The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

VOL. 51 APRIL, 1954 No. 2

An Ecological Study of Invertebrates of Grassland and Deciduous Shrub Savanna in Eastern Nebraska*

Edson Fichter

Department of Zoology, Idaho State College, Pocatello

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Introduction

Several considerations prompt, influence, and lend significance to any serious attempt to add to or improve existing knowledge of animal populations in grassland, namely, (1) the importance of grass to the people of the Great Plains (Allred 1941, U.S.D.A. Ybk. Agric. 1948), (2) the propensities of grassed areas as sources of insect pests destructive to other crops, especially corn (Bruner 1900, Osborn 1917, 1939:16, 29, Herrick 1925:365), (3) the possible role of the ecological method of study in the control of meadow insects (Osborn 1917, 1939:10, Townsend 1924, Chapman 1939, King 1939:281, Smith 1939), (4) current operations of land and wildlife management agencies toward revegetation of exploited and submarginal lands (Robertson 1939:433, Hoover 1939, Graham 1941, Hoover *et al.* 1947), (5) the growth of the bioecological concept (Vestal 1914, Shelford and Olson 1935, Weaver and Clements 1938:478, Carpenter 1939a, and Clements and Shelford 1939), and (6) the decimation of native prairie (Adams 1915, Weaver and Clements 1938:518) accentuating (7) the need for studies on primitive or near-primitive remnants (Carpenter 1939b, Dowdy 1944a:218). The study reported here was undertaken in an effort to determine composition and behavior of the communities of invertebrates as they occurred during the period of the investigations, in a 320-acre remnant of unbroken grassland in eastern Nebraska, and in relatively small areas of two postclimaxes within the tract.

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* Studies from the Department of Zoology, University of Nebraska, No. 266.

When the two-year study was initiated in 1937 it was intended that animals of true prairie were to be under investigation. It become evident, however, that under the impact of three years of drought the characteristic continuous stand of perennial, dominant mid grasses had greatly deteriorated; the more xeric dominants of mixed prairie had invaded. Rainfall patterns remained abnormal, and conspicuous and dramatic changes in the prairie continued through the two years of this endeavor. Drastically reduced plant cover, great and relatively rapid changes in floral composition, and abnormal moisture conditions may have produced invertebrate population patterns not characteristic of remnants of climax true prairie. Relative abundance of the many species of arthropods was probably altered. Osborn (1939:37) has pointed out that "a well known feature of meadow life is the varying abundance of different groups or species in different seasons or years in a series. . . ." Under the vacillating stresses present in the prairie from 1934-41, such shifts in invertebrate populations may have been magnified if not accelerated. Aberrant weather patterns may have been directly reflected in atypical behavior. Previous studies on animal communities in this or comparable tracts of true prairie in this region would have made possible comparison with pre-drought population patterns. Faunal studies should have been in progress throughout the ten-year period of great changes in the grasslands. Here was a magnificent "natural experiment" offering "a chance to deduce the response of a whole community to its weather environment" (Leopold and Jones 1947:117-118). It is regrettable that the study reported here was not continued sufficiently long to measure reliably any drought-induced changes that may have occurred in the invertebrate fauna.

The eight-year period of drought ended and recovery of true prairie vegetation began in 1941 (Weaver and Albertson 1944). Studies on animal communities of that association can again be made; they would probably add significance to much of this report.

Quantitative ecological studies of grassland invertebrates in North America are relatively few in number. King (1927) studied the fauna of native and ruderal associations at Saskatoon, Saskatchewan, with special reference to climatic influence. Prairie invertebrates have been studied quantitatively in Illinois by Shackleford (1929), with emphasis on designation of societies, and by Carpenter (1935) who made his investigations upon the prairie-forest ecotone, emphasizing fluctuations in biotic communities. Carpenter (1939b) again considered biotic fluctuations from the viewpoint of aspection in mixed prairie in Oklahoma, where he found some agreement with the conditions reported by Beed (1936) for short grass plains in Nebraska on a tract grazed only by native mammals. Shackleford and Smith (1928), Shackleford and Brown (1929), and Shackleford (1931, 1935) have studied invertebrate populations of grasslands (pastured in part) in central Oklahoma, with emphasis on seasonal and annual variations.

This paper presents results of the first quantitative ecological study of invertebrates in the true prairie, albeit disturbed by severe drought and in subsere.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the assistance and suggestions accorded me by Dr. Irving H. Blake of the University of Nebraska, under whose direction this study has been conducted. To Dr. David D. Whitney and the Department of Zoology of the

University of Nebraska thanks are due for making possible the construction of field and laboratory equipment. I am indebted to the Nebraska Academy of Sciences for a grant-in-aid which helped defray expenses incurred in transportation and in the construction of a field laboratory. The invaluable help given me by Dr. J. H. Robertson of the University of Nevada in locating the stations is gratefully acknowledged. To Dr. J. E. Weaver of the University of Nebraska appreciation is expressed for helpful advice. For the generosity of the late Mr. T. Flader and his sons in giving me free access to the prairie tract which was under their ownership, I owe a special debt of gratitude. Thanks are due Henry Smith of the University of Nebraska who conducted the soil analyses, William McMann of the Nebraska State Agricultural Conservation Office whose cooperation made possible the inclusion of the aerial photographs, and the following entomologists for the identification of arthropods: Orlando Bare (Formicidae), H. R. Bryson and Roscoe Hill (Coleoptera), H. H. Knight (Hemiptera), Miriam A. Palmer (Aphididae), Raymond Roberts (miscellaneous insects and Ixodoidea), Curtis W. Sabrosky (Diptera), and D. A. Wilbur (Homoptera). To my wife, Ardith Fichter, whose help in organization of data and preparation of manuscript has been indispensable, I am grateful. The efforts of the following men, who as fellow students were helpful in many ways, are acknowledged with thanks: William R. Cunningham, Lloyd Don Davis, Robert Fowler, George Garrison, Merle F. Hansen, Harlan Herman, Albert Lunt, Rufus A. Lyman, Sam Messner, Robert Walstrom, and Robert Worthman.

The specimens taken in this investigation are in storage at the Department of Entomology, University of Nebraska, through the cooperation of H. Douglas Tate. I am grateful to the staff of that Department for their efforts in curating the material, for making any part of it available to other workers (see Muma and Muma, 1949), and for many other courtesies relating to this undertaking.

