiphyseal closure method and the age as determined by the size and condition of the reproductive organs. As will be indicated in the next section, the first young of the 1957 breeding season were born in February. On the assumption that reproduction began at about the same time in 1956, it would appear that this closure takes place at around the age of eight or nine months. Therefore, this criterion could not be used for aging in December and was of limited value in November because the closure of epiphyses and diaphyses in the humeri of jackrabbits born in February had occurred.

No evidence could be found during the study to indicate that female jackrabbits breed during the same breeding season in which they are born. There was also no evidence to indicate that some adult females remain barren throughout an entire breeding season. Because of these factors, young of the year females were easily aged through January by the size and condition of the uterus, ovaries and external genitalia. Many male young of the year jackrabbits were becoming sexually mature in December and by January all males collected were recorded as adult males. Consequently, all young of the year jackrabbits could not be separated from older animals during or after December on the basis of the size and condition of their reproductive organs. By using a combination of the two criteria, size and condition of the reproductive organs and epiphyseal closure, during the months when humeri were collected, it was felt that the November and preceding months' collections were aged accurately. Age determinations were also accurate after March, 1957. Therefore in only Decmeber, January, and February was there any degree of inaccuracy in aging the specimens.

The inability to detect young of the year males during January and February is evident in a monthly age distribution histogram for collected specimens (Fig. 1). The number of animals killed in January and February which were recorded as juveniles was entirely composed of females, while all males collected, whether born in the preceding season or not, were sexually mature animals and classified as adults.

Because jackrabbits were collected by shooting, the age distribution of collected specimens is slightly biased in that no animals too young to be foraging for food were killed. The smallest animal collected weighed 21 ounces and had a total length measurement of 334 millimeters. Haskell and Reynolds (1947) gave weight and total length growth curves for _L. c. californicus_ in Arizona which should be reasonably accurate for _L. c. melanotis_ in this region. The 21 ounce animal, when plotted on the growth curves for Arizona, was apparently about four weeks old. This animal was definitely foraging as its stomach was completely full of green vegetation. The error introduced into the age distribution by the failure to collect animals less than 20 ounces should be constant throughout the breeding season.

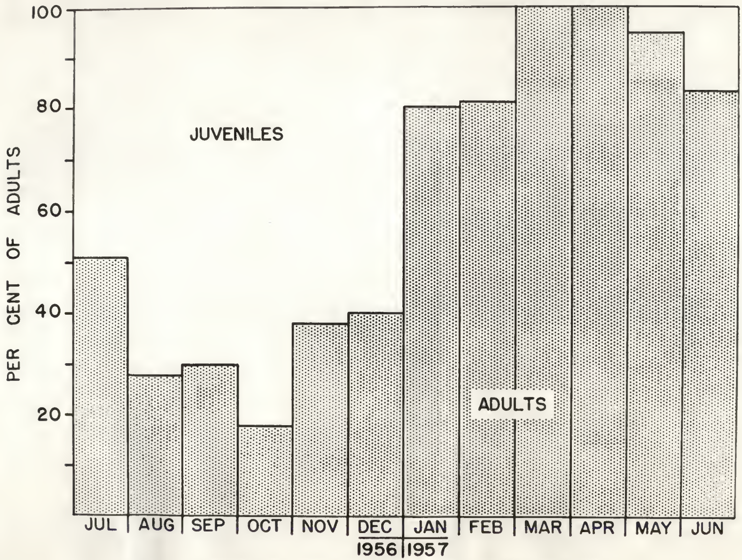

Fig. 1. Monthly age distribution of 696 collected specimens.

On the assumption that the population being sampled is stable, Petrides (1941) gave a formula for computing the average life span of an animal and Burkitt (Petrides, 1951) presented a formula for calculating the population turnover period. As will be shown later, the population was relatively stable during the study period although at a higher level than normal. The average life span of an animal can be calculated by the formula:

$$L = \frac{1}{j}$$ where L = the average life span of those jackrabbits which survive until the end of the year and
j = the per cent of young in the population at the end of the year.

Since aging techniques were not considered to be accurate after November, the per cent of young at the end of the year could be approximated only by using the fall age ratio. This ratio, calculated from the October and November collections was 36 adults to 96 juveniles or a percentage of juveniles in the population of 73 per cent. Therefore the average life span of the jackrabbits in southwestern Kansas would be:

$$L = \frac{1}{.73} = 1.4 \text{ years.}$$

The average population turnover period, which is the time required for the young of one year to be reduced to 0.5 per cent of their original numbers is calculated by:

$$T = \frac{\log .005}{\log (1-j)} = 1$$ where T = the population turnover period and
j = the per cent of young in the population at the end of the year.

Substituting the data from the population studied in southwestern Kansas gives the following:

$$T = \frac{\log .005}{\log .27} + 1 = \frac{7.699 - 10}{9.431 - 10} + 1 = 6.8 \text{ years.}$$

Therefore, should the jackrabbit population remain at its present level of abundance, some of the young born in the 1956 breeding season would theoretically still be active in the population until about 1962 or 1963.

REPRODUCTION

Specimens used to study the reproductive cycle of the jackrabbit were collected within the distances of one-fourth to twenty miles from the principal study area. Jackrabbits were not killed on the study area with the exception of a few specimens shot by landowners and given to the author. Collections were made using a .22 caliber rifle or a 16-gauge shotgun between the hours of 3:00 P.M. and 3:00 A.M. Specimens were then taken to Lakin where the reproductive organs were removed and fixed in 10 per cent buffered formalin. The time between death and examination ranged from a few minutes to approximately 14 hours

All reproductive organs were brought to Manhattan for detailed laboratory examination. Males were examined in the laboratory as follows: The epididymides were stripped off and each pair of testes was weighed on a "Gram-atic" balance. Sperm smears were taken from one testis and epididymis of each animal and examined under a phase microscope. The numbers of sperm were then estimated by use of a 0, 1, 2, 3, or 4 scale of comparative abundance where the figure 0 indicated no sperm present in the smear and the number 4 referred to a maximum number of sperm. The animal was recorded as being capable of breeding, if it had a comparative epididymal smear count of three or four.

Female reproductive tracts were examined as follows: A mean ovary size index was obtained for each specimen using measurements taken with calipers on the width and length of each ovary. The product of these two measurements was averaged with the product of the measurements on the other ovary of each pair to give a mean ovary size index for the animal. The ovaries were then sectioned with a razor blade and the diameter of the larger peripheral follicles, the number of rupture sites, corpora lutea and corpora albicantia were recorded. The animal was designated as parous if the uterus appeared to be longitudinally striated. Lechleitner (1955) used this method of separating parous from nonparous animals. The uteri of jackrabbits become longitudinally grooved during uterine contraction after parturition. Placental scars were counted and recorded. The larger embryos were sexed, all embryos were counted and the zygomatic breadth and crown-rump measurements were recorded.

The 12 monthly collections totaled 696 specimens (Table 2). The 358 males

Table 2. Sex and age composition of 12 monthly collections totaling 696 specimens.

Month	Adult Male	Juvenile Male	Adult Female	Juvenile Female	Total
July '56	23	20	14	15	72
Aug	12	38	13	27	90
Sep	10	24	13	29	76
Oct	7	30	6	28	71
Nov	12	23	11	15	61
Dec	8	26	12	10	50
Jan '57	26	0	16	11	53
Feb	26	0	16	10	52
March	21	0	17	0	38
April	28	0	38	0	66
May	16	1	20	1	38
June	11	1	13	4	29
Total	205	153	191	147	696

and 338 females collected indicated a male:female ratio of 108:100. The fetal sex ratio, using data gained only from embryos with crown-rump measurements of 40 millimeters or over, was 37 males to 30 females. Neither sex ratio was significantly different from a theoretical 50:50 ratio (post-natal ratio $X^2 = 0.58$; pre-natal ratio $X^2 = 0.73$; $X^2_{.05} = 3.84$, 1 D.F.).

A definite annual breeding cycle is exhibited by the Black-tailed Jackrabbit in this area. Males demonstrated this cycle by both an increase and decrease in average testes weight (Fig. 2) and in monthly comparisons of testicular activity (Table 3). From a comparison of the monthly mean testes

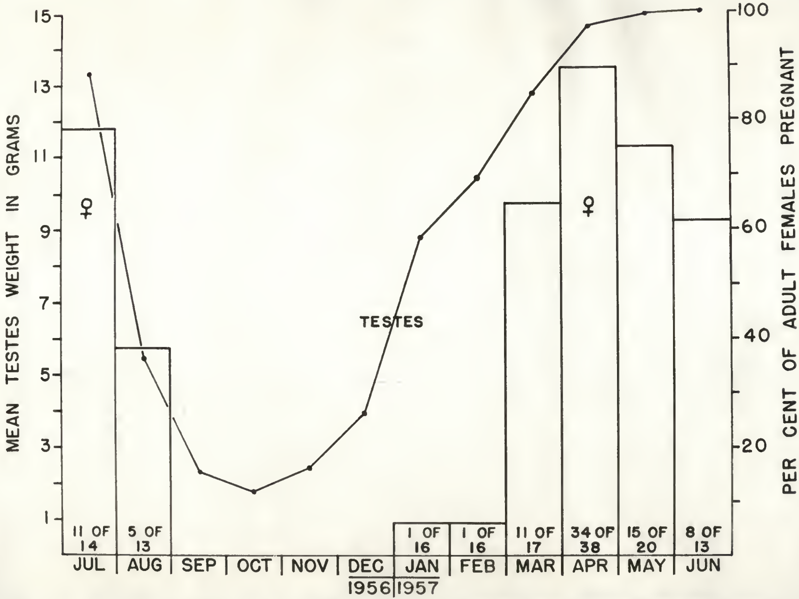

Fig. 2. Mean testes weight and per cent of females pregnant for each month of the study period.

weights it would appear that the peak in male breeding efficiency was in May and June of 1957.

Table 3. Per cent of adult males showing sperm in testicular smears and comparative sperm counts of three or four in epididymal smears.

Smear	'56 July	Aug	Sep	Oct	Nov	Dec	'57 Jan	Feb	Mar	Apr	May	June
Epididymal	100	53.8	10	0	0	15.4	72	100	100	100	100	100
Testicular	100	30.8	0	0	0	15.4	88	100	100	100	100	100

The weight averages and smear analyses indicate that males were incapable of breeding during October and November and the majority were impotent in September and December. Males taken during the non-breeding period had shrunken, flaccid and non-scrotal testes. Testes were scrotal during the breeding season except in cases where shock caused them to be retracted at the time of death. The range in testes weight of males which were recorded as being capable of breeding was from 3.95 to 21.26 grams but sperm production was generally confined to males with testes weight of five grams or over. There was much variation in the testes weight accompanying cessation of sperm production in the fall of 1956. No males aged as juveniles showed evidence of testicular activity until September when a testicular sperm smear from one young of the year hare contained sperm. On the basis of this one individual it would seem that the minimum age at which sperm production begins would be about six or seven months.

