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A Study of Certain PLANT AND ANIMAL INTERRELATIONS on a Native Prairie in Northwestern Minnesota

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The Waubun Prairie Research Area

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ON A NATIVE PRAIRIE IN NORTHWESTERN MINNESOTA

BY

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AND

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Dr. Vincent Schultz of the Atomic Energy Commission offered valued criticisms of the manuscript.

Names of grasses follow Hitchcock and Chase (1950); other plants, Gleason (1952); mammals, Hall and Kelson (1959); and birds, American Ornithologists' Union (1957).

Voucher specimens are filed in the following collections of the University of Minnesota: plants, Herbarium, Department of Botany; mammals and birds, Museum of Natural History; insects, Department of Entomology and Economic Zoology.

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A Study of Certain Plant and Animal Interrelations

INTRODUCTION

ANIMAL populations are closely related to extant vegetation, but the particular characteristics of the vegetation which influence the distribution and abundance of most species of animals are not well defined.

This study, which was carried out from the Lake Itasca Forestry and Biological Station, was conducted to determine the nature of the relations between specific vegetational characteristics of the dominant grasses and litter found on a native prairie in northwestern Minnesota and associated populations of certain birds, small mammals, and insects. The Waubun Prairie Research Area in Mahnomen County was selected as the site for this study.

Quantitative knowledge about the ecological relations among inhabitants of the same locality is necessary for a complete understanding of the structure of the community. Grasslands are well suited to this kind of investigation because major features of the habitat can readily be modified by treatments such as burning, controlled grazing, and mowing, without altering the over-all nature of the community. Subsequent changes in associated animal populations can then be studied.

In addition to contributing to a knowledge of community structure, the results of the investigation have applications in land management. Federal and state governments and conservation-oriented organizations are placing increasing emphasis on the acquisition of natural areas. To get the maximum value from these areas, many of which are in the prairie region of North America, sound management must be developed from basic information. We hope that this investigation will provide information which may be useful in the formulation of such management plans.

The area studied is a 640-acre tract containing approximately 250

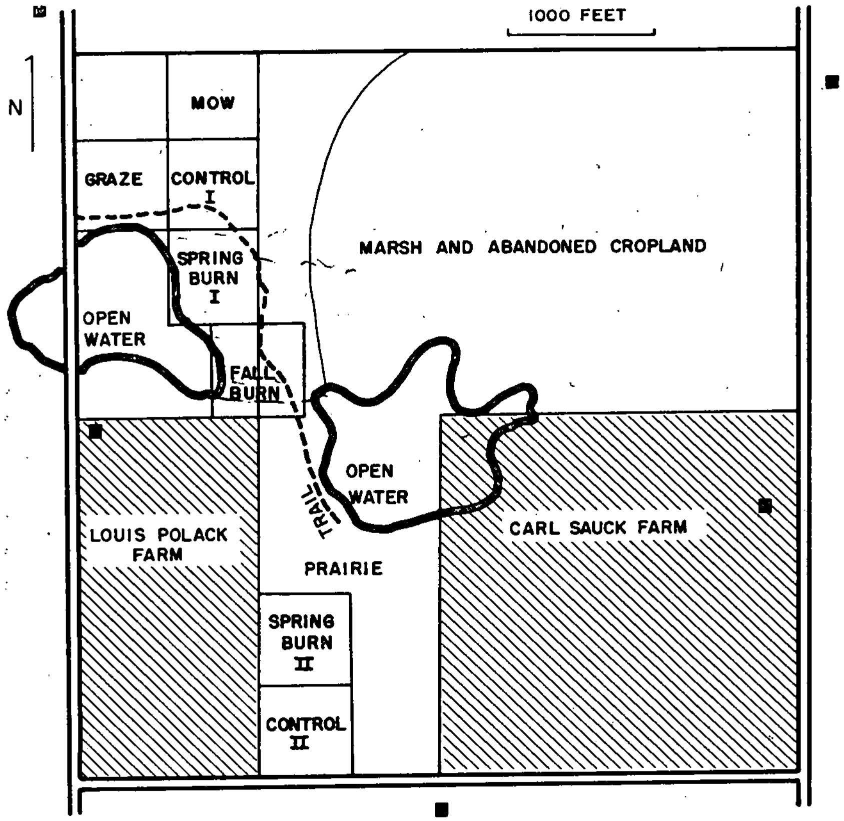


Figure 1. Waubun Prairie Research Area; Section 33, Township 143 North, Range 42 West, 5th Principal Meridian; Mahnomen County, Minnesota

acres of unplowed native prairie. It is 11 miles southwest of the town of Mahnomen in Section 33, Township 143 North, Range 42 West of the 5th Principal Meridian (Fig. 1). This tract was acquired by the Minnesota Department of Conservation in 1954. The entire area has been reserved for basic research and experimental land management.

Louis Polack, who purchased part of this land about 1921 and later sold it to the Minnesota Department of Conservation, has stated that the area selected for study was not plowed during his tenure and that he believed it had never been plowed. The possibility exists, however, that some of it was broken during the period of high land prices in 1917 and 1918. Both grazing and mowing of native hay have been carried out at various times in the past.

No specific information is available on other uses of the land. Mr. Polack said that since 1921 the native hay on the driest portions of the upland had been regularly mowed and that fire and cattle had been kept out. He was unable to give information on these points before 1921. Very probably all three—mowing, burning, and grazing—had occurred.

The Pleistocene history of this portion of Minnesota is not well known at present. This area was covered by continental glaciers during the Nebraskan, Kansan, and Wisconsin stages of the Pleistocene Epoch. The most recent ice covering this area is believed to have been part of the Cary substage of the Wisconsin stage. This ice receded approximately 12,500 years ago (Wright, 1957).

Waubun Prairie lies within a gently rolling recessional moraine about 15 miles wide. This moraine is bounded on the east by the high continuous Big Stone Moraine and on the west by the lower discontinuous Erskine Moraine. The recessional beach lines of glacial Lake Agassiz begin on the western slopes of the latter moraine.

The soils on the upland are predominantly Hamerly and Vallers loams (calcium carbonate solonchak) developed on a poorly drained undulating till plain. A loam to silt-loam texture with weak, fine, granular structure is present in most places to a depth of 14–18 inches. This grades into a clay loam with massive structure at a depth of 36 inches (Rust, 1958).

The climate of the Waubun Prairie region is continental in character and marked by occasional droughts and seasonal extremes of temperature (United States Department of Commerce, 1954; United States Department of Agriculture, 1934 and 1941). The mean annual temperature as recorded at Mahnomen is 40°F and the seasonal means are: winter, 8°F; spring, 40°F; summer, 67°F; and fall, 43°F. Temperatures above 100°F usually occur each summer and winter lows of —20 to —30°F are common. The growing season is approximately 111 days, between the average dates of May 29 and September 17.

Annual precipitation averages approximately 20.6 inches. About seventy five per cent falls during the growing season from May through September. Droughts from one to four weeks long often occur during this period. Snowfall averages 36 inches annually.

The vegetational cover in this portion of Minnesota was originally tall grass prairie with extensive marshes and some thickets of aspen (*Populus tremuloides*) and willows (*Salix* spp.) (Ewing, 1924; Upham, 1884). To the east, a narrow belt of deciduous forests—mainly sugar maple (*Acer saccharum*), basswood (*Tilia americana*), aspen, and oaks (*Quercus* spp.)—largely replaced the prairie at the margin of the Big Stone Moraine. Only a few miles further east, coniferous forests intermingled with the deciduous trees. To the west, the tall grass prairies originally extended over the Erskine Moraine and across the Red River Valley. Some deciduous forest islands appeared on the moraine.

Isolated tracts of native prairie remain, although most of the land is farmed. Waubun Prairie is such a tract that lies in an ecotone between the forests to the east and prairies to the west.

Curtis (1959), after an extensive review of literature pertaining to the origin of the prairie, concludes that the vegetation of any area in the prairie-forest border is determined by a complex of factors. Climatic conditions tolerable to both grassland and forest may exist. Edaphic and/or topographic features may determine the vegetative type, but in most localities fire is the most important determining factor. In such situations, fire favors grassland and kills or suppresses tree growth.

Originally, prairie conditions were probably maintained in the Waubun area by frequent fires set by lightning or Indians (Buell and Facey, 1960; Sauer, 1944; Stewart, 1951). In recent years, with more effective fire control, aspen and willow have spread rapidly. Currently, agricultural drainage and roadside ditching have lowered the water table, allowing extensive cultivation, although numerous marshes and potholes persist.

The vegetation of the uplands of the Waubun Prairie is characterized by big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), Indian grass (*Sorghastrum nutans*), and needlegrass (*Stipa spartea*). In the marshes, cattail (*Typha latifolia*), reed (*Phragmites communis*), bullrush (*Scirpus acutus*), and sedges (*Carex* spp.) are commonly found. The major woody plants are aspen and willows.

A detailed ecological survey of the upland portions of the Waubun Prairie was conducted during the growing seasons of 1957 through 1959. On the basis of the data collected, certain components of the flora and fauna were selected for analysis. The vegetational characters discussed are limited to litter or mulch and the four dominant species in the community: big and little bluestem, Indian grass, and needlegrass. Dominants are the species that have the largest total biomass (Odum, 1959). Rare species, being low in abundance, have little to do with the gross community organization (Hairston and Byers, 1954).

The vertebrates studied were bobolink (*Dolichonyx oryizvorus*), savannah sparrow (*Passerculus sandwichensis*), LeConte's sparrow (*Passerherbulus caudacutus*), masked shrew (*Sorex cinereus*), meadow vole (*Microtus pennsylvanicus*), and the prairie deer mouse (*Peromyscus maniculatus bairdii*). Invertebrate population studies were limited to grasshoppers (order Orthoptera) and beetles (order Coleoptera), the two groups likely to be most abundant in a prairie (Smith, 1940). No taxonomic subdivision was made within these orders.

Many other species of animals live on or range over Waubun Prairie. Those with large home ranges, e.g., red fox (*Vulpes fulva*), and marsh hawk (*Circus cyaneus*), are definitely a part of the population, but their actual density cannot be determined when sample areas are small in relation to the space used by each animal. Censusing these forms was beyond the scope of this investigation.

This paper reports the changes in the components during a three-year period and discusses the relations which exist between them. The vegetation of certain sample plots was altered by fire, grazing, and mowing, whereas other areas were undisturbed. A complete phytosociological analysis will be reported separately.

METHODS

Experimental Treatment

The Waubun Prairie was surveyed and contour-mapped by the Minnesota Department of Conservation as the first step in the present investigation. The survey crew established a grid system with numbered steel posts set in the ground at 300-foot intervals. All phases of the field study were referenced to the grid system.