True Prairie

The vegetational characteristics and relationships, status, and general distribution of the climatic community which, as one of several grassland climaxes, is known as *true prairie* (*Stipa-Sporobolus* association), and of the postclimax tall-grass prairie (*Andropogon* associes) have been treated extensively by Clements, Weaver, and Hanson (1929) Weaver and Fitzpatrick (1934), and Weaver and Clements (1938). Aikman (1929) and Weaver and Clements (1938) have described the postclimax extensions of the oak-hickory association into the prairie climax along stream valleys and dry ravines. The following brief characterizations of the three vegetational complexes involved in this study are drawn from these authors.

True prairie is the characteristic climatic community of the rolling hills of the Missouri Valley within the general limits of 25 to 30 inches of rainfall. Cultivation has erased the true prairie over most of its area and its original limits have been pieced together only within the last twenty years from numerous relatively small and scattered fragments. The dominants of this association are mid grasses of both the sod and bunch life form.

True prairie is most closely related to the mixed prairie on the west and somewhat less closely to the postclimax prairie on the east; it is in contact with both and nearly enclosed by them. Several of the dominant species of true prairie are more abundant in the mixed prairie, and this is strikingly true of the relict short grasses.

Aspect societies are conspicuous and highly developed in the grassland. Four distinct aspects occur in true prairie from early spring through autumn. The number of subdominants in each aspect is usually large; the societies are, therefore, mixed and consist of several fairly abundant species.

TALL-GRASS PRAIRIE

Tall-grass prairie is a postclimax to the true prairie. As the name indicates, it consists of tall grasses, often six to eight feet high and belonging mainly to the sod-forming type. The societies of the postclimax prairie are essentially those of the true prairie, reenforced by additions from the deciduous forest and the meadows included in it; the number of species of composites is considerably larger.

POSTCLIMAX DECIDUOUS SHRUB

Along the Missouri River, which borders Nebraska on the east, a belt of deciduous forest varying in width from two to about ten miles forms a northwestward portion of the oak-hickory association which reaches South Dakota. Extensions of woodland, which are postclimax, border the many tributaries of the Missouri in belts fringing the bluffs, sometimes extending somewhat over the adjacent hills. The extreme outposts of the forest, although represented by relatively few species of trees and shrubs, reach far out into the prairie climax along the creeks and sheltered dry ravines which more or less dissect especially the rolling portions of the prairie. Thus the grassland is in contact over a very extensive marginal area with outposts of the forest. These long, narrow fingers of forest margin conditions reaching into the true prairie form an ecotone where grass meets deciduous woodland or shrub, in response to the operation of compensatory or protective features of topography.

Background of Drought

Weaver (1943), Weaver and Albertson (1944), and Albertson and Weaver (1945) have furnished comprehensive reports on the effects of the great drought of 1933 to 1940 on prairie vegetation, and on trees in the same region. The following account of the drought, of marked importance in this study, is taken from their papers.

That the prairie region of the Middle West was undergoing the most severe drought since the beginning of its recorded weather history was clearly evident by midsummer of 1934. The 12 months following June, 1933, was the driest weather period ever recorded for Nebraska. Rainfall in the summer of 1934 was extremely low, soil moisture became unavailable to a depth of four feet, and a terrific heat wave occurred. In 1935 it was found that losses of plant cover west of the Missouri River were heavy.

Replacement of true prairie by mixed prairie took place as a result of continued drought in an area 100 to 150 miles in width in central Kansas, eastern Nebraska, and eastern South Dakota. Studies in prairie tracts in southeastern Nebraska and northeastern Kansas showed that the formation of mixed prairie became clearly apparent in 1938, and that these grasslands were almost entirely transformed into mixed prairie by 1941.

Predrought vegetation consisted mostly of little bluestem (*Andropogon scoparius*) and big bluestem (*A. furcatus*) with only small amounts of western wheat grass (*Agropyron smithii*), side-oats grama (*Bouteloua curtipendula*), and the short grasses, blue grama (*B. gracilis*) and buffalo grass (*Buchloe dactyloides*). The chief dominant, little bluestem, mostly or entirely succumbed to drought in 1934 and 1936. Big bluestem was greatly damaged. In 1935 with approximately normal precipitation, six-weeks fescue (*Festuca octoflora*), blue grama, and especially western wheat grass, increased greatly. Certain native forbs spread rapidly, and there was invasion by many ruderal forbs. Severe drought in 1936-37 resulted in great advantage to six-weeks fescue, blue grama, western wheat grass, and buffalo grass, with further losses of the less xeric grasses and forbs. Western wheat grass increased in amount and annual weeds were abundant.

Approximately normal precipitation in 1938 resulted in an excellent development of vegetation, thickening of cover, and production of much seed. Wheat grass, blue grama, and buffalo grass continued their spread. Big bluestem, needle grass (*Stipa spartea*), and prairie dropseed (*Sporobolus heterolepis*) thickened their relict stands and increased greatly. Ruderals and native weedy forbs decreased. Spring rainfall in 1939 was followed by severe summer drought. Wheat grass waned in competition with an enormous stand of side-oats grama. Short grasses increased; most other vegetation suffered from severe desiccation.

In the big bluestem type in ravines where *Andropogon furcatus* was the chief dominant, the total cover of grass was not significantly decreased by drought; it was merely changed in composition. The cover of tall grasses, including Indian grass (*Sorghastrum nutans*) and tall panic grass or switch grass (*Panicum virgatum*) became open, and short grasses and wheat grass became abundant in it.

Where postclimax forest extends into the semihumid and dry grassland climates, tree losses were extremely heavy during the decade of drought.

It is obvious that the findings given in this paper must be considered as reflecting composition and behavior of invertebrate populations subjected to aberrant climatic conditions in (1) grassland which was in a generally reverse though fluctuating succession from true prairie to mixed prairie—a prairie subsere induced by recurrent drought and marked by great, rapid, and complex changes in the vegetation, and (2) postclimaxes somewhat less affected by the shifting environment.

Area Studied

The prairie area here reported upon presented (1) a near-primitive and relatively large unit of the once vast true prairie, (2) a grassland area (meadow) bordered by cultivated crops (Fig. 1), and with its included postclimax areas, (3) an opportunity for comparative ecology.

The study was conducted within a continuous tract of upland prairie one-half section in extent (Lancaster County, Township 10 N.—Range 5 E., Section 2, east half), which is located five and one-half miles west and three miles north of Lincoln, Nebraska. Haying operations constituted the only important disturbance to which the vegetation had been subjected by man, with the exception of grazing by a small band of horses during one winter about 1933.