The breeding season extended from late January or early February through August (Fig. 2). Only one pregnant jackrabbit was taken in January and this female was collected on January 27. Although only one pregnant female was collected in February, five of the six non-pregnant specimens taken in March showed evidence of having bred in February. Of these five, two had recently resorbed or aborted their litters and three had recently given birth. The condition of the uteri and placental scars of these three animals indicated that they had given birth within one week of the date of collection. Because the gestation period is 43 days (Haskell and Reynolds, 1947), these animals had successfully bred in the first or second week of February. Therefore, for the purpose of calculating the average production per female per year, it is more accurate to assume that the breeding season began in early February and extended over a period of seven months or approximately 212 days. The estimate of 6.2 per cent of females pregnant which was recorded for February was evidently subject to sampling error and is an inaccurate estimate. No evidence was found to indicate that females breed during the same season in which they are born.

When breeding commenced in the spring of 1957 the population had contained potent males for two months. A large proportion of the females examined in December and January showed signs of copulation but only one pregnant female was examined in that period. Coition was indicated by a stretch or ripped vaginal orifice. In a few instances the orifice was ripped dorsally as far as the anal opening. Because of the common occurrence of infertile coition it would appear that the onset of breeding was dependent upon the occurrence of oestrus in the females. At the end of the breeding season the occurrence of both pregnant females and potent males decreased sharply and simultaneously. Pregnant females and males capable of breeding occurred commonly in collections made during the first part of August but were almost absent from collections made during the last two weeks.

Several techniques commonly used in mammalian reproductive studies were tried in this study in an attempt to gain more information about the reproduction of the jackrabbit. These techniques were analyses of the measurements and number of the larger peripheral follicles, monthly changes in the ovarian size index, and counts of the placental scars and corpora albicantia. These four techniques give little useful information when utilized for studying the reproduction of this species. Because the jackrabbit ovulates only following sexual stimulation, the follicles apparently do not increase greatly in size until after copulation. Marshall (1956) supports this statement. The observed size of the peripheral follicles varied from less than 0.5 to over 2.5 millimeters. The larger follicles were found in ovaries of animals collected both in the breeding and non-breeding season. There was only a small amount of variation in the ovarian size indices through the non-breeding season until breeding actually began in February and functional corpora lutea were present in the ovaries. As was expected, the mean ovarian indices were much larger during the breeding season. Placental scars become rapidly inconspicuous in jackrabbits. Scars could be counted with confidence in a few individuals for as many as three litters; however, in the majority of the uteri examined, only the size of the most recent litter could be determined. Clearing in potassium hydroxide did not facilitate placental scar counts.

The average number per litter was calculated only from litters one-half term or older. A crown-rump measurement of 40 millimeters was assumed to be half-term (Lechleitner, 1955). Thirty-three litters aged as half-term or older contained 79 embryos for an average of 2.4 embryos per litter. However, the litter size did not remain constant throughout the breeding season and this factor should be taken into consideration before obtaining an average number per litter. The mean number per litter increased monthly until the middle of the breeding season and then progressively decreased. Because of the varying percentages of females pregnant during these months, each monthly litter size was weighted according to the per cent of females from which that average was

Table 4. Calculation of the average number per litter by weighting the monthly mean litter sizes according to the per cent of females pregnant for each month.

Month	% of Females Pregnant	Average Litter Size	Coefficient for Weighting Litter Size*	Weighted Component of Mean Litter Size
July '56	78.6	2.5	.19	.48
August	38.4	2.0	.09	.18
Feb '57	6.2	1.0	.01	.01
March	64.7	1.2	.16	.19
April	89.5	2.1	.22	.46
May	75.0	3.6	.18	.65
June	61.5	3.3	.15	.50
Total	415.0	-	1.00	2.47

* Calculated by determining the proportion which each month's pregnancy percentage represented of the sum of these precentages.

calculated (Table 4).

A more accurate estimate of the average number per litter for the study period can now be seen to be 2.47 which will be rounded to 2.5. In this study the difference between the mean litter size calculated from the total number of litters and embryos (2.4) and using monthly weighted averages (2.5) amounted to an increase of only about 0.1 embryo per litter, but possibly in another situation the method of weighting monthly litter sizes could mean a considerable difference in the estimates of the average litter size. Numbers per litter ranged from one to five with only one litter having five embryos.

The presence of considerable prenatal mortality in the early stages of pregnancy is indicated by comparing the average litter size of 2.4 which was calculated from embryos over half-term with an average litter size of 2.6 for those having a crown-rump length of less than 40 millimeters. Another indication of prenatal mortality is found in a comparison of the number of corpora lutea present and the number of embryos found during the study. Caution must be exercised when counting corpora lutea. Corpora lutea atretica, although comparatively rare, do occur in jackrabbits (Lechleitner, 1955).

In general, they are differentiated from the functional corpora lutea of pregnancy by their smaller size and lack of rupture sites. The number of rupture sites and corpora lutea indicated that the females examined during this study had shed 241 ova resulting in only 218 embryos. This would seemingly indicate that there was a 9.5 per cent loss of ova. However, Brambell (1944) pointed out that the difference between the number of ova shed and the number of embryos present is an inaccurate indication of prenatal mortality unless allowance is made for the stage of pregnancy where the loss occurred. Females killed in the early stages of pregnancy could be expected to lose a larger proportion of their litters if they had been allowed to reach full term before being collected. Lechleitner (1955) presented data on the prenatal mortality of L. c. californicus using the more accurate method of analyzing the loss according to the stage of pregnancy where it occurred. Detailed work on this phase of jackrabbit reproduction was not undertaken in this study.

There is a considerable loss of entire litters as units sometime before mid-term in lagomorphs. The method utilized to make an allowance for this loss was the relative frequency with which litters older than half-term occurred in the sample. It was assumed that shooting the specimens resulted in a representative sample of the stages of pregnancy which occur naturally in the population. A sample of pregnant females should contain equal numbers of litters whose embryos have crown-rump measurements of more than 40-millimeters and those containing embryos of less than that measurement if there is no loss of entire litters before mid-term. There were 53 cases of early stages of pregnancy and 33 litters which were older than half-term found during the course of this study. Changing these figures into a per hundred basis, there were 63 stages of late pregnancy for every 100 cases of early pregnancy. The difference between these two figures, 37 per cent, should represent litters which are lost as units sometime before mid-term.

Evidence of resorption in this study supports the contention that while prenatal mortality is heavy in the early stages of pregnancy, litters which survive until mid-term are subject to only negligible mortality from mid-term to parturition. No female in the later stages of pregnancy was found to be resorbing any part of her litter. Seventeen of 218 embryos of all stages, 7.8 per cent, were undergoing resorption when examined. This factor affected 11.6 per cent of the litters in this study. Evidence of resorption of entire litters was found in 5.8 per cent of the total number of litters and affected 4.6 per cent of the embryos.

Evidence of abnormally high resorption was found in March of 1956. The monthly collection which was taken two days after the end of a three-day blizzard revealed that of the 17 adult females killed, four were in the process of resorbing their entire litters and two others had already resorbed or aborted their litters. This would indicate that periods of stress, in this instance a three-day blizzard, may result in the loss of many litters in their entirety.

Brambell (1944) working in England found that resorption of embryos in the European Rabbit occurred usually on the eleventh to thirteenth days of the gestation period and that the process was completed in about two days. If the process of resorption can be assumed to last two days in the jackrabbit, it follows that the ratio of this time interval to the number of days in the initial half-term of pregnancy should be the same as the observed loss of entire litters during that period is to the loss calculated from the frequency of occurrence of early and late stage pregnancies. Five of 53 (9.4 per cent) of the early stage litters examined were in the process of being resorbed in their entirety. The probability of observing this process if it is completed in two days out of a possible 21 days (one-half of the gestation period) would be approximately one in 10.

Therefore the 9.4 per cent observed loss would represent an actual loss of 94 per cent of the litters on the assumption that resorption requires two days. When compared with the 37 per cent estimated loss which was calculated from the frequency of occurrence of early and late stages of pregnancy it is apparent that resorption takes more than two days in the jackrabbit.

If it were not for this loss of litters in their entirety, the prenatal mortality factor could be eliminated from calculations of average production by using only litters containing healthy embryos older than half-term. The average number of young per year produced by a female could then be easily calculated using the per cent of females pregnant during the breeding season as an indication of the average time between pregnancies in the population. Throughout the 212 day breeding season 65 per cent of the adult females were pregnant. The mean gestation period of the jackrabbit is 43 days. By multiplying this period by the per cent of females not pregnant it can be seen that there was an average of 15 days between pregnancies throughout the breeding season. If it takes an average of 58 days (43 + 15) for a female to produce one litter and if all litters were maintained until parturition, then the mean number of litters could be obtained by dividing the number of days in the breeding season by the time required to produce one litter. Applying that formula to the data for this study gives the following:

$\frac{212}{58}$ = 3.7 litters; the mean number per litter of 2.5 X 3.7 = 9.3 young produced per female per breeding season.

The calculation of the average production of young per female per year taking into consideration the loss of entire litters before mid-term will follow the recommendations and the formula given by Lechleitner (1955). A slight bias is present when this formula is used because the oviducts were not flushed to determine if zygotes were present when ovulation sites were found but implantation had not occurred. Only four cases of ovulation without implantation were found so the error is slight. It has been shown that 37 per cent of the litters conceived are lost as units sometime before mid-pregnancy. Since evidence of prenatal mortality was found only in litters less than half-term, an animal which loses its complete litter is probably unable to produce young for approximately one-half the normal gestation period. Lechleitner's formula for calculating average production per year takes this factor into consideration. If Ns equals the number of successful litters per season, then:

$$Ns = \frac{2L}{G} \times \frac{1 - a}{2 - a}$$

where L = the length of the breeding season;
G = the period required to produce ont litter; and
a = the proportion of litters lost as units.

Using this formula and the data from the population sampled in southwestern Kansas, the average production per female per year was:

$$\frac{2(212)}{58} \times \frac{1 - .37}{2 - .37} = 2.8$$ litters per year; $2.8 \times 2.5 = 7.0$ young per female per year.

While females have an average production of young of 7.0, it must be remembered that this is an average of some females which might produce only one or two litters of small numbers of young and some which if breeding continuously and maintaining all litters until parturition could conceivably produce as high as 15 or 16 young in one season. In many lagomorphs, females commonly become pregnant during the post-partum oestrus which would lead to pregnancy after pregnancy with little or no time interval between. These extremes probably are exceptions in the jackrabbit population of southwestern Kansas and the production of the majority of females probably would be between five and nine young per year.

Vorhies and Taylor (1933), working in Arizona, estimated an average annual production of eight young for L. californicus ssp., while Lechleitner (1955) in California calculated the average production to be 9.8 for L. c. californicus. Both studies found evidence of breeding during all months of the year with the peaks of reproduction coinciding with periods of heaviest rainfall. Lechleitner suggests that a nutritional factor affects the reproductive status of the animals. If this hypothesis is true, then it would seem that production of young would have been at a lower rate during the last six months of 1956 when rainfall was still negligible and consequently little green vegetation was available to the animals.