The location of tracts of native prairie present on the area was determined by a preliminary field inspection. A total of seventy acres was suitable for the proposed study. Suitability was determined by topography and by the history of land use, particularly mowing. Field checks and a survey of the literature indicated that a plot size of ten acres would be adequate for studying the relations among some of the dominant flora and fauna. The selected area was divided into seven ten-acre plots, 660 feet square. Each of these was subdivided into quarters for purposes of statistical analysis.

The selection of the treatments for each plot was made subjectively and was based on the location of the plots with respect to potholes and roads, and the nature of use of adjacent agricultural land.

Two plots were used as controls: Control I and Control II. No treatment was applied to these plots during this study.

One plot was burned on October 28, 1957, at approximately 4 P.M. (Fall Burn). Eight men spent two hours conducting this burn. Firebreaks 20 feet wide had been mowed in September. A backfire was set to widen the firebreak to approximately 100 feet. The fire was then allowed to burn across the plot from the windward side.

Two plots were burned on April 11, 1958, from 2 P.M. to 4 P.M. (Spring Burn I and Spring Burn II). Nine men assisted with this burn, using the same technique as above.

The major portion of the burning was carried out with the wind, which was estimated at 15–20 miles per hour by the Beaufort Scale. This resulted in a fire which was hot and fast.

One plot was grazed during the summers of 1958 and 1959 (Graze). Grazing intensity was determined from recommendations by Kieth (1959), Weaver (1954), and Weaver and Tomanek (1951). The first year, 17 Holstein milk cows grazed on the area for ten days during the period of July 17 to August 20 for a total of 170 cow-days. In 1959 the area was grazed by a mixed herd of Holsteins consisting of 6 calves and 10 to 17 cows for a total of 278 cow-days (2 calf-days were considered equal to 1 cow-day). The grazing period in 1959 extended from June 27 to August 11. During both years the periods of grazing were interrupted with periods of no grazing to prevent overuse and to allow the vegetation to maintain vigorous growth (Hayden and Aikman, 1949).

The hay crop on one plot (Mow) was to be harvested each year in September. In 1957 the harvest proceeded as planned. In March 1958, a wild fire burned most of this plot. The hay harvest in September 1958 was only partially completed because the equipment broke down. These incidents were such major disturbances in the treatment plan that this plot was dropped from the study.

Vegetation Analysis

Techniques used in analyzing the vegetation were selected with regard to two objectives: (1) to provide data on the changes in the prairie vegetation, and (2) to determine some of the relations among certain animal populations and prairie vegetation.

Methods of phytosociological analysis have been reviewed by Cain and Castro (1959), Goodall (1952), Greig-Smith (1957), and Oosting (1956). On the basis of these reviews, as well as studies by Curtis (1959) and Kelting (1954, 1957) and consultations with J. R. Bray and D. B. Lawrence, the quadrat method was selected for studying vegetation.

Rectangular quadrats were 1.0 x .5 meter in size as recommended by Bormann (1953), Clapham (1932), Greig-Smith (1957), and others. Preliminary sampling and the use of the species-area technique (Cain, 1938; Moyer, 1953; Rice and Kelting, 1955) revealed that 25 quadrats per ten-acre plot would provide adequate data. Since the plots were divided into quarters, seven quadrats were placed in each quarter, making a total of 28 per plot.

The effect of differences in soil moisture on the vegetation was partially nullified by locating the quadrats only between certain contour intervals. These intervals were selected by recording field conditions on the contour map and then excluding the low, wet sites and the high, dry sites.

The exact location of the quadrats was determined from a table of random numbers (Snedecor, 1956) and referenced to the permanent grid system. Thus a random sample was obtained for certain vegetational characteristics in each quarter of each plot.

Each quadrat was permanently marked on the northwest corner with a numbered aluminum tag attached to a treated wood stake and on the northeast corner by a 60d common spike painted orange.

The percentage of area covered (called "cover" in this report), height, and sociability were recorded in August of each year for each plant species in each quadrat. Areal cover and maximum depth of litter were also recorded. Data on cover, height, and sociability for all plant species will be discussed in a separate report.

The chi-square test for homogeneity based on frequency (Curtis and McIntosh, 1951; Snedecor, 1956) was applied to the four dominant plant species in each of the six plots (plot frequency = sum of frequencies in each quarter). No significant differences among the plots existed, and since the character of a stand is determined mainly by the dominants, the six plots were assumed to be comparable as far as the dominants were concerned.

Areal cover was chosen as the phytosociological character which would provide the best measure of each species with regard to the plant community (Bauer, 1943; Kelting, 1954 and 1957; Penfound, 1948; and Rice, 1952). This character was also considered important in the influence of vegetation on birds by Kendeigh (1945), Lack, (1933), Miller (1942), and Pitelka (1941); on mammals by Eadie (1953), McCabe and Blanchard (1950), Mossman (1955), and Wirtz and Pearson (1960); and on insects by Andrewartha and Birch (1954) and Smith (1940).

The percentage cover was computed from relative cover subjectively estimated in the field. Any species contributing a moderate proportion of the total cover in a quadrat was selected as the base for the relative cover estimate. This species was assigned an arbitrary numerical value, e.g. 100. The amount of cover contributed by each other species in the quadrat was then compared to that contributed by the selected base species. A species contributing twice as much cover was recorded as 200; one contributing a third as much was recorded as 33. The estimates for each quadrat were then converted to percentage values which were used in all further computations regarding cover.

Bird Census

An attempt was made to determine the total breeding population of certain species of birds on each ten-acre plot. The present analysis will include only the three most abundant species, savannah sparrows, LeConte's sparrows, and bobolinks. The census included all parts of the plot, regardless of elevation or relation to wet areas.

Censusing was accomplished by the territory-mapping technique discussed by Bond (1957), Kendeigh (1944), Lack (1937), and Williams (1936). The census is based on observations of singing males: the location of each singing male is marked on a map every time the bird is observed; after a number of surveys of the area, all records for individual species are combined on a composite map. The grouping exhibited by these observations shows the territories of individual pairs. This kind of census is most accurate for birds establishing a "type A" territory (Nice, 1941), i.e., a defended area used for mating, nesting, and feeding. All three species included in the present study are reported to establish this class of territory.

The number of censuses required to provide an accurate estimate of the population on any study plot is subject to a number of variables. Palmgren (1930), using a different method of census, cruised the same area many times and concluded that one survey listed 62 per cent of the total breeding population, two listed 80 per cent, three listed 91 per cent, and four listed 96 per cent. Kendeigh (1944) used a similar technique and found that five censuses were required to list 96 per cent. The actual number of censuses recommended as adequate varies from three (Dambach, 1944; Lack, 1937) to five (Johnston and Odum, 1956; Kendeigh, 1944).

In the present study three censuses were run in 1957 and five in both 1958 and 1959. Censuses were carried out from June 17 to July 4, 1957; May 29 to June 26, 1958; and May 28 to June 28, 1959. The major nesting periods of the three species included in this report fall within these dates in Minnesota (Roberts, 1932). The dates also correspond to those established by Kendeigh (1944) for censusing breeding birds in the middle latitudes of North America.

Preliminary tests revealed that early morning was the best time to observe singing males. Morning observations have been found most suitable for censusing by Bond (1957), Johnston and Odum (1956), Warbach (1958), and others. These observations were supplemented by records kept during the day while other data were being recorded. The existence of a territory was determined subjectively by examining all of the observations of a given species on a given plot during a breeding season. Frequently the discovery of a nest confirmed the presence of a breeding pair.

If a territory overlapped two or three census plots the appropriate fraction in each plot was used to calculate the total population of the species. For example, a territory may have contributed a value of .33 to one plot and .33 to an adjacent plot, while .33 of the territory may have been outside the boundary of the study area.

Mammal Census

Determining the absolute number of individual small mammals living in an area like Waubun Prairie is very difficult. Relative abundance figures for individual species under different conditions are more readily obtained (Blair, 1938; Cook, 1959; Dice, 1941).

Indices of population density of meadow voles, deer mice, and masked shrews were obtained by snap-trapping, using a technique similar to that used by many investigators and summarized recently by Cook (1959). The traps used were of the spring-operated break-back type manufactured under the trade name of Victor Hold Fast. We did not believe that the removal of the small mammals influenced the year-to-year population changes since the life expectancy of these species is very short (Linduska, 1950; Rudd, 1955).

One trapline was established in each ten-acre plot. This line was approximately circular and was within the same contour interval as the vegetation sampling quadrats. It was oriented so that a fourth of the line was in each quarter of the plot.

Twenty-eight stations with two traps each were on the trapline. Stations were thirty feet apart and the traps were placed within two feet of the station. This method of spacing reduces the probability of error introduced by variations in skill and experience in choosing a trap site (Blair, 1938). We used peanut butter for bait in each trapping period.

All plots were trapped twice each year, once in the last week of May and again in the first week in September. The traps were set for 72 consecutive hours during each period. No pre-baiting was done. Trapped animals were removed daily. All plots were trapped simultaneously in order to reduce variability among plot results because of differences in weather.

Insect Census

Indices of the population density of Orthoptera in each of the three years and Coleoptera in 1958 and 1959 within the selected contour interval were obtained by sweep sampling. This technique is widely used (Dice, 1952; Plant Pest Control Division, 1958) and was recommended for this study by Alvah Peterson, Lake Itasca Forestry and Biological Station, and Allan G. Peterson, Department of Entomology and Economic Zoology, University of Minnesota.

Twenty-five individual sweeps (standard 12-inch net—180° sweeps) were made in each quarter of each ten-acre plot. Sweeps were made at approximately 3-foot intervals as the investigators walked through the plot.

Test censuses were run at varying intervals in July, August, and September of 1957. These censuses showed that the largest numbers of grasshoppers and beetles could be captured in mid-August. The data analyzed in this report are from the mid-August censuses for each of the three years. All censuses were taken between 10 A.M. and 2 P.M. Central Standard Time on clear, calm days with temperatures near 85°F. Adherence to these conditions served to reduce the effects of weather variations among plot results (York and Prescott, 1951).

Analysis of Data

Data for each ten-acre plot are presented collectively by histograms. These show both the character of the areas before treatment and the changes that took place after the treatments. "Student's" t test (Snedecor, 1956) was used to interpret differences in sample means of vegetational characters between years in each plot, even though sampling was from a finite population and the observations were not independent. The five per cent level of significance was chosen. Throughout this report the word significant means statistically significant at the .05 or higher level. No statistical comparisons between animal populations were made.

The linear relations between the plant and animal factors are presented as total and first-order partial correlation coefficients (Ezekiel, 1941). This method of analysis was selected so that all possible associations between the variables could be interpreted on a comparable basis.