Climate

Weaver and Himmel (1939) state that "the mean annual precipitation at Lincoln for a period of fifty years is 27.94 inches. Its distribution is of the Great Plains type, between 76 and 79 per cent occurring during the three months of May, June, and July. . . . Less than one-tenth of the precipitation occurs during the three winter months. The average snow fall is about 27 inches." "As a rule snow covers the ground but a few days at a time after each snow storm and the ground is covered with snow less than half of the time even during the months of heaviest snow fall" (Loveland 1920).

The mean annual temperature is 53°F. in southeastern Nebraska. January

Fig. 1.—Aerial view of the half-section tract of unbroken grassland (outlined) and the adjacent areas of cultivated lands.

is the coldest month with a mean temperature of about 23°, July the warmest, with a mean temperature of about 76°. "Maximum temperatures from 96° to 100° usually occur a few times during the warm season, July, August, and the first ten days of September, and temperatures of 110° to 114° have occurred, but they are unusual. Minimum temperatures 15° to 20° below zero occur at intervals during the cold season, the latter part of December, January, and February. Occasionally temperatures 10° lower occur.

"The prevailing direction of wind for the year is from the northwest unless influenced by local conditions. The wind blows from the south or southeast the greater portion of the time during the warm months of June, July, and August, and of course with greater or less frequency during the rest of the year. From the middle of September to the middle of May the prevailing direction of the wind is from the northwest.

"The velocity of the wind has been recorded carefully at only one station in the territory—Lincoln. The anemometer is placed at an elevation of 84 feet and the average velocity is 11 miles per hour.

"The average relative humidity for the year is quite regularly near 70 per cent. It is frequently low during the afternoon in spring or summer, sometimes below 20 per cent.

"The sky is relatively free of clouds; 175 to 185 clear days may be expected, from 81 to 86 cloudy, and the rest of the days of the year will be partly cloudy" (Loveland 1920).

TOPOGRAPHY AND GEOLOGY

The tract is dissected by five major ravines, two draining to the north, two to the south, and one to the east (Figs. 1, 2). The highest of the rolling, flat-topped drift hills is approximately 140 feet above the lowest point. Topographic maps show the 1300 foot interval line traversing the tract. The ravines are of moderate depth, showing no erosion.

SOILS

The soil is Carrington silt loam of glacial origin. Steiger (1930) and Robertson (1939) have pointed out the high water holding capacity of the soil due to the large proportion of very fine sand, silt, and clay. Robertson states that the soil is "dark, granular, friable, and without lime in the first foot but harder, yellow, and speckled with grains of lime at a depth of three feet."

Table 15 represents a summary of data for soil samples taken in the three stations on March 23, 1942. It is notable that percentages of organic matter, volatile matter, nitrogen, and hygroscopic coefficient each show consistent gradients, with the highest values occurring in the shrub station, the lowest in the subseral true prairie station. Hydrogen-ion concentrations likewise conform to a consistent gradient, soil from the true prairie station being most acid, though only slightly so (6.4), that from the shrub station the least acid (6.8).

VEGETATION

In the years 1927 and 1928 Steiger (1930) intensively studied the structure of the prairie vegetation found upon the tract wherein this investigation was conducted. Robertson (1939) reported upon the vegetation of this half-section as he found it during the summers of 1936 and 1937. The following description of the area before and after drought is based largely upon their accounts.

Steiger described what he termed low prairie occupying a broad, nearly level expanse at the foot of a north slope and at that time (1927-28) characterized by a continuous, dense sod, predominantly composed of big bluestem, with the upland or high prairie characterized by more open ground and a varied pattern of little bluestem, needle grass, June grass, dropseeds, grama grass, and a profuse growth of non-grassy subdominants. Robertson states that before the drought the most abundant forbs, in order of decreasing importance, were lead plant (*Amorpha canescens*), prairie cat's-foot (*Antennaria campestris*), goldenrod (*Solidago glaberrima*), and the many-flowered psoralea or wild alfalfa (*Psoralea floribunda*); the many-flowered aster (*Aster multiflorus*) ranked eighth in 1928.

The vegetation of the ravines or draws is more mesic than that of low prairie, the flora varying greatly with depth of the ravines and their exposure to insolation and wind. Trees and shrubs may extend to the heads of ravines on north slopes; in the south-facing slopes trees and shrubs occupy only the lower portion. Boxelder (*Acer negundo*), western cottonwood (*Populus sargentii*), and three species of willows (*Salix cordata, S. amygdaloides,* and *S. nigra*) are the only trees. They are all of relatively small stature and occur in small groups or, more usually, as isolated individuals. Small thickets and scattered clumps of shrubs accompany the trees, often extending farther up the ravines; some of the shrubs, especially poison ivy (*Rhus toxicodendron*) and smooth sumac (*Rhus glabra*), extend into the low prairie. Wild plum (*Prunus americana*), dogwood (*Cornus stolonifera*), elder (*Sambucus canadensis*), sandbar willow (*Salix interior*), and buckbrush (*Symphoricarpos occidentalis*) also occur. Prairie grasses tend to be absent in the partial shade under the woody species where a few mesic woodland herbs, such as bedstraw (*Galium* sp.), find suitable habitat, although frequently the ground layer consists mostly of bluegrass (*Poa pratensis*). The transition from shrubs to grassland is abrupt and follows the line determined by the annual mowing. The more xeric vegetation of the steep banks, where run-off is high, is in striking contrast to that of the moist bottom of the ravine (Fig. 8).

In late July and early August of 1936, during extreme drought, Robertson found that the more mesic grasses of this prairie area were so brittle that stems readily broke off underfoot. Many large cracks were present, especially in bluegrass sod. The most abundant grasses were big bluestem, little bluestem, and prairie dropseed. The last appeared to have come through the drought of 1934 nearly unscathed. Needle grass and side-oats grama were common and of general distribution.

Only the most deeply rooted upland forbs, for example *Amorpha* and *Aster,* were not badly dried. *Aster* had advanced from eighth position to replace *Amorpha* as the most important forb.

In 1937 certain vegetational changes were obvious owing to the drought of the previous year. Much prairie dropseed and bluegrass had been killed, leaving numerous areas protected from erosion only by dead crowns and rhizomes. These and other areas were rapidly being invaded by western wheat grass and *Aster,* in some instances nearly to the bottoms of ravines. The rank growth of *Aster* and other weedy species, coupled with the sparseness of perennial grasses, reduced the value of the hay so that most of the prairie was left unmowed. The loss of bluegrass was due in part to severe injury by grasshoppers. Other perennial grasses which lost ground were side-oats grama, June grass, and the carices. Needle grass and switch grass showed small gains, but wheat grass increased over 40 per cent. Comparable increases were shown by aster, daisy fleabane (*Erigeron ramosus*), and peppergrass (*Lepidium* sp.) —these three species being representative of perennial forbs, annual forbs, and ruderals. Perennial grasses alone were reduced by the drought.