L. c. melanotis of southwestern Kansas produces fewer young than other subspecies in California and Arizona apparently because many females fail to become pregnant during the post-partum oestrus period. The per cent of females pregnant for monthly collections ranged from 6.2 to 89.5 per cent. Vorhies and Taylor (1933) and Lechleitner (1955) found almost 100 per cent of the females pregnant during the majority of the breeding season in Arizona and California. Another factor which limits production of young is the climatic differences between this region and Arizona and California. Winters are much more severe in Kansas and probably because of this reason, the jackrabbits in this state show a breeding season restricted to the seven months of spring and summer rather than breeding sporadically through the winter as was found in the other two states.

A significant difference was found in the numbers of embryos present in the left and right horns of the uterus. There were 124 embryos in the left and 94 in the right horn. These data when subjected to the X^2 test resulted in a value which has a probability of occurrence of four per cent when a theoretical ratio of 50:50 is expected. ($X^2 = 4.12$; $X^2_{.05} = 3.84$, 1 D.F.). Whether this ratio is the result of sampling variation or if there is an actual difference between the number of ova produced by each ovary is not known.

Few authors give more than an opinion of the length of time that young are suckled other than data obtained from pen-raised animals. Animals confined in pens are in unnatural situations and data obtained in this manner are subject to bias. The length of the period when females would be suckling young would be approximately equal to the length of the breeding season. This would be modified only by the difference between one gestation period and the time suckled. The period when a female could be suckling young would then extend from one gestation period after breeding commences until the suckling period after breeding ceases in the fall. The average number of females showing evidence of being suckled during the period of March through September compared to the time required to produce one litter should give a reasonably accurate estimation of the average length of the suckling period. The per cent of adult females showing evidence of suckling during the period was 23 per cent. Since it requires an average of 58 days to produce a litter, the average suckling period would be .23 X 58 = 13 days. So it would seem that the average time that young are suckled in southwestern Kansas is about two weeks. The youngest animal collected by shooting was approximately four weeks old. Since young are suckled for about two weeks, there is evidently a period of about two weeks after weaning during which young jackrabbits remain secreted even when feeding.

Jackrabbit nests have been described in only a few instances. Many hours were spent during the course of this study making observations with the aid of binoculars in attempts to see evidence of nesting or suckling. In addition, various parts of the study area were examined for nests. No nest was found which could be positively identified as having been made by a jackrabbit. It is the author's opinion, that, at least in this area, jackrabbits do not make nests. Probably the young are born in forms or under dense cover such as a sagebrush plant or in an alfalfa field. Vorhies and Taylor (1933) and Lechleitner (1955) reported that the black-tail occasionally makes nests.

Evidence of pseudopregnancy, which occurs in some species of lagomorphs, was not found in this study. Apparently pseudopregnancy is rare, if it occurs at all in the jackrabbit. No case of superfoetation was found during examination of pregnant females. Few abnormalities were noticed during examination of the reproductive tracts. One female was collected which had two embryos in the left uterine horn and one corpus luteum in each ovary. This could have been a case of transmigration of an ovum or a case of polyovulation with the corpus luteum in the left ovary representing a double ovulation. One male was found with both testes descended but the right one represented by what appeared to be a descended but undeveloped testis.

POPULATION DENSITY AND MOVEMENT

Studies were conducted along the southern edge of the Arkansas River valley in eastern Kearny County and in the sand-hills lying to the south of this valley. This range of sand-hills extends from southeastern Colorado eastward through Hamilton, Kearny, Finney and Gray Counties and into the western part of Ford County. The southern edge crosses the northern borders of Grant and Haskell Counties. The soils are sandy with some areas so subject to blowing that no vegetation can exist. In general, these blown-out areas were only a few acres in extent.

The sand-hill region was originally a tall grass region where the climax dominant was little bluestem (_Andropogon scoparius_) with lesser amounts of big bluestem (_Andropogon furcatus_) and turkeyfoot (_Andropogon hallii_) (Gates

1936). Moderate to heavy grazing and drought conditions in the mid-1930's and 1950's have caused secondary succession in most of the region. The principal plants present now are: (a) Grasses: red three-awn (Aristida longiseta), grama grasses (Bouteloua sp.), buffalo grass (Buchloe dactyloides) and sand dropseed (Sporobolus cryptandrus); (b) Weeds: russian thistle (Salsola pestifer), prickly poppy (Argemone intermedia), buffalo bur (Solanum rostratum); and (c) Brush: sand sagebrush, prickly pear cactus (Opuntia sp.) and soapweed. The area surrounding the sand-hills consists mostly of cultivated land where hard winter wheat and milo are grown, and a smaller proportion of short grass pasture land.

The 2240-acre study area, composed of a 1920-acre area on which studies were conducted for one year and an additional 320 acres utilized during the final three months of the study period, was located six miles southeast of Lakin in Kearny County (Fig. 3). The 1920-acre area will hereafter be referred to as the primary study area. This area consisted of approximately 60 per cent sand-hill pasture land and 40 per cent river valley cropland (Fig. 4). The flora of these pastures was similar to that given for the rest of the sand-hills. Milo, winter wheat and alfalfa were grown in the croplands and a majority of these fields could be irrigated by the flood type of irrigation system. Along the irrigation ditches, field borders and in stubble fields dense stands of Johnson grass (Sorghum halepense) and fireweed (Kochia scoparia) were common with a lesser abundance of the following plants: puncture vine (Tribulus terrestris), devil's claw (Martynia louisianica) and prostrate pigweed (Amaranthus blitoides).

The primary study area varies in elevation from 2955 feet in the river valley to 3,020 feet in the sand-hill pastures to the south. At this point the sand-hills extend further south across the northern border of Grant County,

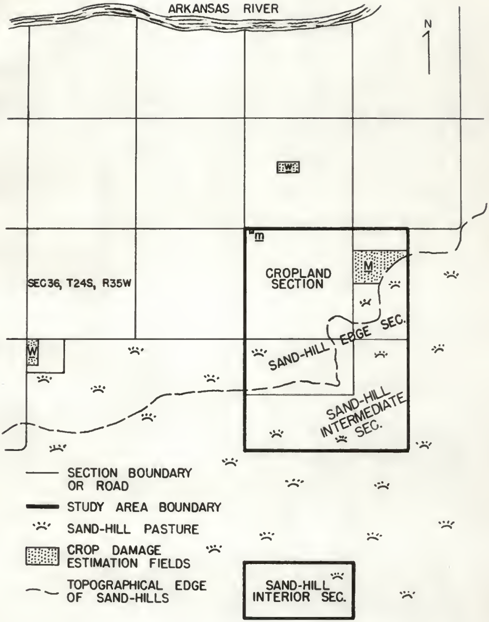

Fig. 3. Map of the region southeast of Lakin, Kearny County, where studies were conducted.

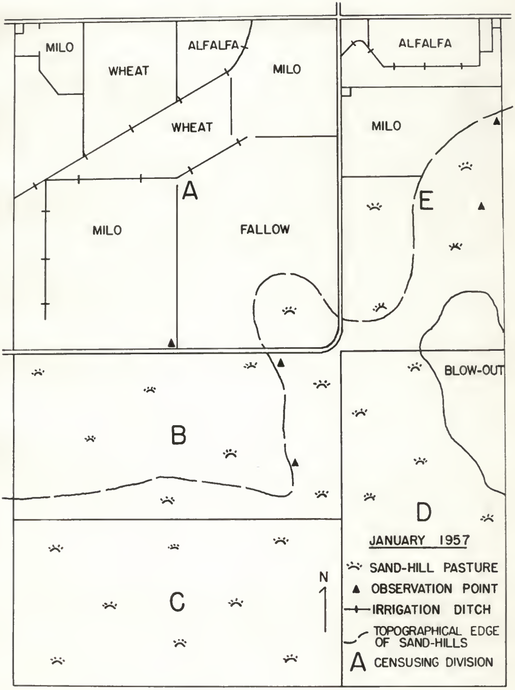

Fig. 4. Map of the primary study area.

a distance of about 12 miles. The average annual rainfall at Lakin is 15.6 inches with most of this amount coming during the spring and early summer months.

During the daytime most of the jackrabbits were found in the sand-hills pasture sections of the study area. Many animals in these pastures displayed a definite daily movement pattern consisting of two major movements. One movement occurred sometime during the evening when the animals moved north into the croplands to feed intermittently throughout the night. The second major movement was the return at sunrise to the hills which served as the hare's daytime resting area. The principal factors affecting the rate and amount of these movements, as in all jackrabbit activities, are wind and the time of day.

In an attempt to get more accurate data on these daily movements, such techniques as sunset road counts, nocturnal feeding counts using a spotlight and trapping and releasing marked animals were tried. Sunset road counts were made on the east-west road lying between the cropland and pasture sections of the primary study area (Fig. 4). Seven-tenths of a mile of this road was marked off by attaching flags to fence posts and, with the aid of binoculars, counts were made on the number of jackrabbits which crossed the road to feed in the cropland to the north. These counts were made during the hour preceding sunset at intervals during July, August and September. This practice was discontinued during the fall months when it became evident that the animals began their feeding trips at approximately the same time every day regardless of the time at which the sun set. While animals moving into the croplands to feed were observed as early as an hour and a half before sunset in the summer, during the winter months this movement did not occur until about two hours after sunset. The results of these sunset road counts are illustrative of the magnitude of this evening feeding movement. An average evening's count consisted of 50 to 70 jackrabbits per hour and on one occasion 91 animals were counted in an hour as they crossed the road to forage in the cropland.

Nocturnal feeding counts using a spotlight and the technique of observing marked animals were not carried on with enough consistency to afford reliable data. The highest spotlight feeding count was recorded in April on a winter wheat field located adjacent to the sand-hills and about two miles west of the principal study area. This 14½ acre field contained a minimum of 203 feeding jackrabbits or a density of 14 per acre.

A majority of the problems arising in populations studies of mammals are caused by a lack of controlled laboratory conditions characteristic of some other branches of the biological sciences. A major problem is the determination of the extent to which populations data obtained in a study is applicable to areas other than that area which was studied. A common error occurs when researchers conduct field studies in atypical areas or areas of insufficient size. For example, much work has been done on institution-owned lands which are seldom subject to the same land management, or the animals residing on those areas subject to the same degree of mortality, as the vast majority of privately-owned land. Another example is the all too common practice in small mammal populations studies of applying data obtained on areas of only one to a few acres to the populations trends shown by the species over a much larger portion of that species' range.

An attempt was made in this study to minimize these sources of error. Population studies were conducted on a relatively large area of 2240 acres located in range and cropland which was entirely privately-owned and hence subject to the typical mismanagement of a great majority of the land in the region. A certain degree of accuracy was sacrificed because of the large area utilized for the study and because conditions on that area were entirely uncontrolled. For instance, man-caused mortality could not be determined with the exception of the number of animals killed by landowners. By using a large area which was representative of the region it was hoped that the loss of accuracy in the mortality factor, which is inherent in such a situation, would be outweighed by the possible application of the study results.