The total correlation matrix (Table 1) was computed on a Remington-Rand Univac using an existing program.

Each quarter of each plot provided one measurement (sample mean for vegetational characters; sample total for animal populations) for each of the thirteen variables. The number of pairs of observations making up each correlation value is 72 (4 quarters $\times$ 6 plots $\times$ 3 years). The t test (71 degrees of freedom) was used to determine whether the observed values were significantly different from zero, i.e., whether the hypothesis of no relationship was contradicted by the data. We made the usual assumptions underlying this test of significance. The assumption of independence of observations may not be justified since measurements were made on the same plots for three consecutive years. In spite of this possible source of error we felt that this procedure would aid in interpreting the data. Correlations greater than .23 were significant at the .05 level and those greater than .30 were significant at the .01 level.

First-order partial correlations were computed for those relations which had statistically significant total correlation coefficients. For example, the association between a given animal and litter cover was computed with the effect of litter depth removed. Next, the association between the animal and litter depth with the effect of litter cover removed was determined. In cases where the partial correlation proved significant (t test; 70 degrees of freedom) the relation was further tested with the effects of each of the individual grass species removed. If the relation shown by the partial correlation was not significant, no further tests were made.

Although an inspection of the correlation matrix revealed that the linear correlations between variables were relatively small, the above procedure was followed in an attempt to interpret the results as observed. We realize that a linear correlation among the independent variables makes it quite difficult to interpret "effects" of any one or a set of variables. Schultz and Brooks (1958) have discussed these difficulties in some detail.

TABLE 1. TOTAL CORRELATION MATRIX FOR ALL PLANT AND ANIMAL VARIABLES

Variable	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needle-Grass	Bobo-link	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Deer Mouse	Masked Shrew	Orthop-tera
Litter cover		.60**	−.33**	−.31**	−.54**	−.38**	.13	.36**	.05	−.04	−.38**	−.04	−.19
Litter depth	.60**		−.11	−.38**	−.47**	−.12	.25*	.23*	.23*	.39**	−.31**	.14	−.55**
Big bluestem	−.33**	−.11		.27*	−.14	.00	.15	−.16	.17	.13	−.15	−.08	.02
Little bluestem ...	−.31**	−.38**	.27*		−.04	.02	−.05	−.13	−.17	.06	−.11	−.26*	.20
Indian grass	−.54**	−.47**	−.14	−.04		.16	.03	−.17	−.07	−.13	.19	.07	.33**
Needlegrass	−.38**	−.12	.00	.02	.16		−.21	.02	−.14	−.12	−.04	.03	−.02
Bobolink	.13	.25*	.15	−.05	.03	−.21		−.21	.41**	.21	−.26*	−.09	−.15
Savannah sparrow..	.36**	.23*	−.16	−.13	−.17	.02	−.21		−.25*	−.09	−.09	−.07	.15
LeConte's sparrow.	.05	.23*	.17	−.17	−.07	−.14	.41**	−.25*		.22	−.14	.02	−.26*
Meadow vole	−.04	.39**	.13	.06	−.13	−.12	.21	−.09	.22		−.07	−.06	−.21
Deer mouse	−.38**	−.31**	−.15	−.11	.19	−.04	−.26*	−.09	−.14	−.07		.07	.01
Masked shrew	−.04	.14	−.08	−.26*	.07	.03	−.09	−.07	.02	−.06	.07		−.05
Orthoptera	−.19	−.55**	.02	.20	.33**	−.02	−.15	.15	−.26*	−.21	.01	−.05	

* Significant at the .05 level.
** Significant at the .01 level.

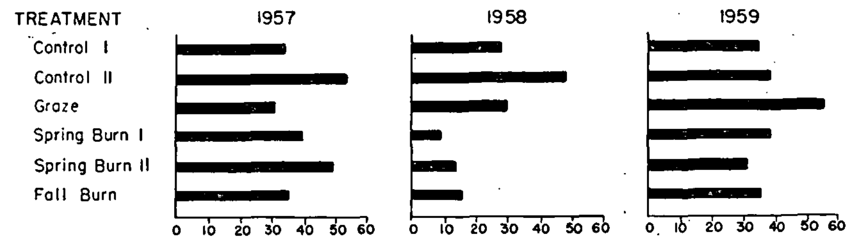
VEGETATION

Litter

Litter or mulch is an integral and important component of grassland vegetation. General characteristics and effects of litter have been discussed by Dyksterhuis and Schmutz (1947), Ehrenreich (1957), Hopkins (1954, 1956), and Weaver and Rowland (1952). All measurements are expressed as sample means (see Appendix for raw data).

In 1957, litter cover and depth in the experimental plots on Waubun Prairie exhibited a wide range of variation (Fig. 2 and 3). The plots labeled Control I, Graze, Spring Burn I, and Fall Burn were in an area which had been mowed annually in late summer before 1957. Litter in these plots was sparse because most of the vegetation produced during each growing season was removed for hay. The average amount of the total cover contributed by litter was 35 per cent. The average maximum depth was 5 centimeters (range: 1–10 centimeters).

Control II and Spring Burn II were in a part of the prairie which was lower and which had more soil moisture. This site had not been mowed since 1951. The litter accumulated during this six-year period constituted 51 per cent of the cover in this area. The average maxi-



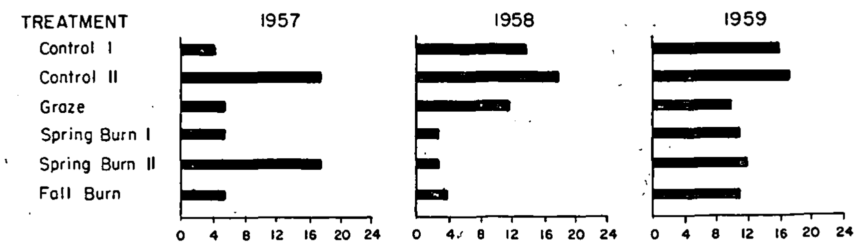


Figure 2. Average percentage of cover contributed by litter. *Figure 3.* Average depth of litter (in centimeters).

mum depth was 17 centimeters (range: 10–25 centimeters). Comparable results were found by Dyksterhuis and Schmutz (1947) who measured 4.5 tons of litter per acre on undisturbed prairie compared to less than one ton per acre on annually mowed prairie in Nebraska.

The pattern of litter cover and depth changed markedly in 1958 after treatments had been applied to four of the plots. Litter cover and depth remained approximately the same in Control II. Depth increased from 4 centimeters to 14 centimeters in Control I as a result of one year's accumulation of vegetation. The percentage of litter cover remained constant in this plot. We believe that the amount of new growth in this plot increased in 1958 as a result of not mowing the previous season. Thus the percentage of the total cover contributed by litter did not change, even though more litter was present.

Litter cover and depth in Graze were approximately the same as in Control I. Grazing intensity in 1958 was light and did not have a noticeable effect on litter.

In all three of the burned plots litter cover was markedly reduced to an average of 12 per cent. Depth in Spring Burn I and Fall Burn was reduced slightly. In Spring Burn II depth was reduced from 17 centimeters to 3 centimeters. The fact that some litter remained after burning may have several causes. Each of these three plots was burned when the litter near the mineral soil was moist. Further, the fires moved over the plots rapidly, and consequently some dead vegetation escaped the burn. In addition, certain prairie plants complete their growth early in the summer and their dried remains contributed to litter as measured in this investigation.

No treatment was applied to the three burned and two control plots in 1959. Litter cover and depth remained approximately the same in Control II. The slight decrease in the percentage of cover in this plot (shown in Fig. 2) we attribute to very heavy rains just before we recorded the phytosociological data. These rains beat down the litter but did not similarly affect the growing vegetation. Consequently the percentage of cover of litter was slightly lower than in preceding years.

In Control I both cover and depth of litter increased as a result of one more year's accumulation.

The three burned plots exhibited similar litter characteristics one year after the fires. Cover increased to an average of 33 per cent and depth increased to an average maximum of 11 centimeters.

Grazing in 1959 was considered moderate to heavy compared to light in 1958. The percentage of litter cover showed a sharp increase because much of the growing vegetation was removed by the cattle.

Average maximum litter depth showed only a small decrease; this is misleading since the actual decrease was very noticeable. Most of the litter in the plot was heavily trampled and was only a few centimeters deep, but small bunches of untrampled litter were present throughout the plot. The sampling technique chosen necessitated that the maximum litter depth for each quadrat be measured, so the data represent the depth of the small scattered untrampled bunches of litter.

The general effects of changes in litter due to burning, grazing and mowing in regard to phenology and growth have been discussed by Aikman (1955), Dix (1960), Ehrenreich (1957), Hayden and Aikman (1949), Hopkins (1956), and others. Effects on soil fertility and organic matter content have been reported by Dyksterhuis and Schmutz (1947), Ehrenreich (1957), Hervey (1949), and Weaver and Rowland (1952).

In addition to substantiating many conclusions reached by the investigators listed above, the data in this study indicate that protection after burning or mowing would result in an accumulation of litter in two or three years similar in depth and percentage of cover to that in an undisturbed area such as Control II. Ehrenreich (1957) found that litter on a burned tract in Iowa accumulated to the level of that on an unburned one in four to six years. Four seasons were required to rebuild the mulch structure on burned prairie in North Dakota (Dix, 1960).

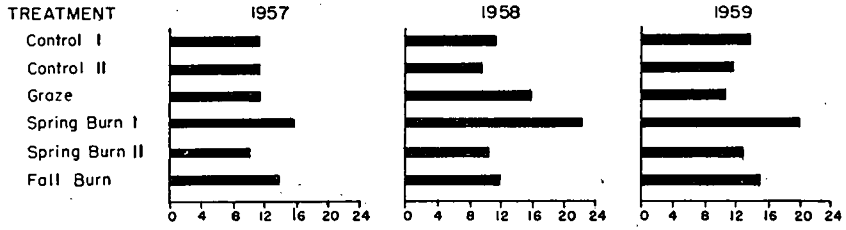
Litter decomposition rates were studied by Hopkins (1954), who says that vegetation placed on the soil and allowed to decompose was mostly disintegrated after three years and that about half of the weight was lost in the first year.

It appears from these findings that on native prairie a state of equilibrium is reached two to six years after protection from burning or mowing begins; in this state the annual increment of new litter is balanced by the decomposition of old litter.

Big Bluestem

Big bluestem, one of the four dominants on Waubun Prairie, made up 10 to 15 per cent of the areal cover in 1957 (Fig. 4). The highest values (14 and 15 per cent) occurred on Spring Burn I and Fall Burn, respectively. This variation is attributed to the topography of these plots. Both are on the highest part of the area studied and thus are the best drained. Soil moisture relationships may be more favorable for big bluestem here than on the other plots.