The south half of the prairie tract was burned by the owners on April 11, 1938. By April 18 much of the burned appearance had been lost due to the rapid growth of the grasses. During the week of May 2-9 many forbs were blooming. By June 17 the picture was dominated by daisy fleabane which was in flower, and by alternes of western wheatgrass. On July 18 it was apparent that the grassland was beginning to lose its green color, due mostly to the browning of needlegrass. The bluestems were putting up flowering stalks, goldenrod was in bloom, with the daisy fleabane noticeably on the decline, the area no longer whitened by its flowers. The prairie was very dry by August 13, leaves of the grasses tightly rolled much of the time, with the general appearance brown except on north slopes and in ravines. The leaves were falling from the wild plum and dogwood in the ravines. Mowing of the prairie hay was begun on August 13 in 1938, hay from most of the north half being in stacks by August 22. Mowing in 1939 did not begin until about September 1.

THE STATIONS

The location of Station 1 (Figs. 2, 5) was chosen after careful scrutiny of the entire half-section in an effort to determine what appeared to be average conditions of slope, exposure, and floristic structure. This station was placed slightly below the rounded top of the next to highest hill of the tract, on a south-southeast slope (high prairie of Steiger 1934). Needlegrass, side oats grama, little bluestem, June grass, and dropseed were the most abundant grasses. Much bare soil surface was evident with little or no litter. The many-flowered psoralea was the most prominent forb. *Erigeron* was markedly abundant in the true prairie subsere substations.

Conditions of tall-grass postclimax considered to be typical for the area were found in a ravine which was centrally located in the tract and which drained to the south-southwest. Station 2 (Figs. 2, 6) was established here, where big bluestem, wild rye (*Elymus canadensis*), switch grass, and bluegrass characterized the vegetation, forming a dense sod, with the many-flowered aster the prominent forb.

Station 3 (Figs. 2, 7, 8, 9) was located near the northeast corner of the tract. Here an area some 20 yards long and about 15 yards wide was rather densely covered by dogwood, wild plum, smooth sumac, buckbrush, and wild grape (*Vitis* sp.).

Substations for the purpose of quantitative sampling were established within the 320 acre tract, five in the true prairie subsere, one in the ravine postclimax tall grass, and two in the ravine postclimax shrub.

Station 1, equipped with meteorological instruments, was put in operation on November 2, 1937, and Stations 2 and 3 on January 4, 1938. Collecting was begun in all three stations on November 2, 1937.

PREVIOUS FAUNAL STUDIES

Whelan has published briefly annotated lists of the Coleoptera (1936a), the Orthoptera (1938), the mammals (1936b), and the birds (1940) of this prairie tract.

Fig. 2.—Aerial view of the half-section tract of subseral true prairie and the included postclimax habitats occupying ravine situations, showing location of stations. 1. Upland true prairie subsere station. 2. Postclimax tall-grass station. 3. Postclimax deciduous shrub station.

Extent and Methods of Study

In this paper the attempt is made to point out some of the measurable factors of the physical environment and the composition of the invertebrate communities in upland true prairie (in drought-induced subsere), and in postclimax tall grass and postclimax deciduous shrub with both of which the true prairie is in contact. Attention is focused upon (1) the differences of the environmental complexes within the three habitats studied, (2) the faunal interrelationships of these three stations, (3) horizontal and vertical movements as exhibited by stratal, seasonal, and daily total population trends, and (4) the strato-seasonal activities of prevalent species with the view of determining any indicator values (Fichter 1939:211, King 1939:281) such numerically prominent species may possess. "In making quantitative sample collections . . . the quality of the work can be greatly improved by seeking out the species occurring in any abundance" and observing their role in the community (Shelford 1930).

No effort is made to estimate the areal numbers of invertebrates. Population trends are sought, and these are considered determinable by comparison of unit collections, especially where it is possible to secure enough samples within a given stratum of a given station to allow for the determination of sample averages within a given season or other unit period. I am in accord

Fig. 3.—General view of the prairie tract, looking southeast from near Station 1, showing postclimax vegetation in ravines and the field laboratory.

Fig. 4.—Field laboratory on the prairie. The construction of this unit was made possible through a grant-in-aid from the Nebraska Academy of Sciences.

with Beall (1935) who writes that "a more legitimate use for the sweep collections of insects and arachnids, than the estimate of numbers per unit area, is to compare those made at different times and to determine population trends."

Park (1939) in emphasizing the desirability of the acquisition of more basic facts about population trends in the field, says that "both the single-

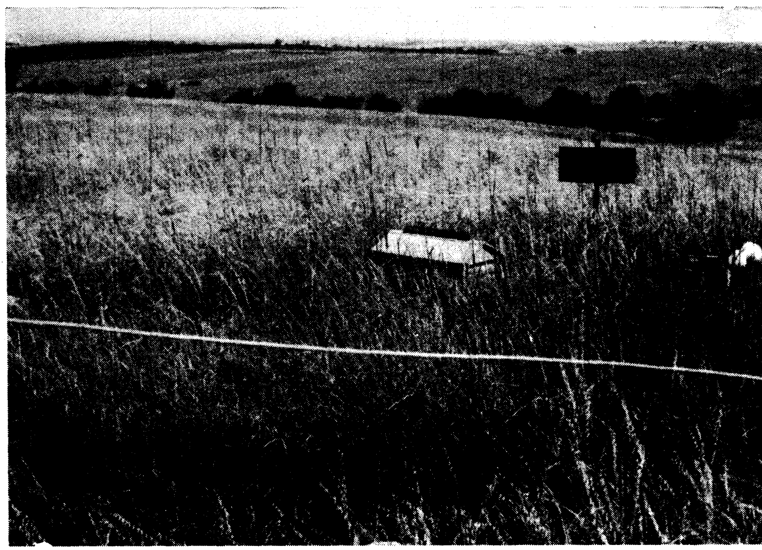


Fig. 5.—Upland true prairie subsere station during late estival aspect, 1938.

Fig. 6.—Postclimax tall-grass station, late estival aspect, 1938.

species population and the mixed-species population possess a structural or quantitative aspect which . . . merits our attention and analysis."

The desirability of designating an animal species which is abundant in its given community by the term *prevalent,* in preference to the word predominant

Fig. 7.—Postclimax deciduous shrub station, estival aspect, 1938.