A second problem in mammal populations work is the choice of the method to be used in density or population estimation. Many mammal censusing methods have been proposed in the literature. The commonly used methods attempt to sample the population by some means and then numerically expand the sample results to fit the entire area under study. Another type of censusing has as its goal an index representing comparative abundance to be related to past and future indices in establishing population trends instead of an exact enumeration of animals. Because of the many-aspected scope of an ecological study of the jackrabbit and the large area to be studied, a method called the strip censusing method was chosen. This method has been used as either a censusing method for enumerating the number of animals present on an area or as a method for obtaining indices of abundance. A variation of this method called the King Strip constitutes an attempt to make this method give more accurate results and is utilized in determining the approximate number of animals residing on an area, the width of the censusing strip being determined by the mean distance at which the animals flush. Too much variation was found in the distances at which jackrabbits flush to use the King Strip in the sand-hills region.

It was felt that trends in population abundance were more important in this study than statistically accurate estimates of the number of animals present on the area for a given time. Methods for the statistically accurate estimation of numbers ofmammals are time consuming and generally are restricted to much smaller areas. The strip method which was used in this study furnished actual counts of animals on designated strips of land and these actual counts were used as indices of abundance by comparing them from one period to the next in establishing population trends. However, the habitat of the study area was of a type to which the strip method could be adapted with reasonable confidence for population and density estimation.

Six indices of comparative abundance were obtained for the study area during the 12-month study period. To facilitate the indexing procedure, the primary study area was first divided into five parts which were named Divisions A through E (Fig. 4). Division A consisted of one-square mile of cropland while the remaining divisions were one-half square mile in extent and, in general, were composed of sand-hill pasture. Counting strips, which were 100 feet wide, were marked off on each division. These strips extended from one border of the division to the other and were laid out at quarter-mile intervals across the division. The strips consisted of a line which was marked at both ends and was walked during the counting. The procedure for obtaining an index of abundance on each division was as follows: The observor walked each of these counting lines and recorded the number of animals which was flushed within 50 feet of either side of the line. After practice, the observor was able to estimate 50 feet with an average error of one to two feet. The original location of all animals that were flushed from the margins of the strip was checked by pacing the distance from the pathway to their forms. The actual number of jackrabbits flushed from within these 100 foot wide strips was recorded and the total number of animals flushed from the total number of strips on a division for each indexing period constituted the index of abundance for that division for that period.

An index of abundance was obtained for Division A by the use of four strips which were one mile long and were laid out in a north and south direction; on Division B there were four counting strips one-half mile long running north and south; Division C had two east-west strips one mile in length; and indices were obtained for Divisions D and E by using two north-south strips on each division which were one-mile long. The 320 acre area (Fig. 3; Plate IV, Fig. 2) was located one mile south of the primary study area and was similarly indexed using two east-west strips of one mile in length. This area was indexed only in April and June of 1957. The total length of all counting strips varied from 12 miles during the first four indexing periods to 14 miles during the last two periods.

Several conditions under which counts for indices were to be made were established at the beginning of the study in an attempt to make each indexing period as environmentally equal as possible. Counts were made on the divisions only between the hours of 10 A.M. and 3 P.M. to insure that movement of the animals in and out of the strips would be negligible. Counting was to be done only when weather was normal; that is, wind at a minimum, no rain or snow falling, the ground dry or relatively so and the temperature normal for the season. These conditions were fulfilled in all but the April indexing period when weather on two of the three days was recorded as windy with light rain falling intermittently. No two adjacent areas were indexed on the same day. To avoid chasing jackrabbits from one area into another area to be indexed that same day counts were made on Division A the first day, Divisions B and D the second and Divisions C and E the third day.

There are two primary sources of bias in the results obtained from this type of indexing method. The largest source of error was that the observor was the sole judge of whether an animal was flushed from within a strip. It was hoped that by following the same strips under conditions as similar as possible that the amount of this personal bias would be constant throughout all indexing periods and that because of this constancy, the trends in population abundance as shown by comparing the indices would be true. The second source of bias was that possibly all animals were not being flushed from the strip or that the seasonal variation in the amount of cover would have some effect on the flushing of the animals. The distances from the observor at which a series of jackrabbits flushed were recorded in April and June of 1957 to determine whether an area of 50 feet on either side of a line was too large a strip, and to determine the effect of the amount of vegetation on flushing distances. In April, when the amount of cover was believed to be at a minimum for the study period, 20 flushes occurred at a mean distance of 140 feet from the observor. The range for these flushing distances was 20 to 320 feet with only one animal flushing at less than 50 feet. Heavy rains during the spring produced a larger amount of cover in June than at any other time during the study period. The mean flushing distance of 13 jackrabbits in that month was 147 feet with a range of 28 to 357 feet. Again only one jackrabbit flushed at a distance of less than 50 feet. Thus it can be seen that there was little variation in flushing distances even when cover was considerably heavier. Part of this lack of variation can be attributed to the open cover type of the sand-hills where the vegetative cover, with the exception of soapweed and sagebrush plants, does not extend above eight to 10 inches. Because of this lack of variation in flushing distances and the fact that only two animals out of 33 flushed at a distance of less than 50 feet from the observor, it has been concluded that the strip method of obtaining comparative indices gave valid data in the cover types where it was employed.

In order to see the dynamics behind movement and crop damage, the divisions of the primary study area were aggregated according to their type of habitat and location into three groups and named as follows: Division A became known as the cropland section; Divisions B and E were known as the sand-hill edge section; and Divisions C and D were named the sand-hill intermediate section. The 320 acres comprising the indexed area one mile south of the primary study area was known as the sand-hill interior section (Fig. 3). Each section contained a homogeneous cover type with the exception of 160 acres of cropland in the sand-hill edge section. With that exception, the sand-hill edge, sand-hill intermediate and sand-hill interior sections all consisted of pasture land but differed in their location in the sand-hills.

The change in abundance of animals on the primary study area (Fig. 5) reveals a graphical pattern completely unlike the pattern shown by a normal, stable mammal population. In terms of the annual reproductive cycle of the jackrabbit, a stable population would be expected to increase until August when reproduction ceased, decrease sharply throughout the critical winter period and then increase again when reproduction began in late February and March. The number of flushes per 12 miles of indexing strips on the primary study area when graphed, produced a pattern with increases and decreases almost opposite to that of the expected pattern of a normal, stable population. The number of animals on the study area did not decrease sharply during the winter period but did decrease within two months after reproduction started. The number of jackrabbits flushed on the 12 miles of indexing strips in the area decreased by only 20 per cent during the eight month period of September through April. During this eight month period the total mortality on the area was undetermined but was known to be heavy. The known mortality for the area during this period including predator, highway and landowner kills amounted to 186 animals. Since eight per cent of the study area was sampled and assuming

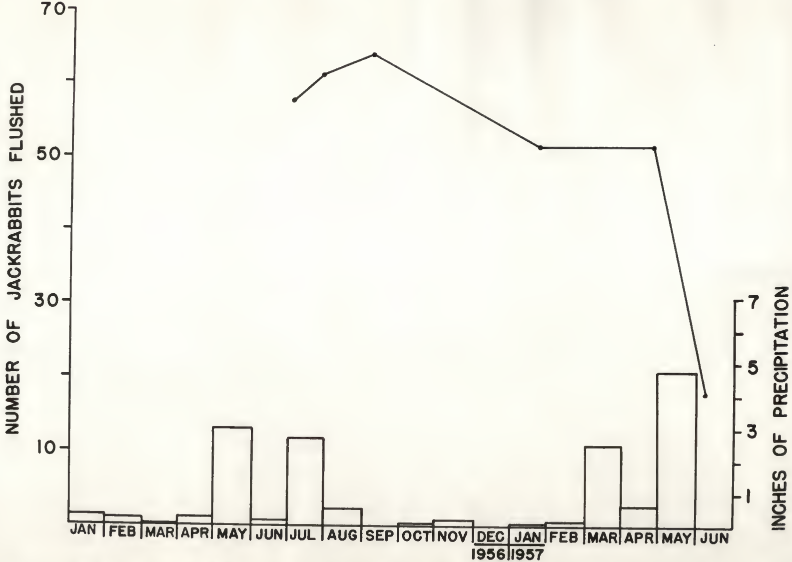

Fig. 5. Relationship between the amount of precipitation and changes in the indices of abundance for the primary study area.

that the indexing strips were representative of the area, this drop of 20 per cent in the comparative indices would amount to 169 animals for the entire area. Therefore, in crude figures, the known mortality for the study area amounted to more jackrabbits than the indices showed were lost from the area.

During three months of this period, Kearny County paid a five-cent bounty for jackrabbits and meat buyers paid 10 to 20 cents for jackrabbit carcasses. Hunting mortality on the area because of these factors could not be estimated but was known to be high. Landowners told of as many as six carloads of hunters patrolling the roads and shooting jackrabbits in the study area during a single night. The author recorded the presence of three carloads of hunters on the area in one night. Thus it is apparent that many more animals were killed on the area than the results of comparing the indices of abundance revealed.

The answer to the question of why the number of animals on the primary study area failed to decrease even though mortality was exceptionally heavy is obviously immigration into the area by jackrabbits from other areas. The location of these other areas will be taken up shortly.

The amount of natural food available played an important role in changes in population abundance of jackrabbits. Because moisture is the limiting factor in plant growth in southwestern Kansas, a review of monthly rainfall records for the region reveals the cause for these changes in abundance (Fig. 5). The sand-hill area had been subjected to almost constant drought conditions since 1952 and the vegetative cover in these hills had been badly damaged by drought and overgrazing by cattle. The area was in a state of secondary succession. Rains in May of 1956 totaled a near normal amount but were of sufficient intensity to promote only a limited growth of forbs and grasses in the sand-hills. No rains were recorded in the spring of 1956 which were of an intensity of over one-half inch and therefore a large proportion of the precipitation was lost to evaporation before it could be utilized by plants. Because of heavy grazing by cattle and jackrabbits and because the amount of forage was limited by insufficient rainfall, the natural food supply soon failed. As the drought intensified through the summer of 1956, the grasses became dormant and unpalatable and most of the forbs which had not been eaten earlier were killed. This failure of the natural food supply in the hills caused jackrabbits to concentrate in low areas where some food remained or along the periphery of the sand-hills where food in the form of milo and alfalfa was available on their nightly foraging trips into the croplands. Two observation trips into the center of the sand-hills in September revealed the presence of few jackrabbits in that area. The condition of the vegetation was such that there was little available food in the area (Plate II, Fig. 1 and 2). Winter conditions and the almost complete loss of natural food caused all animals to move out of the center of the hills and to concentrate along the edges. Thus the number of jackrabbits in the primary study area, which was located along the edge of the hills, did not decrease sharply as normally would be expected during the winter months. Large amounts of precipitation in March, April and May of 1957 produced a large growth of forbs and grasses in the sand-hills. Because a large quantity of natural food was again available, the jackrabbits migrated from the sand-hill edges back into the hills. This dispersion accounts for the sharp drop in the number of animals on the area between April and June. During the late April indexing period many small forbs were in evidence but the majority had just begun to grow. On the May field trip, few jackrabbits were in evidence along the edge of the hills. The dispersion movements of the concentration of jackrabbits along the edge of the hills therefore must have occurred during the early part of May.