The changes in the percentage of cover of big bluestem from 1957



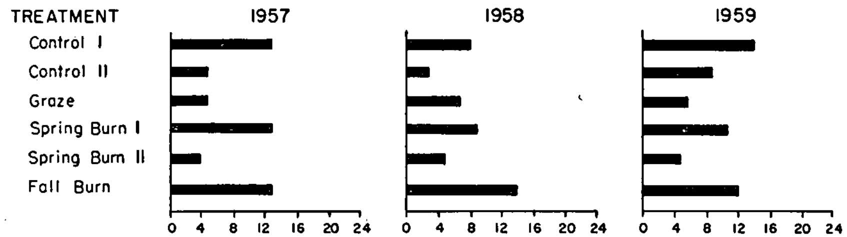


Figure 4. Average percentage of cover contributed by big bluestem. *Figure 5.* Average percentage of cover contributed by little bluestem.

to 1958 are not statistically significant except for the increases in Graze and Spring Burn I.

The significant (t = 2.10; 54 degrees of freedom) increase under grazing is contradictory to most other studies of comparable nature as summarized by Dix (1959) and Weaver (1954). No explanation of this apparent discrepancy is postulated at the present.

The significant (t = 2.15; 54 d.f.) increase in big bluestem cover which took place on Spring Burn I corresponds to increases observed by Aldous (1934), Ehrenreich (1957), Kelting (1957), and others. A similar increase was expected on Spring Burn II but, for reasons unknown, did not occur.

The only significant (t = 3.22; 54 d.f.) change in percentage of cover of big bluestem in 1959 was the reduction from 16 to 11 per cent in Graze. The more intensive grazing during this period is believed to account for the decrease.

Little Bluestem

In 1957 the percentage of cover of little bluestem (Fig. 5) was approximately 5 in three plots and 13 in the other three. This species has been found to attain its optimum growth on dry uplands (Curtis,

1959; Weaver, 1954). The low amounts in Control II and Spring Burn II were expected, because these plots are in a wetter site than the others. The reason for the low amount in Graze is not known.

The only significant (t = 4.80; 54 d.f.) change shown by the data for 1958 was the small reduction in Control II. This change of only 2 per cent is significant because of the low variability of little bluestem cover in this plot.

Similarly, in 1959 the only significant (t = 18.95; 54 d.f.) change was an increase from 3 to 9 per cent in Control II. No explanation for this change is available at the present.

None of the burned plots nor the grazed plot exhibited significant changes in little bluestem cover. The findings in the literature about the effects of burning on this grass are contradictory: Dix and Butler (1954) and Hopkins, *et al.* (1948) say that little bluestem cover is reduced and that the plants may be killed by burning, whereas Aldous (1934 and 1935) found that it increased with burning.

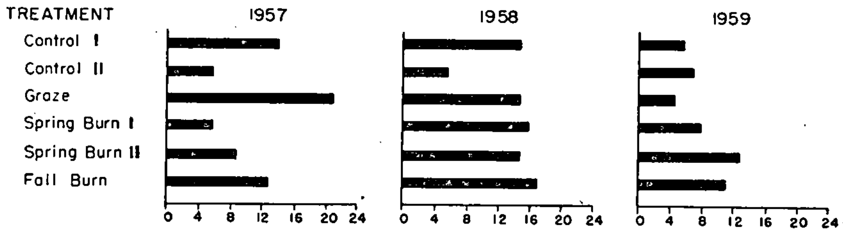
Intensity appears to be the critical factor in determining the effect of grazing on little bluestem. Kelting (1954) and Robocker and Miller (1955) found this grass favored by moderate grazing or clipping, and Dix (1959) and Weaver (1954) say that it is reduced by heavy grazing. Apparently the grazing in the present study was too light to affect little bluestem.

Indian Grass

The reason for the variability in percentage of cover of Indian grass (Fig. 6) in 1957 is difficult to explain. This distribution pattern may be a response to edaphic or topographic conditions not revealed in the investigation, or it may result from the variableness of the species (McMillan, 1959).

In 1958 no significant changes were observed in Controls I and II. Graze showed a significant (t = 5.17; 54 d.f.) reduction, which reflects cattle's strong preference for Indian grass (Dix, 1959; Weaver, 1954). Both Spring Burn plots showed highly significant (t = 7.50, 13.53; 54 d.f.) increases, increases similar to those observed by Aldous (1935) and Robocker and Miller (1955). However, Aldous (1935) states that the burn must take place in late spring, whereas Dix and Butler (1954) reached the opposite conclusion: that spring burning caused a marked decrease in Indian grass cover. The data from Fall Burn, although not statistically significant, point toward an increase in Indian grass cover.

Results from the third season of the study reveal no significant



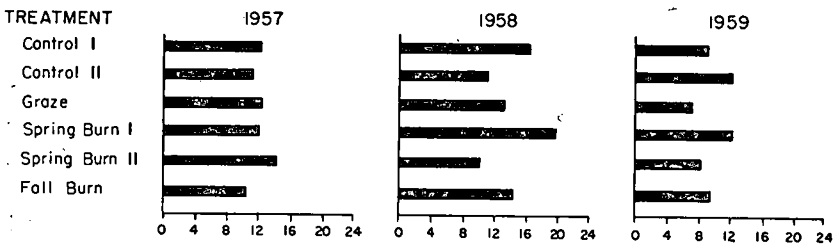


Figure 6. Average percentage of cover contributed by Indian grass. *Figure 7.* Average percentage of cover contributed by needlegrass.

change in Control II and a significant (t = 11.44; 54 d.f.) decrease in Control I. Reasons for this decrease are not known.

The more intensive grazing in 1959 continued to reduce Indian grass cover in Graze. All three burned plots show a decline in this species in the second growing season following the fire. However, only the decrease in Spring Burn I is significant (t = 4.29; 54 d.f.). Dix and Butler (1954) found that fire effects were very slight during the second growing season.

Needlegrass

Needlegrass, the fourth dominant on Waubun Prairie, made up approximately 12 per cent of the cover in each plot in 1957 (Fig. 7). The only significant changes in 1958 were an increase in Spring Burn I (t = 6.34; 54 d.f.) and a decrease in Spring Burn II (t = 5.17; 54 d.f.). The reasons for this apparent anomaly are not known.

In 1959 needlegrass in Control II remained the same but in Control I it decreased significantly (t = 6.19; 54 d.f.). No explanation can be given for this change. The significant (t = 9.36; 54 d.f.) decrease in Graze reflects the preference of cattle for needlegrass as reported by Voigt and Weaver (1951) and Weaver (1954).

Needlegrass decreased in each of the burned plots. However, the

reduction was significant (t = 5.97; 54 d.f.) only in Spring Burn I. It appears that the unknown factor or factors which caused the large increase in this plot the first growing season after the fire were not operating in the second season.

BIRD POPULATIONS

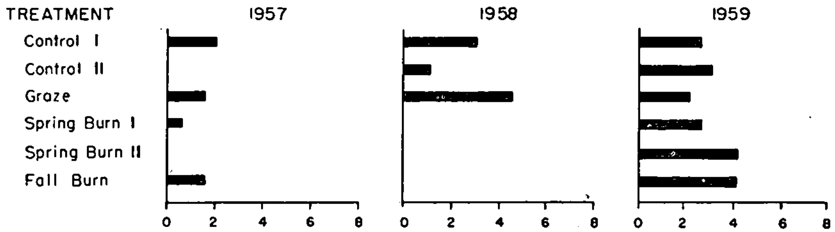
Changes in the distribution and abundance of three species of birds—bobolinks, savannah sparrows, and LeConte's sparrows—were investigated on Waubun Prairie. The changes will be analyzed in terms of the vegetative changes brought about by the treatments applied to the study plots.

When considering populations of migratory birds, it must be kept in mind that changes in abundance may be related to the numbers of a given species available to nest in a specific area. During years of high populations, submarginal habitats may be occupied, whereas in years of low populations only the more suitable sites will be used. Unfortunately, the actual abundance of each species in this region during the period of the study is not known and no estimate can be made from the available data.

Bobolink

Breeding pairs of bobolinks, as indicated by singing males, were present in all four plots on the mowed portion of the prairie in 1957 (Fig. 8), but there were none in the unmowed area (Control II and Spring Burn II). In 1958 no bobolinks were observed on the three burned plots; 3 territories (see p. 8) were observed on Control I and 4.5 on Graze; 1 territory appeared on Control II. The following year, 1959, 2.5 territories were present on Spring Burn I; Fall Burn and Spring Burn II each contained 4 territories; the other three plots held approximately 2.5 breeding pairs each. Territories in Graze were reduced from 4.5 in 1958 to 2 in 1959.

The relations between these changes and the vegetation were analyzed by comparing the number of bobolinks (Fig. 8) with the vegetational characteristics represented by Figures 2–7 and by correlation analysis. The total correlation matrix for all plant and animal variables has been presented in Table 1. First order partial correlations for bobolinks and vegetative characters are shown in Table 2. These data indicate that distribution and abundance of bobolinks is associated to some degree with litter. The absence of this species in both of the unmowed plots in 1957 (Fig. 8) suggests that, under some cir-



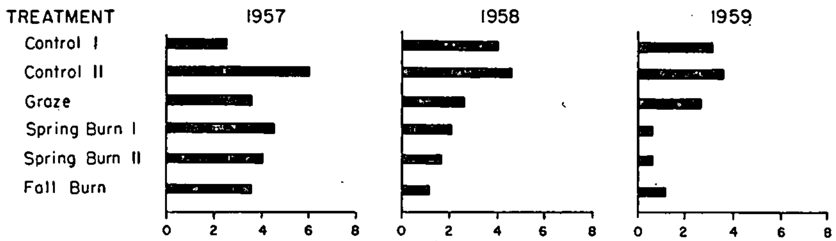


Figure 8. Number of bobolinks. *Figure 9.* Number of savannah sparrows.

cumstances, areas with very deep litter are not occupied. In 1958 and 1959 Control II was occupied, perhaps due to changes in absolute numbers of bobolinks present in the region.

In contrast to areas with deep litter, all of the burned plots contained very small amounts of litter in 1958, the season after the fires. No bobolink territories were located in these plots.