Fig. 8.—Interior of postclimax deciduous shrub station, estival aspect, 1938.

as suggested by Shelford (1926) "as covering all organisms of outstanding abundance or obvious importance," has been pointed out (Fichter 1939). Prevalent species are determined on the basis of strato-seasonal abundance, i.e., that species which shows the highest seasonal population within a given stratum thereby attains prevalent rank for that season, a designation which indicates only that the species has prevailed numerically in that stratum. Such a determination of prevalents, as carried out in this study, does not purport to lend basis to the naming of societies.

Shelford (1932:107) has proposed "the importance of the abundant or otherwise significant species" in the classification of communities, and the value of characteristic though less abundant species as indicators. I am in accord with the principles of ecological classification stated by Shelford (1932:107-108), and with his suggestion that "a definite assemblage of organisms" can be relied upon as a safe criterion in the classification of communities, but I cannot subscribe to such nomenclatural appointments founded on short-time studies, especially on remnant areas. It is improbable that the existence and nature of any "definite assemblage" of terrestrial organisms can be reliably determined within the period of time given to any ecological study made to date. Osborn (1939:25) has pointed out that quantitative determinations on insects of grasslands "in any one place or for any one season cannot be assumed to represent the general [characteristic] condition . . . even for meadows of different history in the same locality." Blake (1931:524) has shown that species of animals, on which have been based application of detailed nomenclature to terrestrial animal communities, "may fail to appear in important numbers and relations in" similar studies "made on the same ground at a different time."

A species which exhibits a seasonal population less than that of the prevalent, and which may or may not equal the frequency values of the prevalent, but which exceeds the population values of the latter at one or more brief intervals, even in any one sample collection, is considered as possessing *sub-*

Fig. 9.—Postclimax deciduous shrub station, hiemal aspect, 1938-39.

prevalent rank. All prevalent and subprevalent species among the invertebrates as determined by this study are reported in this paper, with special reference to the prevalents. A few characteristic and conspicuous forms which did not attain prevalent or subprevalent rank are considered.

Four strata were studied in the true prairie subsere and postclimax tall-grass stations; namely (1) soil, (2) litter, (3) soil surface, and (4) herb, with the addition of (5) the shrub stratum in the postclimax deciduous shrub station. The soil stratum was sampled to a depth of four inches (10 cm.), always beneath the one square foot of litter collected for examination from the litter stratum. The soil surface invertebrate fauna was studied by use of an alcohol pitfall, designed to trap "those species which travel, for the most part, over the surface of the ground, and, though closely associated with the litter as material for abode, constitute when active (not resting, hiding, or hibernating), a distinct society" (Fichter 1941). This apparatus does not measure any given unit of soil surface population at any given time but does appear to indicate population trends. The population of the herb and shrub strata were sampled by the sweep net method of previous workers at 0-75 cm. in the herb and 1-2 meters in the shrub.

While the litter stratum in the shrub station approaches the condition found in climax deciduous forest, and should perhaps be more properly designated as litter-duff, the term litter will be retained here.

Field operations began on November 2, 1937, and terminated on November 4, 1939. The seasonal studies (sweeps, and litter and soil sampling) were carried on from November 2, 1937 to March 20, 1939, the day-night studies (sweeps only) from June 12 to October 29, 1938, and the pitfall studies from April 8 to November 4, 1939. A total of 187 unit day sweep collections in the herb stratum of the three stations yielded 44,418 specimens, while 2,782 specimens were taken in 24 unit sweep collections in the shrub stratum. Night sweep collections numbering 52 in herb and shrub strata collected 17,779 specimens. Soil collections numbered 63, producing 689 specimens, litter samples 102 with 4,982 specimens, and 76 pitfall collections secured 11,161 specimens. This study is thereby based upon the examination of 81,811 specimens of invertebrates taken in 504 collections.

From June 17 to August 15, 1938 I maintained a field laboratory and living quarters on the prairie tract (Figs. 3, 4). This floored and screened tent made it possible to take samples with greater regularity and to care adequately for large numbers of specimens. An average of five days and nights out of each week were spent on the area during this two-month period.

The term invertebrate as herein employed includes only the phyla Annelida and Mollusca and the classes Arachnida and Insecta; although members of the orders Acarina (mites), Collembola (springtails), Thysanoptera (thrips), and Corrodentia (psocids and book-lice) were taken they are not included in this study. It must be stated, however, that the importance of these latter groups, particularly of the mites and springtails, is thoroughly recognized.

The inclusion of small, postclimax areas in an ecological study of true prairie animals seemed advisable because of the juxtaposition of these vegetational units and the more or less universal occurrence of such postclimax vegetation throughout the prairie formation (Weaver and Clements 1938:85). These more or less distinct local habitats are expressions of immediate physiographic features and each presents an ecologic problem of its own (Osborn 1939:16).

The seasons as delimited in this paper are based upon the vegetational aspects of the prairie outlined by Weaver and Fitzpatrick (1934). The prevernal and vernal are combined to form the prevernal-vernal, and the serotinal of Weese (1924) and others is included in the autumnal.

The time basis, other than the natural aspectional divisions, employed in this paper for the expression of data is the two-week period. Three short periods appear in the tabulations: a seven-day period of December 14-21, 1937, a period of thirteen days from January 18-31, 1938, and one of twelve days from September 12-24, 1938. The transition from one aspect to another is, of course, a gradual one. To facilitate seasonal study of collections made in the prairie tract it was necessary, however, to define aspectional limits. The following dates were established to keep intact the two-week periods which occurred at these transitional periods and at the same time conform closely to the normal aspect limits given by Weaver and Fitzpatrick (1934): Hiemal, November 2, 1937 to March 28, 1938; Prevernal-vernal, March 28 to May 23, 1938; Estival, May 23 to August 1, 1938; Autumnal, August 1 to October 22, 1938; Hiemal, October 22, 1938 to March 25, 1939; Prevernal-vernal, March 25 to May 20, 1939; Estival, May 20 to July 29, 1939; Autumnal, July 29 to October 22, 1939; and early Hiemal, October 22 to November 4, 1939.

This population study is neither comprehensive nor exhaustive. The lack of correlated laboratory experimentation (King 1939:284) is an admitted weakness. Relatively few conclusions can be drawn from these findings. They are offered, however, as the results of a further effort in the vast amount of work known to "be necessary before valid generalizations can be drawn" regarding terrestrial invertebrate populations — generalizations which, it is hoped, will "in turn serve as valuable guides to both economic and general work" (King 1939:281). Most of the data gathered are presented in order that workers less "handicapped by unwillingness or inability to correlate and fully utilize the data secured" (King 1939:284) may have access to them.