Further evidence of these concentration and dispersion movements can be found in an analysis of the changes in numbers of animals in the three sections of the primary study area and the interior section (Fig. 6). The major concentration of animals throughout the study period was found in the sand-hill edge and intermediate sand-hill sections. However, there was a definite shift in abundance of animals from the intermediate to the edge section. When the study began in July, 1956, jackrabbits already were concentrated in the intermediate and edge sections with four miles of counting strips in each revealing an actual flushing count of 21 jackrabbits in the edge and 32 in the intermediate section. The sand-hill intermediate section reached a peak in density in September when 34 animals were flushed from the strips and then declined steadily until June 1957 when only nine jackrabbits were flushed from the four miles of strips. The sand-hill edge section, however, increased during the critical winter period from 23 hares flushed in September to 27 in April. The number of animals flushed in this section then dropped 65 per cent between April and June as the jackrabbits spread throughout the hills. It can now be seen that the 20 per cent drop in the population which took place between September and April on the primary study area can be attributed entirely to the sand-hill intermediate section. Within the intermediate section these decreases in abundance of jackrabbits occurred almost completely on the strips located closest to the center of the hills. This constitutes additional evidence of the concentration through the summer, fall and winter months for the purpose of feeding on the croplands to the north of the sand-hills.

The interior section, which was located one mile further into the hills than the intermediate section and about two miles from the border of the cropland section, had no jackrabbits residing on the area in April of 1957. No actual indexing was done on the area prior to April. However, observation trips

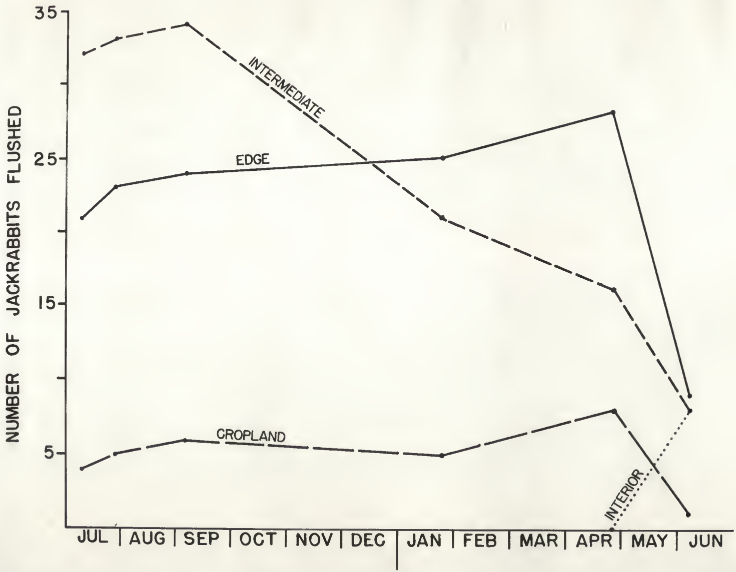

Fig. 6. Seasonal changes in indices of abundance for the cropland, sand-hill edge, sand-hill intermediate and sand-hill interior sections.

through this and other areas located near the center of the sand-hills during the winter months revealed that no jackrabbits were present. In June, four animals were flushed on two miles of indexing strips indicating that jackrabbits had moved into the area during the dispersing movements. The cropland section maintained a low and relatively stable number of jackrabbits until the onset of the spring rains when food was again available in the hills. In the June indexing period, only one jackrabbit was flushed while walking four miles of strips on this area.

The abundance of jackrabbits along the edges of the sand-hills was the result of local concentrations of jackrabbits which had moved out of the center of the hills rather than an overall increase in the species' population. Because of the abundance of animals in the hills, concentration would have occurred during the winter months despite the amount of rainfall. However, because of summer drought and accompanying overgrazing, jackrabbits began concentrating during the summer months.

The indexing strips covered eight per cent of each division. Assuming that these strips were representative of each division indexed and that the number of animals flushed on these strips represented eight per cent of the population, density and population estimates may be made for these areas (Table 5). It must be emphasized that any method of sampling a population is only as accurate as the proportion of the population sampled. Consequently, density and total number estimates given are accurate to the extent that sampling intensity was eight per cent.

If it were not for the concentration factor, the density of jackrabbits in the croplands of the Arkansas River valley would probably not have been above one jackrabbit for every 50 acres during the study period. It is obvious that the natural or preferred habitat for the jackrabbit in this area is the

Table 5. Numbers of animals flushed on indexing strips expanded to population and density estimates.

Indexing Period	Cropland Section	Sand-hill Edge Section	Sand-hill Inter-mediate Section	Primary Study Area	Sand-hill Interior Section
Early July '56:					
Number flushed	4	21	32	57	
Population estimate	52	277	416	745	
Density estimate*	0.08	0.43	0.65	0.39	
Late July:					
Number flushed	5	23	33	61	
Population estimate	65	299	434	797	
Density estimate	0.10	0.45	0.68	0.42	
September:					
Number flushed	6	24	34	64	
Population estimate	78	312	442	832	
Density estimate	0.12	0.49	0.69	0.43	
January '57:					
Number flushed	5	25	21	51	
Population estimate	65	325	273	663	
Density estimate	0.10	0.51	0.43	0.35	
April:					
Number flushed	8	27	16	51	0
Population estimate	104	351	208	663	0
Density estimate	0.16	0.55	0.33	0.35	0
June:					
Number flushed	1	9	8	18	4
Population estimate	13	117	104	234	52
Density estimate	0.02	0.18	0.16	0.12	0.16

* Density given as parts of a jackrabbit per acre.

sagebrush pasture lands of the sand-hills where under conditions of an abundant food supply, the population showed a density of about 0.16 jacks per acre or about one jackrabbit for every five acres (Table 5). In periods of food shortage the hares concentrated in the periphery of the sand-hills reaching an abundance in September, 1956 of 0.69 per acre or about one jackrabbit for every 1.4 acres. If man-caused mortality had not been so heavy on the study area, the density in the edge region probably would have reached about one jackrabbit per acre during the critical winter months.

A density of 0.1 to 0.2 jackrabbit per acre, which was found in the sand-hills when food supply was abundant, is not a high figure. Vorhies and Taylor (1933) estimated the population density of their study area in southern Arizona to have been about 0.5 jackrabbit per acre. Wooster (1939) recorded an average density of 0.3 per acre for a one-square mile plot of mixed prairie in Ellsworth County, Kansas. The highest density estimation that was found recorded in the literature was on a waterfowl refuge in California (Lechleitner 1955) where densities of 1.2 jackrabbit per acre were found. When food was not available for the jackrabbits within the sand-hills they migrated to the periphery where maximum densities of about 0.7 was recorded. When these animals along the periphery moved into the croplands to feed at night the highest density recorded was 14 jackrabbits per acre on a winter wheat field. This definitely constitutes a high density.

The average home range was not calculated in this study. The size of a jackrabbits' daily home range would be subject to much variation depending upon the location and abundance of food. During their evening foraging trips, animals moving out of the hills to feed had recorded linear distances of over one mile. These distances were determined by observing the animals through binoculars from a hill. When the animals were dispersed throughout the sand-hills, as they were when food was available in the hills, it is probable that their home range was not extensive.

The known mortality on the study area was 294 jackrabbits. This total consisted of 255 animals killed by hunting, 26 predator kills and 13 highway kills. The 255 animals recorded as hunting kills were shot by landowners with the exception of an estimated 25 jackrabbits killed during a drive held on the area by a group of farmers and residents of Lakin. As stated earlier in this section, only a part of the mortality on the area caused by hunting was recorded because during the winter months, hunters picked up the animals they had killed for bounty and carcass payments. Also because an average of only three or four days per month was spent on the area during the winter months, only a fraction of the predator and highway kills were detected.

The only predator of consequence on adult jackrabbits is the coyote (Canis latrans). Coyotes were observed occasionally and heard almost nightly on or near the primary study area. On one occasion three small separate groups were heard howling in the vicinity of the study area. In all probability coyotes depend heavily on the jackrabbit as a food source, particularly when the hares are concentrated during the winter time. A few of the larger mammals present on the area such as the badger (Taxidea taxus) and the striped skunk (Mephitis mephitis) could conceivably catch and kill young jackrabbits but neither of these mammals were present in sufficient numbers to be of any consequence as predators.

Four of the larger hawks and two of the larger species of owls were observed on the study area. Of these, only the American Rough-legged Hawk (Buteo lagopus sancti-johannis) and the Swainson's Hawk (Buteo swainsoni) were recorded as common on the area. Three instances were noted of these two larger hawks feeding on adult jackrabbits. All three jackrabbit carcasses were examined and none were found to have been fresh kills. Popular opinion to the contrary, it is doubtful that these large hawks are capable of or have the inclination to prey upon adult jackrabbits. On one occasion, a group of three large sagebrush plants about ten feet apart was observed to have an American Rough-legged Hawk and two adult jackrabbits resting in the shade. Neither of the jackrabbits appeared to be concerned about the presence of the hawk. However, on other occasions, jackrabbits showed fear when one of the larger hawks chanced to fly close to them. Three instances of Swainson's Hawks preying upon cottontail rabbits (Sylvilagus audubonii) were observed and in all probability the larger hawks also prey upon young jackrabbits.

The blizzard of March, 1957, which deposited 24 inches of snow on the level and contained winds of 60-70 miles per hour in Garden City, killed few jackrabbits on the study area but dead jackrabbits were noted in the flat cultivated lands to the north of the Arkansas River. Several residents of the area reported many jackrabbit carcasses found in borrow pits of east-west running roads after the snow melted. Evidently the animals had taken refuge in these ditches from the strong winds and blowing snow and had been covered up, as the snowfall continued for more than two days.

CROP DAMAGE

The Arkansas River valley in Kearny County is an area of intense farming where irrigation is heavily relied upon as an agricultural aid. The principal crops are hard winter wheat, milo, alfalfa and feed sorghums. The study area was chosen at the location south of Lakin because it was thought to be representative of areas along the edge of the sand-hill region where crop damage had been heavy in the winters of 1954-'55 and 1955-'56. Specifically, the degree of crop damage was estimated for the following reasons: (1) to determine if damage was limited to the most readily available fields in relation to the sand-hills or if it was general throughout the valley; (2) to determine the effect of buffer fields upon the amount of damage in a field; and (3) to gain some information about the distances jackrabbits moved from the hills during their nightly feeding trips.

No attempt was made to evaluate the total loss resulting from the feeding activities of the hares on the study area. Rather it was hoped that a comparison of the amounts of damage in different fields would indirectly give information about the nocturnal movements of the animals and the relationship between the amount of damage and the distance from the animal's daytime resting areas. Accordingly, four fields, two each of wheat and milo, were chosen for damage estimation studies. One field of each crop was located so that it was readily accessible to the jackrabbits as they initially began their feeding trips at sunset. The other field of each pair was chosen at least one mile from the edge of the sand-hills and situated so that fields of the same crop, acting as buffer fields, lay between this field and the sand-hills edge.