During the entire investigation all plots with litter depths between the extremes discussed above were occupied by breeding pairs of bobolinks. Dambach and Good (1940) found more bobolinks in good

Table 2. Partial Correlations between Bobolinks and Vegetational Characters

Variable Tested	Variable Removed	Partial Correlation
Litter cover	Litter depth	—.03
Litter depth	Litter cover	.22
Litter depth	Big bluestem	.27*
Litter depth	Little bluestem	.25*
Litter depth	Indian grass	.30**
Litter depth	Needlegrass	.22

* Significant at the .05 level.
** Significant at the .01 level.

quality wild hay meadow or alfalfa than in thin cover in Ohio. Observations by Kendeigh (1941) on a restored prairie with two to three inches of dense litter in Iowa revealed numerous bobolinks. Roberts (1932) associates the species with upland prairie and hay meadows. These findings are in general agreement with those of the present study which suggest that depth of litter is the most important vegetational character, of those measured, which can be related to bobolink occurrence.

Savannah Sparrow

Breeding populations of savannah sparrows were present in all plots in all three seasons (Fig. 9), but marked reductions took place in each of the burned plots in 1958 and further reductions in 1959 in both Spring Burn I and II.

The correlation data (Table 1 and Table 3) indicate a positive association between savannah sparrows and litter cover. The significant decrease in litter cover after burning (Fig. 2) apparently made this habitat less suitable in both 1958 and 1959. The reason for the continued decline in numbers in the spring-burned plots in 1959 is not known. It appears that this species requires more than two years' accumulation of litter following fire.

Table 3. Partial Correlations between Savannah Sparrows and Vegetational Characters

Variable Tested	Variable Removed	Partial Correlation
Litter depth	Litter cover	.02
Litter cover	Litter depth	.28*
Litter cover	Big bluestem	.33**
Litter cover	Little bluestem	.34**
Litter cover	Indian grass	.33**
Litter cover	Needlegrass	.42**

* Significant at the .05 level.
** Significant at the .01 level.

Savannah sparrow habitat is described by Roberts (1932) as the rank growth of meadows and low-lying fields and prairies and also thickets on the upland prairie. Linsdale (1938) concluded that the factor determining the local presence of this species in the Great Basin was the dense cover of low vegetation. Johnston and Odum (1956) noticed a reduction in numbers of grasshopper sparrows (*Ammodramus savannarum*), a closely related species, in an oat field after mowing in May. These studies together with the current data support the conclusion that litter cover is one of the most important features of savannah sparrow habitat.

LeConte's Sparrow

No LeConte's sparrows were observed on the study area in 1957 (Fig. 10). Parts of territories were in Control I and Control II and one entire territory was in Graze in 1958. No LeConte's sparrows were seen in Control I and II in 1959. Partial or entire territories were located in each of the other four plots in 1959.

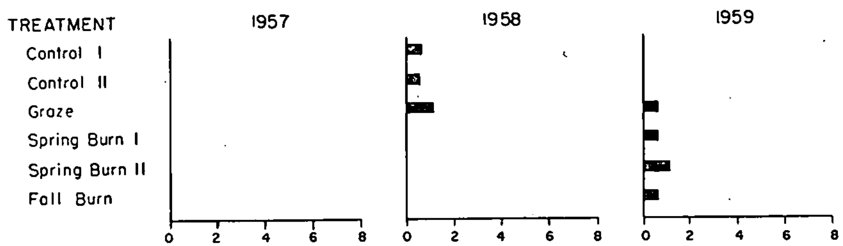


Figure 10. Number of LeConte's sparrows.

The correlation analyses (Tables 1 and 4) suggest that an association exists between litter depth and distribution of this species. However, we feel that because LeConte's sparrows were nearly always found in a wet site the methods of vegetation measurement used do not provide suitable data for determining relations. Roberts (1932), Peabody (1901), and Walkinshaw (1937) also say that this species is most frequently found in marshy places.

Field observations have led to a tentative evaluation of the LeConte's sparrow's habitat. They appear to need a moderate amount of litter combined with much new grass rising 30 centimeters or more above the litter. In 1957 the mowed plots may have had too little litter and the unmowed plots too much for these sparrows (Fig. 2 and 3).

TABLE 4. PARTIAL CORRELATIONS BETWEEN LECONTE'S SPARROWS AND VEGETATIONAL CHARACTERS

Variable Tested	Variable Removed	Partial Correlation
Litter cover	Litter depth	—.12
Litter depth	Litter cover	.25*
Litter depth	Big bluestem	.26*
Litter depth	Little bluestem	.19
Litter depth	Indian grass	.23*
Litter depth	Needlegrass	.21

* Significant at the .05 level.

In 1958 Control I and Graze had a year's accumulation of litter and an abundant growth of new grass. The presence of LeConte's sparrows here shows that the habitat was suitable. The partial territory in Control II cannot be explained. In contrast, the three burned plots contained almost no litter the first season after burning and no LeConte's sparrows.

The next year the burned plots had accumulated one year's litter and had much new growth; the species was present. It was also present in Graze, attributable to the fact that the cattle grazing the preceding year had kept the amount of litter within the acceptable range. No LeConte's sparrows were observed in either control. Their absence from Control I may be due to the increase in litter.

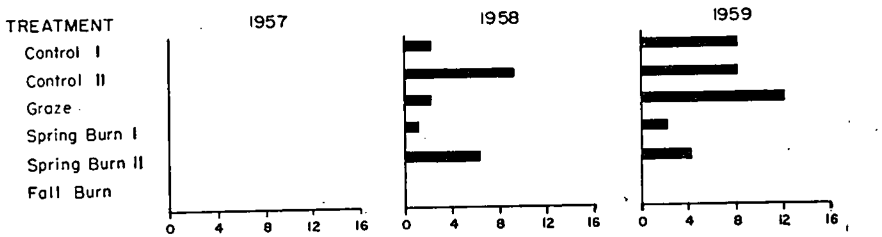
The total number of breeding pairs of LeConte's sparrows on the Waubun Prairie at any time was very low. This might be because of the general character of the vegetation as discussed above, or it may be that the entire population in the region was low. According to unpublished United States Weather Bureau Station reports at Mahnomen, this area in Minnesota had been undergoing a period of moderate drought before the study, and Peabody (1901) says that dry weather is detrimental to LeConte's sparrows.

MAMMAL POPULATIONS

The distribution and abundance of three species of small mammals —meadow voles, prairie deer mice, and masked shrews—will be considered. Populations of voles, mice, and other mammals undergo wide fluctuations; the reasons for many of these fluctuations are as yet unknown. Errington (1957) and Odum (1959) include reviews of this complicated phenomenon. Because of this known fluctuation the study plots were trapped twice in each season. These data will be considered in terms of vegetational changes and of possible population fluctuations operating independently of the vegetation.

Meadow Vole

No voles were trapped in the spring of 1957 (Fig. 11). In the fall the only voles captured were taken in the two unmowed plots (Con-



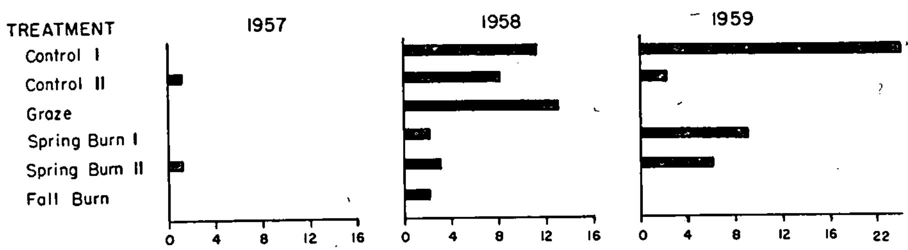


Figure 11. Number of meadow voles captured during spring trapping period.
Figure 12. Number of meadow voles captured during fall trapping period.

trol II and Spring Burn II), and only one was trapped in each of these plots (Fig. 12).

In the spring of 1958 nine voles were caught in Control II and six in Spring Burn II and smaller numbers in each of the plots in the mowed area, except Fall Burn. By the fall of 1958 populations had increased markedly in Control I and II and Graze, but in each of the three burned plots the number of voles was very low.

This same general pattern of abundance was exhibited in spring 1959, except for the absence of any captures in Fall Burn. In fall 1959, a wide range in population size was revealed. Control II captures increased to 22 animals, Control I decreased to 2, Graze decreased to 0, both Spring Burns increased, and Fall Burn remained at 0.

The correlation analyses in Table 1 and Table 5 indicate that an abundance of meadow voles is associated with litter depth and in part with litter cover (partial correlation removing effect of litter depth equaled —.37). We believe that this negative correlation between voles and litter cover is the result of the phytosociological methods used rather than a true ecological relationship, since deep litter was not always consistent with high litter cover values (see VEGETATION section). The relatively high positive correlation between

TABLE 5. PARTIAL CORRELATIONS BETWEEN MEADOW VOLES AND VEGETATIONAL CHARACTERS

Variable Tested	Variable Removed	Partial Correlation
Litter cover	Litter depth	—.37**
Litter cover	Big bluestem	.00
Litter cover	Little bluestem	—.02
Litter cover	Indian grass	—.13
Litter cover	Needlegrass	—.10
Litter depth	Litter cover	.46**
Litter depth	Big bluestem	.40**
Litter depth	Little bluestem	.44**
Litter depth	Indian grass	.39**
Litter depth	Needlegrass	.37**

** Significant at the .01 level.

voles and litter depth we believe real in spite of the apparently independent population fluctuations.

Figures 11 and 12 show that the vole population was very low over the entire Waubun Prairie in 1957. The only animals captured were taken in the two plots containing the deepest litter, Control II and Spring Burn II.

Populations increased during the fall and winter, and by the spring trapping period voles were present on most of the plots. The largest numbers were taken in the unmowed plots, which had had the deepest litter during the winter. It is interesting to note that a high relative population was indicated in Spring Burn II even though the census was run after the fire and there was only a small amount of litter remaining at this time. It appears that voles increased during the winter in this deep-litter habitat and that many persisted in the plot for a period following the burn. High mammal survival rates following fires have been reported by Howard *et al.* (1959).

Small populations are indicated in the spring of 1958 in Control I, Graze, and Spring Burn I. These plots had one year's accumulation of litter during the winter, which apparently proved suitable for voles. Those captured in Spring Burn I must have stayed on the plot after the fire.

In contrast to these three plots, no voles were trapped on Fall Burn. Since this plot was burned in October 1957, practically no litter cover was available during the winter and no vole population became established.

By the fall of 1958 the effects of the burning on the vole populations became more apparent. High relative populations were indicated in the two controls and in Graze compared to low populations in each of the burned plots. Litter was comparatively deep in the first three plots and shallow in the last two.

The following spring, the same abundance pattern existed for both voles and litter depth except that, for reasons unknown, no voles were present in Fall Burn.

During the summer of 1959 some factor or factors other than the measured characteristics of the vegetation exerted an influence on certain of the meadow vole populations. Relative numbers increased in Control I, but decreased in Control II. Litter depth and cover were nearly identical in these plots. No explanation is postulated for these population changes.