INSTRUMENTATION

The environmental factors, soil temperature, air temperature, relative humidity, wind, and evaporation stress were studied in each of the three stations. Precipitation was measured in a rain gauge at the true prairie station (Station 1). Light intensity (Table 14) was measured in foot candles at the surface of the soil in each station. This admittedly inadequate information on light was secured on July 1, 1938 between 11:30 A.M. and 12:30 P.M., at which time the sky was entirely clear; readings were taken with a Weston photometer at intervals of 1 meter over a 9 meter random transect in each station. Hygrothermographs were in operation in Stations 1 and 3 from the time these stations were established until the end of the period of study, and in Station 2 from August 12 to November 4, 1939. Station 3 was equipped with a soil-air thermograph from January 4, 1938 to April 29, 1939. Only air temperature was recorded in Station 2 from April 29 to August 12, 1939. Soil temperature was recorded by soil thermograph in Station 1 from November 2, 1937 to November 5, 1938 and in Station 3 from January 4, 1937 to February 11, 1938. Three-cup anemometers recorded total miles of wind in Stations 1 and 3, while Station 2 was equipped with a four-cup anemometer.

Livingston cylindrical porous cup atmometers with non-absorbing mountings were operated in duplicate in all stations from June 20 to September 12, 1938. These atmometers were so placed in the herb stratum that the evaporating surface fell between 30 and 40 cms. above the soil surface, a level approximating one-half the height of the herb stratum, and the level through which passed the greater portion of the arc of the sweep net stroke; those in the shrub stratum of Station 3 were placed two meters above the ground. Anemometers were mounted with their cups at ½ meter above the surface of the ground, the hygrothermographs with their sensitive units at approximately 10 cm., and the soil thermograph sensitive units at 10 cm. beneath the soil surface. All of the recording instruments were housed in screened and ventilated wooden shelters.

It is to be noted that the inherent difficulties incurred by the use of instruments was apparently somewhat aggravated in the present instance by frequency of dust storms during the study. Such atmospheric conditions, while not particularly severe at any time, and often of local nature, made it impossible to keep recording instruments as free of disturbing elements as desired. It is my opinion that further inaccuracies in recorded meteorological data are introduced by the use of green shelterhouses; while green offers a desirable camouflage, shelters painted this color tend to absorb radiant energy, and, in spite of apparently adequate ventilation, thereby alter the conditions of temperature (and possibly relative humidity) to which the instrument is exposed, with respect to those in the surrounding vegetation. It is suggested that recording instruments in all studies in the field be housed in shelters painted *white* and equipped with a *double roof*.

Further difficulties were caused by crickets and spiders finding their way into certain of the shelters. Hygrothermograph hairs were eaten by crickets in two instances. The spiders spun webs in the sensitive units.

Drifting snow often completely filled the shelterhouses and covered wind gauges.

COLLECTIONS

The sweep net method of quantitative sampling was employed in the herb and shrub strata. Fifty uniform strokes of a sweep net measuring 30 cm. in circumference, with a 35 cm. handle, constituted a unit sweep collection at 0-75 cm. above the surface of the ground in the herb stratum of the true prairie subsere and tall grass stations. In the shrub station the average single stroke of the sweep net in the herb stratum was of necessity about two-thirds that in the more open vegetation; seventy-five strokes, therefore, formed a unit sweep collection here at 0-75 cm. above the surface of the ground. Ten strokes were taken as a unit collection at the 1-2 meter level in the shrub stratum, and these on the periphery of the shrubs. Invertebrate population values obtained in the shrub stratum were mutliplied by five to allow comparison with samples from the herb stratum. The impossibility of accurately establishing and maintaining a standard stroke of the sweep net in different types of vegetational complexes demands that the investigator must admit the probability of discrepancies in his findings. These inherent difficulties make desirable the securing of large numbers of samples. The fluctuations which invertebrate populations exhibit may, thereby, be more exactly traced.

Litter samples were taken with the enclosed quadrat, a 12x12 inch sheet iron box, open at the bottom, and equipped with a handle and a corked aperture on the closed top. After the instrument is placed quickly over the spot to be sampled, the edges are forced into the soil an inch or so. Ether is introduced through the hole in the top, which is then corked. After the litter inhabitants are sufficiently anesthetized, the litter is gathered by hand into a paper sack and removed to the laboratory for examination. The soil beneath the now bared area is removed to a depth of 4 inches (10 cm.) and placed in tin pails for transportation. In this study the soil was treated with sodium bicarbonate (1 heaping tablespoonful to 1 gallon of water) for 4 to 6 hours to partially break down the flocculation. Then it was put through a soil washer (Shelford 1929), an apparatus which is effective in securing only the larger forms in the soil, its successive screens measuring 2, 4, 8, and 16 meshes to the linear inch.

The square foot sample from the litter stratum, even when "used to an extent within the limitations of a single investigator" does not furnish desired information on species that may be noted as abundant on the surface of the soil (Fichter 1941). That the square foot sample appeared to fall below the minimal area requirements for the quantitative study of soil surface forms in spruce-fir forest has also been noted (Blake 1945). The alcohol pitfall, previously referred to as designed for the comparative study of the wandering, relatively swiftly moving, ground surface arthropod populations, secured continuous collections in each of the three stations while in use.

Environmental Studies

Precipitation records taken in Station 1 (Table 1) show a yearly total (March 28, 1938 to March 25, 1939) of 32.37 inches, 4.43 inches above the mean annual value of 27.94 given by Loveland (1920). The total rainfall figures for the estival periods of 1938 and 1939 are 8.71 and 8.82 inches, respectively. The prevernal seasons of the two years are at considerable variance, however, 8.64 inches of rain being recorded in that season of 1938, and only 2.9 inches in 1939 (Figs. 10, 12).

It is felt that precipitation values secured in this station during the winter months may have been somewhat high due to inaccuracies introduced by melting snow.

Air temperatures (Tables 2, 3, 4) during the period of the study appear to have maintained approximately normal values. The mean temperature in Station 1, as calculated from thermograph records, was 54.2°F., 1.2° in excess of the mean annual level of 53.0° for southeastern Nebraska. Means determined for the postclimax tall-grass and deciduous shrub stations still more closely approached the fifty year mean, being 53.5° and 53.6° respectively (Table 16).