Jackrabbit damage inflicted upon milo plants ranged from eating a part of the leaves to eating the entire plant (Plate III, Fig. 1 and 2). Jackrabbits feeding milo fields were observed through binoculars on several occasions. During the month of August and September, when milo fields were being heavily utilized as food sources, several fields were inspected to obtain information upon the type of damage. The most typically damaged plants had only a stump remaining. The animals chewed through the stalk at a point one to three inches above the ground and fed upon a part of this cut-off portion. The seed head alone was occasionally eaten but only one instance of this type of feeding was observed. The jackrabbit stood on its hind legs, using its front paws to hold the plant steady while feeding upon the mature head.

Milo damage was estimated on two fields which were named Fields M and m (Fig. 3). The per cent of damage in these fields was obtained by choosing specific rows within a field and counting the number of damaged and undamaged plants in a certain number of random one-yard samples for each row chosen. The location of these one-yard samples was obtained through use of a table of random numbers in Snedecor (1956). Milo damage estimates were made on September 28 and 29, 1956, approximately one month before the harvest time for this area.

Field M, a 55-acre field located in Division E of the study area, was situated with the south and east borders lying adjacent to the edge of the sand-hills. This field was divided for sampling into the following three subdivisions: Area M_1, which consisted of the south 17 rows; Area M_2 which was a strip 50 feet wide along the southeast and east borders of the field; and Area M_3 consisting of the remainder of the field. Therefore, damage in this field was estimated for a strip composed of Areas M_1 and M_2 along the field borders which were adjacent to the daytime resting area of the jackrabbits and the rest of the field was composed of Area M_3. Damage estimates were made on these areas in the following manner: In Area M_1, 20 samples were taken on every fourth row; because the rows were laid out running east and west in this field and Area M_2 had its long axis lying across the rows, Area M_2 was sampled by two one-yard samples on every tenth row; and in Area M_3, 20 samples were taken on every fortieth row.

Field m, a five-acre field, was located in the extreme northwest corner of the study area approximately one and one-fourth miles from the nearest daytime concentration of jackrabbits. There were several buffer fields of milo between this field and the hills.

By omitting Area M_2, because it is comparable to Area M_1, in that both are field borders lying adjacent to the sand-hills edge, a row by row analysis shows heavy damage on the rows nearest the sand-hills and lighter damage through the remainder of the field (Table 6). Further evidence that jackrabbits feed on the most accessible rows, in relation to the sand-hills, was found in the rows closest to the daytime resting area where there was a preponderence of damaged plants which had been eaten when young. Heavy damage extended into the field for about 75 to 100 rows. The majority of the field had damage ranging from 10 to 20 per cent.

Table 6. Per cent of damaged milo plants by row number on Areas M_1 and M_3* exclusive of M_2.

Row Number	Per Cent of Damage	Row Number	Per Cent of Damage
1	93.2	155	18.0
5	90.0	195	5.6
9	72.2	235	5.7
13	73.9	275	12.2
17	44.7	315	14.9
35	42.4	355	15.5
75	24.4	395	12.4
105	14.4		

* Rows numbered with Row Number 1 being located on the south edge of the field and being the closest row to the sand-hills edge.

Table 7. Milo damage estimates on Fields M and m.

Field	Number of Plants Examined	Number of Plants Damaged	Per Cent Damaged	Range of Damage By Rows
Field M				
Area M_1	397	290	73.0	93.2 - 44.7
Area M_2	353	227	64.3	100.0 - 0.0
Area M_3	740	126	17.0	42.4 - 5.6
Field m	192	2	1.0	4.3 - 0.0

When the results of damage estimations for Fields M and m are compared it would seem that one and one-fourth miles would be beyond the average distance traveled by jackrabbits during their nightly foraging trips in the late summer and fall months (Table 7). The low per cent of damage on Field m probably resulted because of the presence of buffer fields, rather than because of the distance factor. Field m was adequately buffered by milo and alfalfa fields and had an irrigation ditch to the south of it. In the late summer and fall the distances which jackrabbits travel into the valley on foraging trips apparently are directly dependent upon the location of the nearest food source. During evening observations in August and September several large concentrations of jackrabbits were noted in milo and alfalfa fields more distant from the hills than Field m. In almost all instances these fields were the nearest food sources to the edge of the hills

It must be emphasized that both fields would have been economic losses to the landowners even without the presence of jackrabbit damage. Both had been irrigated at the beginning of the growing season but because of the drought this practice had been discontinued. Consequently neither field was harvested. A possible source of bias when comparing the amount of damage in the two fields is the fact that irrigation was stopped earlier on Field m and possibly the plants of this field had lost their palatability to the jackrabbits before they could be heavily damaged. This would not account for the large difference between the per cent of damage on the two fields.

Estimating the amount of damage done to wheat by grazing is a complex problem. Anderson (1956) stated that a certain amount of grazing will not materially reduce grain yields and often the yield will be somewhat increased by moderate grazing. Winter grazing may maintain the soil moisture until it is needed by the plant for the heading-out process. In general, providing it has become well established in the fall, wheat can be moderately grazed until the jointing stage without serious reduction in grain yields.

Pulling or digging out the roots by the hares was the principal complaint of wheat growers in the river valley. Since wheat damage estimation work has not started until the last week of March, this type of damage was not evaluated. Consequently, none of the wheat damage figures can be taken as the total damage attributable to jackrabbits on the wheat field where those figures apply. As in the milo studies, the damage estimation studies for wheat had the objective of determining if the damage was a local problem confined to fields lying next to the hills or if it was general throughout the valley.

In July of 1956, original plans were made to utilize fields on the study area for both wheat and milo damage studies. Because of the drought and a change in tenants, the fields originally planned for wheat damage checks were not planted. Two wheat fields named W and w were chosen in the area surrounding the principal study area for wheat damage estimation (Fig. 3).

Field W, located two miles west of the study area, was situated approximately one-fourth mile from the edge of the hills. There were no buffer fields present. This field was not a pure stand of wheat but had some alfalfa planted on it. Because the exclosure method of damage estimation was used, the presence of two types of plants would have no effect on the difference in per cent of damage for the grazed and ungrazed plots. Field w was located one-half mile north of Division A of the study area and was approximately one and one-fourth miles from the nearest sand-hill pasture land. There were several buffer fields of wheat between this field and the sand-hills.

On March 27 and 28, 1957, ten 4 x 4 foot exclosures (Plate IV, Fig. 1) made of two-inch hexagonal chicken wire were placed in each field as control plots using a table of random numbers for the determination of each plots' location. The method of random paired observations was used to eliminate the variable of a patchiness type of grazing. The test plots to be checked for grazing loss consisted of the 16 square feet lying to the south of each exclosure.

The exclosures were removed and a sample of wheat was harvested from each grazed and control plot on June 10 and 11, 1957. A one-eighth inch steel wire hoop, having an area of 2.6 square feet, was placed in the center of each plot and the heads of all plants contained within the hoop were collected. The samples from each plot were placed in numbered paper bags and brought to Manhattan where the stems were trimmed to a uniformly short size and the heads weighed on a gram balance to the nearest 0.5 gram (Table 8).

The difference between each set of paired plots was calculated and the resulting figures grouped according to fields and subjected to the t-test.

Table 8. Weight of harvested samples from Fields W and w.

Enclosure No.	Field W		Field w	
	Grazed	Control	Grazed	Control
1	12.5 gr.	56.0 gr.	24.5 gr.	25.5 gr.
2	28.5	53.5	16.5	24.5
3	48.0	48.5	20.5	25.5
4	27.0	71.0	19.0	22.0
5	36.0	58.5	20.5	21.0
6	53.0	56.0	18.0	5.5
7	37.0	81.5	19.0	11.0
8	53.5	63.0	12.0	21.5
9	70.5	87.0	16.5	13.5
10	41.5	58.5	21.0	20.0
Total	407.5	633.5	187.5	190.0
Mean Differences	22.6 gr.		-0.8 gr.	

The differences between grazed and ungrazed plots on Field W, the unbuffered field, was significant at less than the one per cent level indicating a definite loss in wheat because of the grazing activities of jackrabbits ($t = 4.30$; $t_{.05} = 2.26$, 9 D.F.). Field w showed a mean difference between the grazed and control plots of minus 0.8 grams indicating that no loss occurred because of the grazing activities of jackrabbits.

At the time wheat damage samples were collected, it was noticed that a 25 to 50 foot wide strip of plants along the south border of Field W had not headed out. Apparently jackrabbits had fed upon these plants after the jointing stage. As discussed earlier, the heavy rains in the spring of 1957 had provided sufficient natural food to prevent heavy damage to wheat after the jointing stage and the loss of this strip of wheat probably occurred just before the dispersing movements which took place in May.

During a two and one-half week period beginning in the third week of April, the landowner pastured approximately 10 to 15 cattle on Field w. It is evident that this amount of grazing by cattle did not significantly reduce the yield of wheat in this field while continual grazing by jackrabbits on Field W during the winter and spring months did materially decrease the amount of wheat. Several nocturnal feeding counts were made on Field W during the winter and spring months. The procedure for these counts was to drive slowly along the road bordering this field and count all jackrabbits observed in the field. Feeding counts on Field W ranged from 66 to 203 jackrabbits. As stated previously, the highest count of 203 jackrabbits was calculated to be a density of 14 per acre. It can readily be seen why the results of tests on grazed and ungrazed plots show a significant loss of wheat on Field W. Only one feeding count was made on Field w and on that evening there were only four jackrabbits in the field.

As in the milo damage studies, it has been concluded that wheat damage in the region of the Arkansas River valley is local and that jackrabbits moving out of the sand-hills on nocturnal foraging trips feed on the most available wheat fields. Unbuffered fields lying adjacent to the sand-hills edge would be expected to receive heavy damage by night-foraging jackrabbits when the population of jackrabbits in the sand-hills is at the high-level of abundance that it has been for the last three years.

POPULATION FLUCTUATIONS

Despite the heavy crop damage accompanying jackrabbit population increases and the opportunities for ecological study on this species, the jackrabbit has been the subject of comparatively few ecological researches. This is true not only in Kansas but for the majority of the western states. It is amazing that so interesting a mammal and one which occurs in densities which are favorable for ecological study has been so neglected in population studies. The jackrabbit population throughout much of its range exhibits marked fluctuations in numbers. An answer to the question of why a population of jackrabbits increases so markedly at certain times is beyond the scope of this study. A thorough understanding of the causes of jackrabbit fluctuations would require a long-term investigation not only of the ecology of the population, but also of the physiology of this species. However, during the course of a one-year investigation of the basic biology of this mammal, several factors which affect the fluctuations of jackrabbits have become apparent.

There is little doubt that a relationship exists between the occurrence of jackrabbit population eruptions in western Kansas and the occurrence of drought conditions. Both the drought period of the mid-1930's and the recent five-year drought (1952-'57) were accompanied by large increases in the numbers of jackrabbits in the western part of the state. These are established facts, familiar to most residents of that region.

The present eruption was first noticed during the winter of 1953-'54. By questioning landowners, game wardens and county agents, it was revealed that these hares were never abundant and only locally common during the period between the eruption which occurred in the 1930's and the population increase of the present drought period. The majority of the people questioned also stated that there were many more jackrabbits in the 1930's than during the present drought period.