No voles were captured in Graze. This is attributed to the reduction in litter depth because of trampling by cattle.

Vole populations continued to show a relative increase in both Spring Burns as litter conditions became more favorable. The continued absence of voles in Fall Burn cannot be explained.

Many workers have reported that meadow voles are most frequently captured in areas of dense vegetation (Beckwith, 1954; Frenzel, 1957; Johnson, 1926; Linduska, 1950; Ogilvie and Furman, 1959; and Sanderson, 1950). Eadie (1953) found a significant association between meadow voles and air-dry weight of the vegetation. Areas with the most vegetation were occupied by the highest numbers of voles. An inverse relation between the abundance of small mammals, taken collectively, and the amount of light penetrating the vegetation was discussed by Mossman (1955).

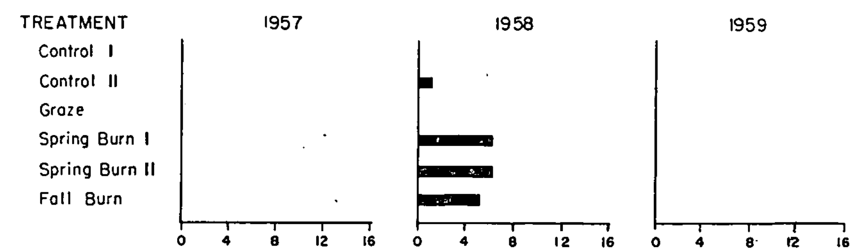
In investigating changes in vole populations in an alfalfa field, LoBue and Darnell (1959) found high numbers in the dense vegetation before mowing and low numbers in the same area after mowing had removed most of the cover. Cook (1959) says that voles require a year's accumulation of litter as cover for surface runways. He based this conclusion on the rate at which populations built up following a wild burn. The growth form of the vegetation is considered by Pearson (1959) to be of first importance in determining small mammal distribution and density. By testing responses of captive animals to simulated habitats Wirtz and Pearson (1960) found that meadow voles had a positive orientation based on visual response toward the densest cover.

The changes in meadow vole distribution and abundance attributed to changes in both cover and depth of the litter as observed in the present study correspond closely with the findings of other investigators, suggesting that the characteristics of litter are important influences on the meadow vole.

Prairie Deer Mouse

The distribution and relative abundance of deer mice are shown in Figures 13 and 14. None was trapped in 1957. In the spring of 1958 the species was common in each of the three burned plots. One was caught in Control II: it may have moved into this plot from the adjacent Spring Burn II. By the fall of 1958 deer mice were more numerous in Spring Burn II, but declining in the other two burned plots. None was found in the unburned areas. The only deer mouse captured in 1959 was trapped in the fall in Graze.

A negative association between deer mice and litter cover and depth appears to be the most important relationship revealed by the correlation analyses presented in Table 1 and Table 6. The population data (Fig. 13 and 14) indicate that the deer mice were common in the burned areas when the least litter was present and that they decreased as the litter cover and depth increased. No deer mice were observed in plots where an abundance of litter had accumulated except for the suspected stray in Control II.



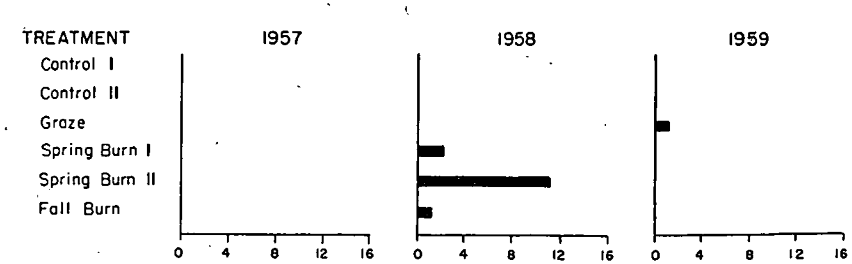


Figure 13. Number of prairie deer mice captured during spring trapping period.
Figure 14. Number of prairie deer mice captured during fall trapping period.

TABLE 6. PARTIAL CORRELATIONS BETWEEN PRAIRIE DEER MICE AND VEGETATIONAL CHARACTERS

Variable Tested	Variable Removed	Partial Correlation
Litter depth	Litter cover	—.12
Litter cover	Litter depth	—.25*
Litter cover	Big bluestem	—.46**
Litter cover	Little bluestem	—.44**
Litter cover	Indian grass	—.34**
Litter cover	Needlegrass	—.43**

* Significant at the .05 level.
** Significant at the .01 level.

It is important to note that the only deer mouse captured in 1959 was taken in Graze. This plot had been heavily trampled by the cattle and only a small amount of litter cover was present. Dambach (1944) and Phillips (1935) found deer mice more numerous in overgrazed than in ungrazed habitats.

Many different species of deer mice have been studied. In nearly every case where habitat is discussed the sparseness or lack of vegetational cover is considered a characteristic feature of areas occupied by these species (Allen, 1938; Beckwith, 1954; Dice, 1932; Frenzel, 1957; Hays, 1958; Tevis, 1956). Increases in deer mouse populations following burns are reported by Gashwiler (1959), White and Pearson (1959), and Williams (1955). Blair (1938) mentions that the deer mouse was the most abundant mammal in bluestem prairie in Oklahoma, but that the prairie vole (*Microtus ochrogaster*) is most characteristic of this habitat. He also says that the study area had been burned a short time before his censuses. LoBue and Darnell (1959) found that deer mice increased in an alfalfa field after most of the vegetative cover had been removed by mowing. As the amount of cover increased following the mowing, the numbers of deer mice declined. Johnson (1926) concludes that the prairie deer mouse is characteristically an inhabitant of open fields and that it does not belong to a climax prairie community but rather to some subclimax stage. In discussing habitat requirements, Brant (1953) says that the deer mouse is not dependent on surface runways, but does require a permanent nesting site such as an underground burrow or clump of brush or rocks.

The close correspondence of the results of these widespread investigations with the findings in the present study suggest strongly that the sparseness of vegetational cover is a most important factor in determining the distribution and abundance of prairie deer mice. This study tends to show that litter is a very important facet of cover.

Masked Shrew

Populations of masked shrews fluctuated over wide ranges in all of the study area during the three years (Fig. 15 and 16). Only a few animals were captured during each of the spring trapping periods. By the succeeding fall period numbers had increased and masked shrews were found living over most of the study area. Larger relative populations are indicated in the unmowed plots than in the mowed plots in fall, 1957. No other definite patterns of changes in distribution and abundance were detected from the field data.

The correlation analyses (Tables 1 and 7) suggest that a negative association exists between masked shrews and little bluestem. This might be related to soil moisture or humidity, since little bluestem is most abundant on dry sites and shrews are generally believed to be somewhat restricted to moist sites (Chew, 1951; Pearson, 1947 and 1948; Pruitt, 1953). In sampling numerous upland and lowland habitats in Michigan, Pruitt (1953) found masked shrews only in bogs.

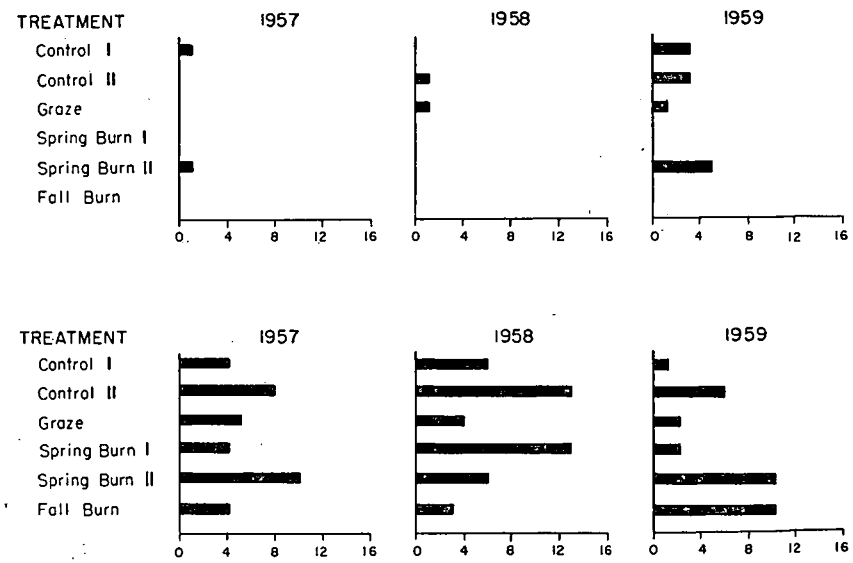


Figure 15. Number of masked shrews captured during spring trapping period. *Figure 16.* Number of masked shrews captured during fall trapping period.

TABLE 7. PARTIAL CORRELATIONS BETWEEN MASKED SHREWS AND VEGETATIONAL CHARACTERS

Variable Tested	Variable Removed	Partial Correlation
Litter cover	Litter depth	—.15
Litter depth	Litter cover	.20
Litter depth	Big bluestem	.15
Litter depth	Little bluestem	.04
Litter depth	Indian grass	.19
Litter depth	Needlegrass	.14
Little bluestem	Litter depth	—.23*
Little bluestem	Litter cover	—.29*
Little bluestem	Big bluestem	—.25*
Little bluestem	Indian grass	—.26*
Little bluestem	Needlegrass	—.26*

* Significant at the .05 level.

The large relative populations in the unmowed plots in fall 1957 suggest a relation with the dense litter cover in this area. Pearson (1959) found masked shrews most abundant in habitats with heavy ground cover and Jameson (1949) believes that a positive relation exists between the number of smoky shrews (*Sorex fumeus*) and the amount of humus and matted litter.

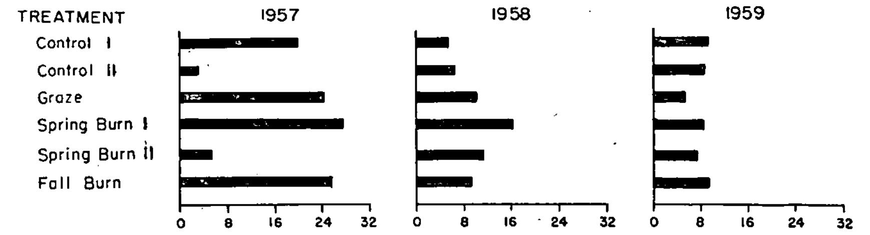
In contrast to these implications concerning habitat selection, Hamilton (1939) reports that the masked shrew "occupies diverse ecological niches." Our study would seem to support his statement.

INSECT POPULATIONS

Relative indices of the abundance of Orthoptera (grasshoppers) were obtained during each of the three years. Populations of Coleoptera (beetles) were censused only in 1958 and 1959. Changes in numbers of individuals of these groups of insects will be considered in relation to the treatments applied to the study plots.