The maximum air temperature value for the period, 112°F., was recorded by the thermograph in Station 1 as occurring during the two-week period ending August 15, 1938 (Table 2). As previously stated, it is possible that temperatures higher than the true air temperature may at times occur inside the instrument shelters. The lowest air temperature recorded during the study was –22.0°F., this level being reached in the tall grass station (2) during the

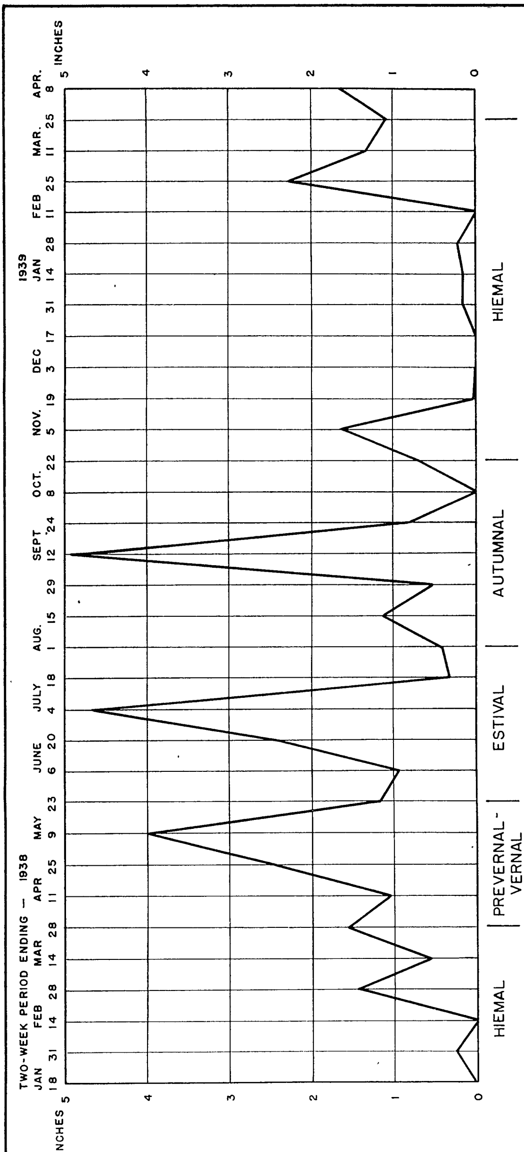


Fig. 10.—Amount of precipitation recorded by rain gauge in the prairie tract (Station 1), January 4, 1938 to April 8, 1939, expressed as total inches per two-week period.

two-week period ending January 31, 1938 (Table 3). The lowest fortnightly mean minimum and lowest fortnightly mean air temperature values, 16.4° and 19.0° respectively, also occurred in Station 2 during the two-week period ending February 25, 1939 (Table 3). The corresponding two-week period of the preceding year, that ending February 28, 1938, shows the fortnightly mean air temperature of 29.5° as the low for that winter (Fig. 11).

A single marked annual peak of fortnightly mean air temperature occurred early in the autumnal season of 1938, the two-week period ending August 15 producing a high mean of 83.7°F. in the true prairie subsere station (Fig. 11). A lesser though well defined temperature peak is shown for the same season, produced eight weeks later by the mean for the two-week period ending October 8. In 1939 an estival temperature peak constituted the annual peak, as

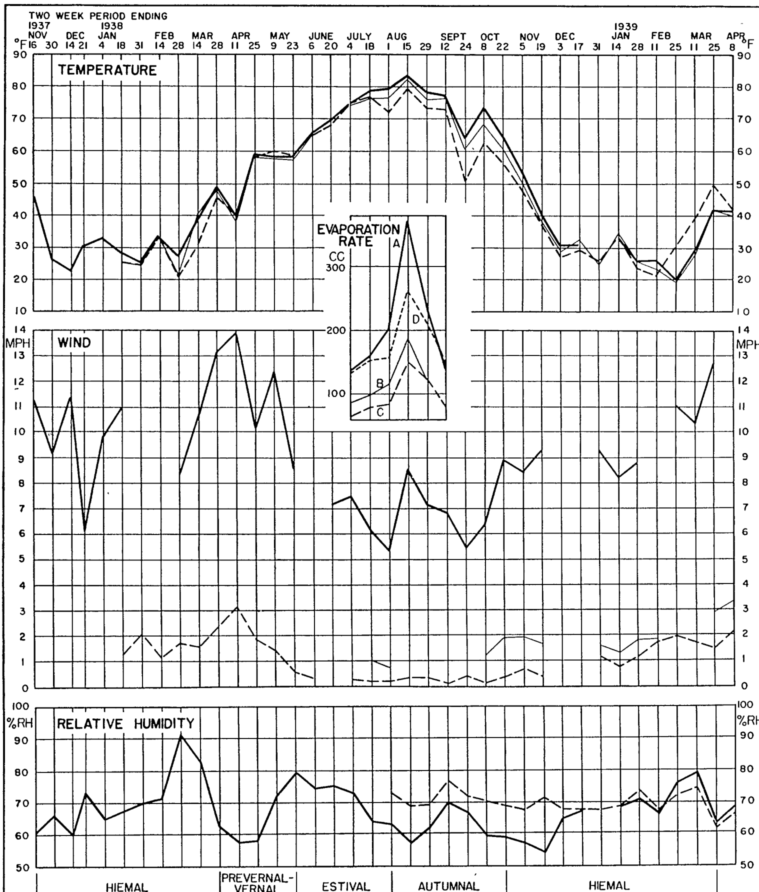


Fig. 11.—Physical factors of the atmosphere, November 2, 1937 to April 8, 1939. Discontinuous lines indicate mechanical failure of recording apparatus. *Temperature* (mean °F. per two-week period, in the herb stratum): Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line). *Evaporation rate* (loss in cubic centimeters from standardized atmometers per two-week period, June 20 to September 12, 1938): Subseral true prairie, herb stratum (line A); Postclimax tall grass, herb stratum (line B); Postclimax deciduous shrub: Herb stratum (line C); Shrub stratum (line D). *Wind* (mean MPH per two-week period at 0.5 meter): Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line). *Relative humidity* (mean per cent per two-week period in herb stratum): Subseral true prairie (solid line); Postclimax deciduous shrub (broken line).