It has been shown that during the period when the reproductive cycle was studied, female jackrabbits produced an average of about seven young per breeding season and since the sex ratio of collected specimens was essentially a 50:50 ratio, there were about 3.5 young produced for every adult in the population. Assuming that the average production in 1956 was about the same as was calculated for the last part of that breeding season and the first part of the 1957 season, a figure for the survival of juveniles during the breeding season can be obtained by comparing the adult:juvenile age ratios after reproduction ceased with the number of young produced (Petrides, 1941). Reproduction ended in August, however, it has been shown that young jackrabbits do not appear in collections until they are about one month old. The fall age ratio, consisting of the collections made in October and November, should be a reliable index to the number of young-of-the-year that lived from the time they were born to the beginning of the critical winter period. The age ratio for these two months was 36 adults to 96 juveniles or approximately a ratio of 1 adult to 2.7 juveniles. If the population had not been subjected to mortality, there should have been a ratio of 1 adult to 3.5 juveniles during these fall months. It would appear that there was a juvenile mortality during the breeding season of 23 per cent. This comparison does not take into consideration the loss in adults during the breeding season. The mortality of adults would tend to increase the apparent survival of young by increasing the proportion of juveniles to adults in the fall population. Consequently, the 23 per cent loss of young is accurate only as a minimum mortality figure for juveniles. A 23 per cent loss of young during the summer and fall months cannot be considered as heavy mortality in the young-of-the-year of a polyoestrus mammal.

Unless significant juvenile mortality occurs during the breeding season, the winter months comprise a period when a population, if it is to remain stable, must be reduced by mortality to a degree where the survivors of this period will be essentially the same in numbers as the survivors of the preceding winter period. If survival is high during this period more potential breeders will be present at the onset of the reproductive season and the population will increase. Providing also that the habitat is capable of supporting that increase.

Juvenile mortality during the critical winter period can be approximated even though aging techniques for young-of-the-year males are inaccurate after

November. Juvenile females could be accurately aged until breeding began in February. The January collection consisted of 53 jackrabbits, of which 11 were juvenile females. By January, all young-of-the-year males had become sexually mature and so could not be differentiated from the older males. Since the sex ratio is essentially 50:50, it follows that there would be an approximately equal number of young-of-the-year males in the collection as juveniles females. The ratio, after an adjustment to account for the inability to detect young-of-the-year males, would be about 22 young of the year out of the 53 animals collected. The age ratio, therefore, had decreased to 1 adult for every 0.7 juveniles. Although the breeding season began in February, only one pregnant female was taken in that month's collection, and that collection revealed a strikingly similar ratio of 20 juveniles out of the 50 animals collected.

The change in ratios was based on the assumption that mortality is negligible in adults and this was undoubtedly a false assumption. Also in all probability there was a differential mortality among adults and juveniles. The number of young-of-the-year would normally be expected to decrease faster than the number of adult animals. Since a change from a ratio of 1:2.7 during the fall to 1:0.7 during the critical winter period would indicate a minimum mortality for the region, it is obvious that the mortality loss in young-of-the-year was exceptionally heavy during the months of December and January. A characteristic of an increasing population is the preponderence of young in that population which survive to breed the following year but there was definitely not a preponderence of young present during the critical winter period. Further evidence of this is the low proportion (20 per cent) of females which were pregnant but non-parous during the first three months of the 1957 breeding season. It is now evident that the population of jackrabbits in the sand-hills which had been increasing rapidly since 1953, must have become stabilized, or at least began increasing at a much less rapid rate during 1956. The probable history of the 1950's drought period eruption would then be: the population began increasing in 1953, increased rapidly until 1956 and became stable or relatively so during 1956 and through the first part of 1957. Field observations for the study period and conversations with residents support this sequence of events.

There was no way of obtaining information on the exact, or even the approximate, percentage of increase in the population during the drought period. However, it is felt that the increase has appeared to be larger than it actually was because of two factors which had the effect of concentrating the animals. The first is the concentration of the animals in the vicinity of the croplands when the natural food supply of the animal became depleted because of the overgrazing and drought conditions. Concentrations of animals feeding on the croplands would be more readily noticeable than if the food was abundant and they were dispersed throughout their normal habitats. On the study area, the dispersion and concentration migrations recorded in the sand-hills edge is illustrative of this point.

A second and a more minor factor is the shrinkage of the actual area of available habitat in the region. Exact figures on the changing land use pattern were not available. During the drought period the acreage of the available habitat in some areas probably decreased because of some exceptionally heavy overgrazing and an increase in the amount of fallow land. Vorhies and Taylor (1933), working in areas of varying grazing intensity, showed that overgrazing and subsequent secondary succession of an area creates a preferred habitat for jackrabbits, but that the animals were not abundant in areas that were severely overgrazed. The carrying capacity of an area for jackrabbits was increased to a maximum by overgrazing and then more severe overgrazing reduced the carrying capacity. Overgrazing has been a common practice in southwestern Kansas during the five-year drought. Part of the rangeland has been depleted to such an extent that it is unsuitable habitat for jackrabbits, thereby concentrating the animals in a somewhat smaller area. However, the majority of the pasture land had probably been depleted only to the state where the carrying capacity for the jackrabbit population was increased.

This concentration of animals because of a lack of suitable habitat was not as noticeable in the sand-hills as it was in the flat crop and pasture land to the north of the Arkansas River. In these areas jackrabbits spent the daytime in brushy draws or in some instances in wheat stubble fields. The jackrabbits left their resting areas at night to feed on the surrounding croplands. The movement in these areas was much the same, only on a smaller scale, as the daily movement pattern of the animals residing in the sand-hill edge sections. However, jackrabbits concentrated along the edge of the hills because of the food factor while the animals north of the river concentrated in brushy draws because this was the only habitat available for resting areas.

A factor which would tend to give the populace an impression that jackrabbits were more abundant than was really the case and consequently that crop damage was heavier than it actually was, is that inherent quality in man which makes him prone to exaggerate. One illustration of this will suffice: The January index of abundance on Division B of the primary study area was 14 flushed animals, giving a population estimation of about 180 jackrabbits for that division. The following day after indexing had been completed, a group of local residents held a "rabbit drive" on this division. The author and another worker observed this drive and estimated that about 25 jackrabbits had been killed. When the drive had been completed and the hunters were gathered to await transportation to another area, the author questioned the group about their opinions of the number of animals killed and the number which had escaped from the field. The concensus was that about 55 had been killed and between 400 and 500 jackrabbits had escaped the hunters' guns. Their estimate of the number of animals in the field was therefore about 450 to 550 animals when the censusing procedure on the preceding day had indicated about 180 jackrabbits in that area.

In an attempt to gain information about the past fluctuations of the jackrabbit population, commissioner's journals of Kearny, Grant, Haskell and Finney Counties were reviewed from 1900 to date. Dates were recorded by month when either jackrabbit bounty was paid or for other indications of a high jackrabbit population, and these months were graphed in relation to the mean annual rainfall for the four counties (Fig. 7). The category named "other indications" included such entries as payments for "strychnine for jackrabbits", "advertising rabbit drives" and "moving rabbit fencing". When periods of abundance are compared to the average annual precipitation, a relationship between peaks of abundance and drought since 1930 is indicated. Because of a state law requiring counties to pay bounty in the 1920's, no relationship can be seen during that period.

Carter (1939), using data obtained exclusively from questionnaires, showed that when settlers first came to western Kansas there were few Black-tailed Jackrabbits. As the native prairies were put under cultivation, this hare increased in numbers. This increase was gradual and the animals reached maximum abundance around 1920 with the exception of the population eruption in 1934.

By utilizing the above mentioned information and the results of the survey of county records, it would seem that as the climax grassland decreased

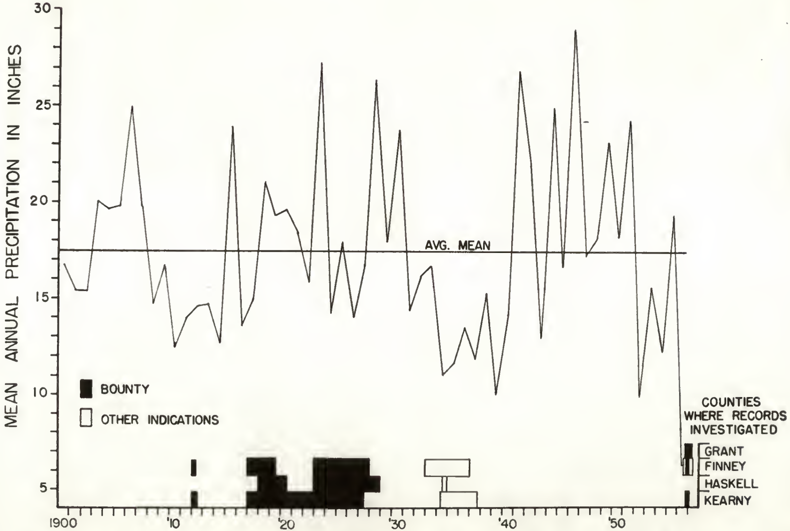

Fig. 7. Relationship between mean annual precipitation and indications of high jackrabbit populations as found in county records of four southwestern Kansas counties.

because of cultivation and grazing, the jackrabbit increased it's range and numbers in western Kansas. All indications were that once the maximum amount of land was being utilized by man, the jackrabbit population became relatively stable with the exception of population eruptions during the two drought periods. Questionnaires and county record surveys are not accurate sources of information. Because the jackrabbit has such a profound effect on agriculture, it is felt that at least the years of peak abundance were obtained. Undoubtedly there have been many minor fluctuations in the levels of population abundance. With the exception of the eruptions occurring in the two drought periods, no evidence was found to indicate that these fluctuations were anything more than random changes in abundance that could be expected in any animal population.

Taylor, et al. (1955) and Vorhies (1936) developed the concept of the jackrabbit as an "animal weed". They showed that jackrabbits are an effect and not a cause of overgrazed conditions. Secondary succession resulting from overgrazing, unless exceptionally heavy, creates in some way a more preferred habitat for the jackrabbit. These authors were of the opinion that a preference for annual instead of perennial vegetation as food was the cause for jackrabbits preference of overgrazed situations. It would appear that drought and the increase of overgrazing which accompanies drought conditions in western Kansas increased the carrying capacity of rangeland in a manner not fully understood but related to secondary succession. A flaw in this hypothesis is that many western Kansas areas were in a state of secondary succession before the drought period. Probably the degree of a secondary succession and the change in plants associated with this stage of succession could account for the increased carrying capacity. At any rate, it is apparent that overgrazing in combination with drought conditions in some way increase the carrying capacity of an area. An increased carrying capacity does not necessarily constitute an actual increase in numbers of jackrabbits.

An animal population to increase in numbers must be liberated to some degree from certain limiting factors. The two most important limits on population size are factors decreasing the reproductive potential and mortality factors. It is beyond thelimits of a one-year study to determine whether increased reproduction or decreased mortality is responsible for jackrabbit population increases. It would seem probable that increased reproduction would occur under conditions of food abundance and it has been shown that food was not abundant during the breeding season of 1956. Rather, it seems more probable that survival of the precocious young would be higher during dry weather and that this factor might account for an increase in numbers. Juvenile survival was relatively high throughout the breeding season in the dry year of 1956. However, survival of young-of-the-year was low during the critical winter period. It is entirely possible that during the critical winter period, the carrying capacity of the habitat had been reached and that other factors were limiting the population at that time.