Orthoptera

Relatively high populations of Orthoptera were present in each of the plots on the mowed area in 1957 (Fig. 17). Both of the plots in the unmowed section (Control II and Spring Burn II) had markedly lower populations. The following year the number of grasshoppers remained approximately the same in Control II; decreased markedly in Control I, Graze, Spring Burn I, and Fall Burn; and increased in Spring Burn II. In 1959 numbers of Orthoptera were relatively simi-



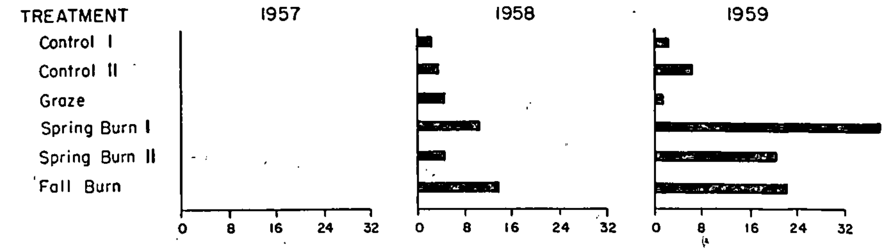


Figure 17. Number of Orthoptera captured. *Figure 18.* Number of Coleoptera captured.

lar in all plots. A slight decrease was noted in each of the burned plots and in Graze.

The correlations in Table 1 and Table 8 show a negative association between grasshoppers and litter depth. The deep litter which had accumulated for several years in the unmowed plots apparently did not provide a satisfactory habitat for grasshoppers. Litter conditions in the four mowed plots in 1957 were apparently more satisfactory for these insects.

The possibility that the sweep-census technique is not suitable in areas with heavy cover might have affected the indices of abundance. Flush counts in this same habitat, however, made to check the sweep-census method, also indicated very low populations.

The fire reduced litter cover in Spring Burn I and Fall Burn to a level which appears to be below the optimum for grasshoppers as shown by the decline in numbers. Similar treatment in Spring Burn II, which originally had much more litter than Spring Burn I, may have brought the litter down to an optimum level for grasshoppers. This possibly accounts for the larger numbers of these insects. The increase in litter above the possible optimum in Graze and Control I is believed responsible for the reduction in numbers of Orthoptera in these areas.

TABLE 8. PARTIAL CORRELATIONS BETWEEN ORTHOPTERA AND VEGETATIONAL CHARACTERS

Variable Tested	Variable Removed	Partial Correlation
Litter cover	Litter depth	.33**
Litter cover	Big bluestem	—.19
Litter cover	Little bluestem	—.14
Litter cover	Indian grass	—.01
Litter cover	Needlegrass	—.22
Litter depth	Litter cover	—.56**
Litter depth	Big bluestem	—.55**
Litter depth	Little bluestem	—.52**
Litter depth	Indian grass	—.47**
Litter depth	Needlegrass	—.55**
Indian grass	Litter cover	.28*
Indian grass	Litter depth	.10

* Significant at the .05 level.
** Significant at the .01 level.

The similarity of the relative populations in the two control plots and the three burned plots in 1959 indicates that habitat conditions were comparable in all of the areas. This suggests that one to two years' litter accumulation has about the same effect as six to eight years' accumulation.

The effect of grazing on the abundance of grasshoppers on Waubun Prairie appears to be negligible, since populations on Graze followed a pattern of abundance similar to Control I. This is attributed to the relatively low intensity of grazing. Carpenter (1939), Smith (1940), and Weaver and Flory (1934) report higher populations of grasshoppers on disturbed and heavily grazed prairie than on undisturbed grasslands.

In general the data presented above suggest that, on native prairie, grasshoppers are most abundant where there is a light to moderate amount of litter. Increasing or decreasing the amount of litter appears to make the habitat less suitable.

Clark (1948) found that the most important feature of vegetation affecting the abundance of grasshoppers in England was the amount of direct sunlight reaching the soil. The shading effect of litter may account for the smaller populations of grasshoppers in sites with heavy litter.

Uvarov (1928) discovered the highest numbers of locusts in areas of thin vegetation. Dempster (1955) and Richards and Waloff (1954) determined that certain species of grasshoppers showed a preference for tall grass and others showed a preference for short grass. Isley (1937) concludes that in some instances grasshopper populations may be influenced by specific food plants, but that they are chiefly determined by relations between vegetational cover and climate.

These studies tend to support the findings on the Waubun Prairie that the amount of litter is an important factor influencing numbers of grasshoppers.

Coleoptera

Relative numbers of those beetles which could be censused by sweeping in the study plots in 1958 and 1959 are shown in Figure 18. In 1958, populations were comparatively low in both controls, Graze and Spring Burn II, and high in Spring Burn I and Fall Burn. The following year, populations were low in each of the three unburned plots and high in each of the burned plots.

No correlation coefficients were calculated for beetles and vegetational characters because data were not available for the first year of the study. But inspection of Figures 2–7 and 18 suggests that high populations of beetles are associated with sparse litter. The separation of the effects of litter cover and litter depth cannot be made with the available data.

The 1958 census reveals the highest populations in Spring Burn I and Fall Burn. Litter cover and depth were low in both of these plots. Similar litter conditions existed in Spring Burn II, and a relatively high beetle population was to be expected here. The reasons for the indicated low population are not known.

In 1959 the apparent relationship with sparse litter was much more striking. Large numbers of beetles were present in each of the three burned plots where litter was still comparatively sparse. In the three unburned plots, where litter was dense, strikingly smaller populations were revealed.

Carpenter (1939) found total insect populations higher on burned areas and in seral stages than on undisturbed prairie. In contrast, Wehlan (1927) says that burning destroys much of the wintering habitat of beetles and that this, in turn, causes a reduction in populations.

The relation between an abundance of beetles and litter as influenced by fire requires further investigation. The delayed effect as indicated by the increase in numbers in the burned plots from 1958 to 1959 appears especially interesting. No explanation for this effect is known.

DISCUSSION

Our purpose in this section is to point out the factors limiting the interpretation of the findings of the investigation and to advance those interpretations we consider valid.

The changes and relationships observed in the Waubun Prairie flora and fauna studied may have spatial and temporal relations which would limit application of the findings. The position of the study area in the ecotone between prairie and forest must be given special consideration in any interpretation of these results. The time element must also be taken into account, particularly in terms of the weather and population levels, since the cumulative and year-to-year effects of weather were not measured in this study. In addition, the general level of populations of the resident small mammals in the area and the numbers of breeding migratory birds available in the region are both unknown. The variation in soils, although believed to be slight (Rust, 1958), must also be considered.

Certain generalizations regarding the effects of land use or treatment on the vegetation appear valid:

1. Mowing was included as a treatment in the original design of the study, but because of unforeseen problems this treatment was omitted in 1958 and 1959. But when 1957 data from the four plots in the area which had been mowed annually are compared with the data from the two plots in the unmowed area an assessment of the effects of mowing on native prairie can be made.

No differences in species composition of the four dominant native prairie plants resulting from mowing were recorded. This is in agreement with Weaver (1954). The removal of the annual growth of vegetation as hay, however, results in a habitat in which new growth is erect and relatively evenly distributed while litter is sparse in both cover and depth. In contrast, undisturbed sites have deep, dense litter and uneven or clumped new growth.

2. Similar characteristics of species composition, new growth, and litter as discussed above exist in areas which have been burned as compared to undisturbed areas.

3. Grazing brings about more complex changes. The observed responses of the dominant grasses suggest that each species has its characteristic reaction to grazing of a given intensity. A detailed analysis of the changes in all plant species on the Waubun Prairie resulting from grazing will be reported separately.

Data for litter, as measured in this study, indicate an anomalous situation. The percentage of cover contributed by litter appears to

increase because of removal of the current growth, whereas the actual cover on the plot provided by litter may decline as grazing continues.

The animal populations responded in various ways to the changes in vegetational cover brought about by mowing, burning, and grazing. Some species or groups of related species increase, some decrease or even disappear from a particular locality, while other populations appear to be unaffected. Some are affected immediately following application of a treatment and others exhibit a time lag.

Inspection of the distribution of significant correlations in Table 1 reveals that most of the animals studied show a linear association with litter depth or litter cover rather than with particular dominant plant species. Similar associations of animals with the physical nature of the vegetation rather than with specific plants have been discussed by Dice (1952), Hardy (1945), Kendeigh (1945), Miller (1942), and Pitelka (1941).

In the present investigation, litter cover and litter depth are closely related (.60). We believe that this correlation would be even higher if the methods of vegetation analysis had been specifically designed to measure such conditions. Ezekiel (1941) states that a test of whether a given variable may be related to a dependent variable, even if it shows no apparent correlation, is whether the first variable is correlated with other independent variables which in turn are correlated with the dependent. The recognition of this relation leads to the conclusion that the litter, whether measured in terms of areal cover or depth, is an important influence on the distribution and abundance of certain animals in grasslands.

The present study clearly points out the importance of litter. Since the methods were not specifically designed to measure the physical aspects of litter, the observed relationship may be even more valid than indicated by the analysis of these data. Further, when one considers that the biological processes governing the formation of litter are little known, the basic factors at play here are obscure. For these reasons, more research on litter itself will be required before the fundamentals underlying these relations can be documented.

Interspecific associations between the animal populations studied on the Waubun Prairie are suggested by the significant correlations shown in Table 1. Most of these correlations decreased below the selected levels of significance when the effects of litter cover or depth were removed by the partial correlation technique. But one cannot conclude that two populations of animals are not associated because they show no correlation. The lack of correlation may result from the compensating influence of other variables which conceal the true relation (Ezekiel, 1941). Only two interspecific correlations remained statistically significant when analyzed as partial correlations.

The total correlation of —.21 between bobolinks and savannah sparrows increased to —.28 and —.29 when the effects of litter cover and depth, respectively, were removed. These correlations indicate that some factor other than those investigated was influencing the association of these two species—perhaps space for breeding territories. A more detailed analysis of the relations among the species of birds inhabiting the Waubun Prairie Research Area will be presented separately.

The other significant interspecific animal association pointed out by the study was a correlation between savannah sparrows and grasshoppers. The partial correlations were .24 and .35 with the effect of litter cover and litter depth, respectively, removed. The explanation for this association is not definitely known at present, but it appears likely to be part of a food chain situation. Martin *et al.* (1951) and Roberts (1932) say that grasshoppers make up a large portion of the summer diet of savannah sparrows. Smith (1940) reports that grasshoppers are more universally accepted by birds as food than any other insects. These findings suggest that savannah sparrows may be attracted to areas with high or potentially high populations of grasshoppers.