No evidence was found in this study to indicate that the Black-tailed Jackrabbit is cyclic in Kansas. If these populations were to be thoroughly studied for a longer period of time, jackrabbit fluctuations probably could be explained by factors pertaining to the stage of succession of the rangeland and the effect of drought conditions on the survival of young in the population. It is further asserted that the population subjected to a long-term study would not exhibit the cyclic phenomenon so noticeable in some of the more northerly residing species of mammals.

SUMMARY

The Black-tailed Jackrabbit has been the subject of comparatively few

ecological researches. The literature was reviewed and contradictory evidence was found during this review as to whether the jackrabbit's populations display the phenomenon of cyclic levels of abundance.

The study on the ecology of this hare extended over a period of 12 months (July 1956 to June 1957) and was initiated because of reports that a population eruption, and consequent heavy crop damage, had occurred in southwestern Kansas. Field work was conducted in four southwestern Kansas counties but principally along the Arkansas River Valley and the sand-hills lying to the south of that river in east-central Kearny County.

The jackrabbit is not gregarious except in the breeding season. Interactions are few but responses from interactions which do occur may take the form of head-butting, running in circles, biting or jumping into the air. Activity in this species is almost exclusively crepuscular or nocturnal and wind was found to be the chief limiting factor on the amount of activity.

Sexual dimorphism was evident in the total length and weight of adults. Female jackrabbits averaged about 18 millimeters larger and 11 ounces heavier than males. Specimens were aged by the size and condition of the reproductive organs and by the degree of closure of the epiphyses and diaphyses of the humeri.

Monthly specimen collections for study of the jackrabbit's reproductive cycle totaled 696 animals. The breeding season extended from early February through August. No pregnant females were in evidence during the months of September through December and no males showing evidence of testicular activity were found in October or November. The onset of the breeding season was determined by the condition of oestrus in females but pregnant females and potent males disappeared from the collections at about the same time when the breeding season ended in August.

The average number per litter increased from 1.0 in February to 3.6 in May and then decreased to 2.0 in August. The mean litter size for all months was 2.5 and the range was one to five. The mean number of litters per year was calculated to be 2.8 or an average of 7.0 young produced per female per year. The comparatively severe winters and the failure of many animals to become pregnant during the post-partum oestrus caused the population of jackrabbits studied to produce fewer young on the average than in comparative studies in Arizona and California.

Considerable evidence of prenatal mortality was found in litters which were aged at less than half-term. It was estimated that 37 per cent of the litters which were conceived were lost in their entirety sometime before mid-term. Following a severe blizzard in March of 1957, six of the 17 adult females collected showed evidence of resorbing their entire litters, possibly indicating that periods of stress can cause rescrption.

The suckling period was calculated to be two weeks. No young jackrabbits were collected which were aged at less than one month and it is evident that after weaning, young jackrabbits remain comparatively secretive for an additional two week period. The jackrabbit probably does not make nests in southwestern Kansas.

Six comparative indices of population abundance were obtained for the 1920-acre primary study area and two indices were obtained for a secondary 320-acre study area by using the strip censusing method. By comparing these indices and relating the population trends to the amount of rainfall, it was evident that the abundance of jackrabbits in the sand-hills changes seasonally according to the availability of food. Overgrazing by cattle and a lack of rain during the summer of 1956 quickly depleted the supply of grasses and forbs in the sand-hills. Because of this failure of the natural food supply, the animals concentrated along the edge of the sand-hills where they would be in a position to obtain food on their nightly foraging trips into the croplands. When the drought was broken in the spring of 1957 and a good supply of grasses and forbs was again available, the jackrabbits dispersed throughout the sand-hills.

Eight per cent of the area was sampled in obtaining the indices of comparative population abundance. Assuming that the indexing strips were representative of the area and therefore the number of flushed animals was in proportion to the population of the remainder of the area, population and density estimates were made. According to the level of abundance shown by the population in 1956 and 1957 and when food was available in the sand-hills, there was about one jackrabbit per 50 acres in the cropland region and one for every five acres in the sand-hill pastures. When food was not available in the sand-hills, density estimates reached about one animal per 1.4 acres along the edge of the sand-hills in the daytime as the animals concentrated in those areas and a maximum count of 14 per acre on a winter wheat field adjacent to the hills during the night.

Only a fraction of the mortality could be detected on the area. Adult jackrabbits are killed by man and preyed upon by coyotes while young hares are subject to predation also by the buteonid hawks found on the area.

Crop damage was estimated on two milo fields and two wheat fields to ascertain if damage was local, the effect of buffer fields on the amount of damage to a field and to gain some conception of the nocturnal movements of the jackrabbits. Results from damage estimation on both crops showed that serious damage was limited to the crop fields nearest the daytime resting area of the hares and that buffer fields between a field and the sand-hills were effective in reducing damage. On their nocturnal foraging trips into the croplands, jackrabbits moved only as far as the closest food source whether this food source was located 100 feet or one mile from the edge of the hills.

Little information was available on the past fluctuations of the jackrabbit population. Various persons were interviewed and county records were surveyed in an attempt to add more data to the small amount of information that was available in the literature. Even though interviews and county record surveys are not reliable sources of information, it was hoped that since the jackrabbit does have a profound effect on agriculture, at least the peaks in population abundance were apparent. All evidence indicated that the jackrabbit increased in range and abundance as the climax grasslands were lost to cultivation and grazing. The population reached a comparatively stable level around 1920. The levels of abundance were uncertain for the period 1920 through 1930. Since about 1930, the population has maintained a relatively stable level with the exception of population eruptions in the two drought periods (1930's and 1950's) which have occurred in that time interval.

The present population eruption began in 1953 and by comparing age ratios at intervals with the known average reproduction as an indication of juvenile survival, it was ascertained that the population became relatively stable in 1956. The percentage of increase could not be determined. Certain factors related to the drought tended to concentrate the jackrabbits and gave the impression of a larger increase in numbers than actually occurred.

The jackrabbit is probably not cyclic in Kansas but is subject to eruptions during drought periods because of a change in the carrying capacity of the rangeland. This increased carrying capacity resulting from overgrazing and drought is not clearly understood but is apparently related to the degree of secondary succession and the changes in the habitat accompanying such successions. Juvenile survival may be greater in drought years and this factor would enable the population to increase in numbers as the carrying capacity of the habitat increases.

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APPENDIX

EXPLANATION OF PLATE I

Fig. 1. The Black-tailed Jackrabbit, pregnant female.

Fig. 2. Concentration of jackrabbit pellets caused by rain run-off carrying the pellets into low areas.

PLATE I

Fig. 1.

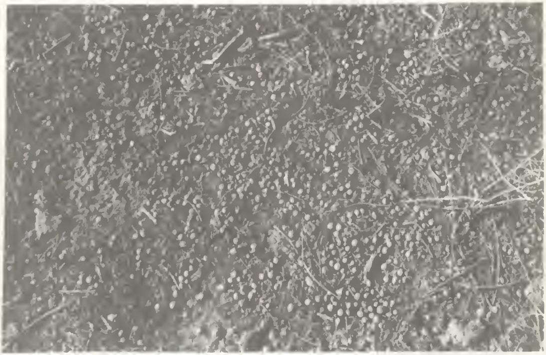

Fig. 2.

EXPLANATION OF PLATE II

Fig. 1. View looking east in the sand-hills showing the depleted food supply caused by overgrazing and drought conditions. Taken in early April of 1957.

Fig. 2. Close-up view of the foreground in the picture above.

PLATE II

Fig. 1.

Fig. 2.

EXPLANATION OF PLATE III

Fig. 1. Milo field on the east border of Division E of the primary study area showing the effects of the feeding activities of jackrabbits moving out of the sand-hills (upper right) on nocturnal foraging trips. Taken in August of 1956.

Fig. 2. Close-up of plants taken from the field in the picture above showing types of damage inflicted on the plants by feeding jackrabbits.

PLATE III

Fig. 1.

Fig. 2.

EXPLANATION OF PLATE IV

Fig. 1. Close-up of one side of an exclosure used for wheat damage estimation on Field W showing the effects on the wheat of grazing jackrabbits. The ruler is six inches in length. Photo was taken in April of 1957, 25 days after exclosures were set up.

Fig. 2. View looking west across the interior sand-hill section of the study area. Taken in April of 1957.

PLATE IV

Fig. 1.

Fig. 2.

THE ECOLOGY OF THE BLACK-TAILED JACKRABBIT (*Lepus californicus melanotis*, Mearns) IN SOUTHWESTERN KANSAS

by

FRANKLIN HERBERT BRONSON

B. S., Kansas State College of Agriculture
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Reports of heavy crop damage by Black-tailed Jackrabbits in the western part of Kansas during the winters of 1954-'55 and 1955-'56 indicated a population increase of this species. A review of literature revealed that even the most basic ecological facts about this hare were unknown for the central region of the United States. An ecological study of the jackrabbit in southwestern Kansas was conducted from July, 1956 to June, 1957. The majority of the 88 field days was spent in the sand-hill region and the Arkansas River valley of Kearny County. It was hoped that the basic data obtained from this study could be utilized in understanding the population fluctuations of this species.

Methods were: (1) a collection of 696 specimens was examined to determine the reproductive cycle; (2) population trends on a 2240-acre study area were recorded as well as data on mortality, variations in the natural food supply, crop damage and observations of the animals' movements and habits; and (3) county records were examined and residents were questioned about certain aspects of the population eruption.

One reproductive cycle was recorded. The average number per litter was 2.5 and the average number of litters per year was 2.8 or an average production per female per year of 7.0 young. Considerable evidence of prenatal mortality was found. Comparatively severe winters and failure of many females to become pregnant during the post-partum oestrus cause the jackrabbit in southwestern Kansas to have a lower production than that which was found by investigators in California and Arizona. The suckling period was calculated to be two weeks. Aging was accomplished by the size and condition of the reproductive organs and the degree of epiphyseal closure.

Six indices of population abundance were obtained by periodically walking a set pattern of censusing strips and counting the flushed hares. By relating the trends in population density to the amount of precipitation, it was evident that drought conditions and overgrazing caused a failure of the natural food supply which in turn resulted in a migration of the jackrabbits from the center of the sand-hills. Concentrations of animals along the edge of the sand-hills were the sources of the heavy wheat and milo damage which had been reported in the Arkansas River valley.

Crop damage was estimated on two wheat and two milo fields. It was concluded that damage was local and that the presence of buffer crop fields materially reduced the amount of damage.

Information obtained through a literature review, resident interviews and a survey of county records indicated that the jackrabbit population has remained relatively stable since the late 1920's with the exceptions of population eruptions in the drought periods of the 1930's and 1950's. By comparing age ratios and the known average production, it was shown that the population, which had been increasing since 1953, became relatively stable during 1956.

Drought conditions and overgrazing increase the carrying capacity of rangeland in some manner, probably by a change in the type and amount of vegetation. Either increased reproduction or increased juvenile survival, probably the latter, would enable the population to increase in numbers as the carrying capacity is increased.