All of the plant and animal species in a community are involved in the energy relations of the ecosystem (Odum, 1959). Certain obvious relations exist in prairies: for example, meadow voles and deer mice feed on plant materials and savannah sparrows eat grasshoppers. An understanding of these energy relations is dependent upon absolute quantitative data on total biomass of the organisms. The relative population indices used for censusing mammals and insects in the present study preclude a further analysis of interspecific association on the energy level.

Some of the dynamic aspects of a climax prairie community have been illustrated in this investigation. The species studied, though few, characterize certain aspects of the community and give it a fundamental unity. The relative numbers of the animals censused on the Waubun Prairie varied considerably in time and space. The differences in distribution and abundance have been shown to be at least partially dependent upon the history of the land treatments such as mowing, burning, and grazing. Comparable changes in species composition in a given locality owing to the impact of physical forces have been discussed by Elton and Miller (1954). Thus, land use has an important influence on animals in a given community even though it may not actually alter the climax status of this community.

SUMMARY

1. A field study to determine the nature of the relations between specific vegetational characteristics of the dominant grasses and litter found on a native prairie and changes in distribution and abundance of certain birds, mammals, and insects was carried on at the Waubun Prairie Research Area in Mahnomen County, Minnesota during the growing seasons of 1957, 1958, and 1959.

2. A total of 70 acres of relatively undisturbed native prairie was selected within the 640-acre tract. On five 10-acre plots mowing, grazing, or burning was carried out. Two plots were left untreated and held as controls.

3. Detailed descriptions of these treatments; of the methods of vegetation analysis; of censusing populations of three species of birds, three species of small mammals, and two groups of insects; and of the techniques of statistical analyses including test assumptions are given.

4. Striking changes in the percentage of areal cover and depth of the litter took place as the result of the treatments. The changes in percentage of cover of big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), Indian grass (*Sorghastrum nutans*), and needlegrass (*Stipa spartea*) were small.

5. There were important changes in the distribution and abundance of breeding pairs of bobolinks (*Dolichonyx oryzivorus*), savannah sparrows (*Passerculus sandwichensis*), and LeConte's sparrows (*Passerherbulus caudacutus*). On the basis of correlation analysis these changes appeared to be most closely associated with changes in litter.

6. Changes in populations of the meadow vole (*Microtus pennsylvanicus*) were positively associated with increasing litter. Those of the prairie deer mouse (*Peromyscus maniculatus bairdii*) were negatively associated with increasing litter. Numbers of the masked shrew (*Sorex cinereus*) seemed to be independent of the vegetative characteristics measured.

7. Analysis of the data for the two groups of insects indicated that while grasshoppers (Orthoptera) were most abundant where light or moderate amounts of litter were found, large beetle (Coleoptera)

populations appeared, on the other hand, to be associated with sparse litter.

8. Some of the dynamic aspects of a climax prairie community are discussed on the basis of this study. The influence of land use on the organisms studied is demonstrated even though the climax status of the community did not appear to be actually altered by two or three years of treatments by mowing, burning, or grazing.

APPENDIX TABLES AND LITERATURE CITED

APPENDIX TABLE 1. RAW MEASUREMENTS OF VEGETATIONAL CHARACTERS AND ANIMAL POPULATIONS IN CONTROL I

Year and Quarter	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needlegrass	Bobolink	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Prairie Deer Mouse	Masked Shrew	Orthoptera
1957													
1	39%	4 cm	8%	6%	22%	13%	.25	.50	.00	0	0	2	7
2	33	4	8	12	16	15	1.00	1.00	.00	0	0	1	7
3	31	3	13	12	13	13	.75	.50	.00	0	0	0	2
4	33	4	14	20	9	8	.00	.50	.00	0	0	1	4
1958													
1	27	12	8	6	23	16	1.00	1.50	.00	2	0	1	1
2	32	16	9	6	15	14	1.00	.00	.50	4	0	5	1
3	27	11	9	9	16	19	.50	1.00	.25	0	0	0	2
4	28	16	17	11	7	14	.50	1.50	.25	5	0	0	1
1959													
1	32	14	18	10	7	11	.75	1.25	.00	2	0	1	3
2	40	16	12	9	5	9	.50	.50	.00	10	0	0	1
3	41	16	14	12	8	8	.75	.50	.00	3	0	0	1
4	33	17	13	21	3	8	.50	.75	.00	7	0	0	4

APPENDIX TABLE 2. RAW MEASUREMENTS OF VEGETATIONAL CHARACTERS AND ANIMAL POPULATIONS IN CONTROL II

Year and Quarter	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needlegrass	Bobolink	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Prairie Deer Mouse	Masked Shrew	Orthoptera
1957													
1	58%	17 cm	10%	3%	4%	13%	.00	.25	.00	0	0	2	0
2	48	15	15	5	3	12	.00	1.75	.00	1	0	1	1
3	52	16	8	6	10	11	.00	1.50	.00	0	0	1	2
4	53	18	10	5	9	10	.00	2.50	.00	0	0	4	0
1958													
1	48	17	8	2	3	16	.50	1.00	.50	1	0	0	2
2	41	18	15	4	5	12	.50	1.25	.50	2	0	5	0
3	55	19	7	2	8	6	.75	1.00	.00	2	0	2	1
4	44	18	9	2	8	12	.25	1.25	.00	3	0	6	3
1959													
1	41	18	11	5	5	20	.50	.50	.00	0	0	1	2
2	38	15	15	9	5	13	1.25	1.00	.00	0	0	1	1
3	39	16	10	11	9	7	1.00	1.00	.00	1	0	3	1
4	37	17	12	9	8	10	.25	1.00	.00	1	0	1	4

APPENDIX TABLE 3. RAW MEASUREMENTS OF VEGETATIONAL CHARACTERS AND ANIMAL POPULATIONS IN GRAZE

Year and Quarter	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needlegrass	Bobolink	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Prairie Deer Mouse	Masked Shrew	Orthoptera
1957													
1	25%	4 cm	11%	7%	20%	13%	.25	.50	.00	0	0	2	3
2	32	6	7	10	18	16	.25	.50	.00	0	0	1	4
3	26	4	16	4	24	12	.75	1.00	.00	0	0	2	9
4	40	5	9	2	23	6	.25	1.50	.00	0	0	0	8
1958													
1	26	11	16	6	17	16	1.25	.00	.50	2	0	2	3
2	30	14	13	6	17	16	1.50	.75	.25	1	0	1	2
3	28	13	19	7	15	12	1.00	.50	1.00	7	0	0	2
4	38	11	16	9	11	7	.75	1.25	.25	3	0	1	3
1959													
1	60	8	10	5	6	5	.50	.50	.00	0	0	1	2
2	54	12	12	5	4	7	.50	.75	.50	0	0	0	1
3	57	9	11	8	3	7	.50	.75	.00	0	1	1	1
4	52	11	13	5	7	8	.50	.50	.50	0	0	0	1

APPENDIX TABLE 4. RAW MEASUREMENTS OF VEGETATIONAL CHARACTERS AND ANIMAL POPULATIONS IN SPRING BURN I

Year and Quarter	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needlegrass	Bobolink	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Prairie Deer Mouse	Masked Shrew	Orthoptera
1957													
1	45%	4 cm	13%	16%	5%	10%	.50	2.00	.00	0	0	0	7
2	27	4	21	14	5	14	.00	.00	.00	0	0	1	7
3	39	5	13	12	6	12	1.00	.50	.00	0	0	3	6
4	42	5	12	10	9	12	.00	2.00	.00	0	0	0	7
1958													
1	5	2	13	8	22	15	.00	.00	.00	2	0	4	5
2	7	2	17	12	10	18	.00	.75	.00	0	1	6	3
3	8	4	22	8	9	24	.00	.75	.00	0	0	2	3
4	11	3	15	10	20	19	.00	.50	.00	0	1	1	5
1959													
1	33	13	17	17	5	13	.25	.25	.50	3	0	0	3
2	20	11	29	11	8	11	.50	.25	.00	2	0	0	1
3	43	9	13	10	3	10	.50	.00	.50	2	0	2	2
4	29	10	22	6	15	11	1.25	.00	.00	2	0	1	2

APPENDIX TABLE 5. RAW MEASUREMENTS OF VEGETATIONAL CHARACTERS AND ANIMAL POPULATIONS IN SPRING BURN II

Year and Quarter	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needlegrass	Bobolink	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Prairie Deer Mouse	Masked Shrew	Orthoptera
1957													
1	45%	17 cm	10%	4%	12%	15%	.00	.25	.00	1	0	3	0
2	51	16	4	5	8	18	.00	1.00	.00	0	0	2	1
3	52	17	9	4	9	13	.00	2.00	.00	0	0	2	2
4	46	17	15	3	7	10	.00	.75	.00	0	0	3	2
1958													
1	15	4	7	6	18	8	.00	.00	.00	1	1	2	3
2	19	4	8	5	12	13	.00	.50	.00	1	2	1	1
3	13	3	7	5	19	10	.00	.50	.00	1	6	3	3
4	4	2	17	4	9	10	.00	.50	.00	0	2	0	4
1959													
1	30	12	15	6	13	7	.25	.00	.50	2	0	7	3
2	36	12	8	5	12	8	1.25	.00	.50	0	0	1	1
3	34	12	11	7	15	9	1.25	.00	.00	4	0	1	2
4	25	10	18	4	12	6	1.25	.00	1.00	0	0	1	1

Appendix Table 6. Raw Measurements of Vegetational Characters and Animal Populations in Fall Burn

Year and Quarter	Litter Cover	Litter Depth	Big Bluestem	Little Bluestem	Indian Grass	Needlegrass	Bobolink	Savannah Sparrow	LeConte's Sparrow	Meadow Vole	Prairie Deer Mouse	Masked Shrew
1957												
1	37%	4 cm	10%	9%	16%	9%	.25	1.00	.00	0	0	2
2	39	6	11	13	15	12	.75	.00	.00	0	0	0
3	34	4	15	15	12	12	.00	1.50	.00	0	0	1
4	34	4	19	16	7	10	.50	1.00	.00	0	0	1
1958												
1	8	3	13	18	27	10	.00	.50	.00	0	1	0
2	12	4	13	18	22	16	.00	.50	.00	1	0	1
3	16	4	12	14	14	18	.00	.00	.00	0	0	1
4	23	4	8	16	8	12	.00	.00	.00	1	0	1
1959												
1	37	9	15	12	11	7	1.00	.00	.50	0	0	2
2	37	13	19	12	15	6	1.00	.00	.00	0	0	4
3	33	10	14	13	14	11	1.00	.50	.50	0	0	2
4	37	10	11	14	3	12	1.00	.50	.00	0	0	2

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