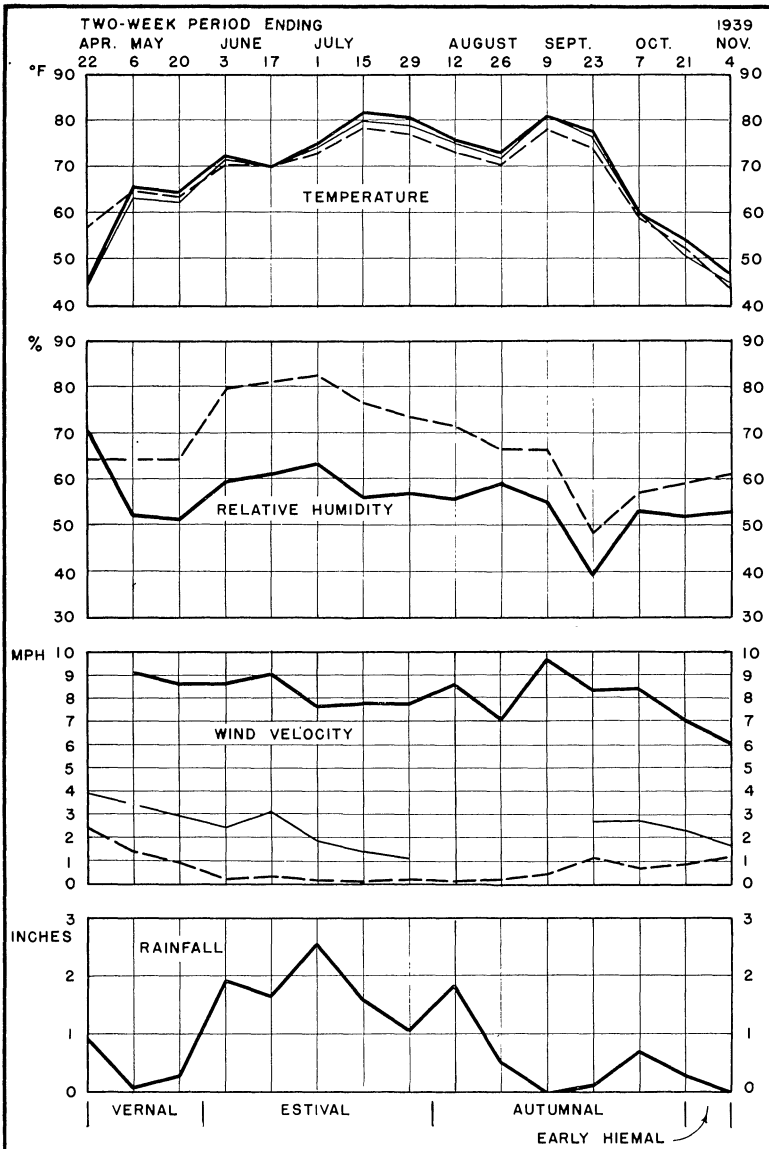


Fig. 12.—Physical factors of the atmosphere, April 8 to November 4, 1939. Discontinuous or omitted records indicate mechanical failures of recording apparatus. *Temperature, relative humidity, and wind velocity:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line, omitted in relative humidity graph); Postclimax deciduous shrub (broken line). *Rainfall:* Includes all precipitation as measured by rain gauge in the subseral true prairie station.

based on averages for two-week periods, coming a month earlier than the 1938 peak (Fig. 12). It is of special interest to note that in this second year of study a second fortnightly mean temperature peak again occurred, and again followed the major peak by eight weeks; in this instance, however, the second peak was of nearly the same magnitude as the first.

The mean relative humidity for Stations 1 and 3 as calculated from hygrograph records (Tables 5, 7) was 64.1% and 69.3%, respectively, (Table 16), the latter more closely approaching the "near 70 per cent" annual value previously quoted from Loveland (1920). Periodic means of relative humidity, of two-week intervals in this instance, usually showed slight though irregular variations from a comparatively uniform annual level. Records from this study (Station 1) show, however, a definite high for the two-week period ending February 28, 1938 followed by consistently decreasing values and a distinct low with means of 57.7% and 58.1% for the two-week periods ending April 11 and 25, respectively. This low is in turn followed by a definitely constant increase to a lesser peak of 75.3% for the two-week period ending June 20. While the curves of relative humidity show, for the most part, vacillations which in some cases are apparently not correlated with temperature differences, a condition reported by Blake (1926:47[411]) for pine-hemlock forest in Maine, it seems significant here that the one marked high of relative humidity is coincident with the 1938 low of temperature already noted, although they occurred in different stations (Fig. 11).

Also noteworthy are the concurrent fall in relative humidity and sharp rise in temperature in the spring of 1939; a marked autumnal low of relative humidity lags somewhat behind the autumnal air temperature peak (Fig. 12).

The annual mean wind velocity of 8.82 MPH for the upland true prairie subsere station was 2.18 below the Weather Bureau mean of 11.0 MPH for the Lincoln area. This variance is possibly accounted for by the differences in placement of anemometers relative to the surface of the earth and to vegetation. The anemometer in the subseral prairie station, being near the top of a hill and in comparatively low vegetation (drought-stricken grasses), was in a relatively exposed situation. The record from this instrument would thereby be expected to approach that of the Weather Bureau anemometer, about seven miles separating the two stations. Wind velocity was greatest during the latter half of March and the first half of April, a fortnightly mean of 13.92 MPH recorded between March 28 and April 11, 1938, in Station 1 forming the peak. The two-week period showing the lowest mean wind velocity in Station 1 is that ending August 1, 1938 (Table 8). The following fortnight produced an early autumnal peak, of considerably less magnitude than the prevernal-vernal high, but well defined and coincident with the high in air temperature for that year (Fig. 11). Similarly, an autumnal peak of mean wind velocity coincides with the autumnal air temperature peak of 1939 already discussed (Fig. 12).

Soil temperatures (fortnightly means, Tables 10, 11, 12; Fig. 14) show the usual lag behind air temperatures in the attainment and relative constancy of the hiemal low and the late-hiemal upturn in March of 1939. Those for the winter of 1937-38, however, show the late-hiemal rise beginning in mid-February, roughly a month earlier than in the following year. This suggests relatively higher insolation values in the winter of 1937-38 and the production of soil temperatures which show little or no lag behind air temperatures. This condition may have been a correlative of the "general recovery" of vegetation, "thickening of cover," and "decrease in amount of bare soil" reported for the growing season of 1938 by Weaver and Albertson (1944:403).

The lowest soil temperature that occurred during the period of the study was recorded in Station 1, when the 22.5°F. level was reached during the fortnight ending February 14, 1938. Station 1 also produced the maximum soil temperature during the study, a value of 90.0°F. This peak occurred in the two-week period ending August 29, 1938, exhibiting the usual lag behind air temperature, the 1938 peak of which was attained in the two-week interval preceding, i.e., ending August 15 (Fig. 11).

Of more interest in this problem than the general weather picture is the comparison of climatic factors in the three biotic communities investigated. Pertinent comparative data are summarized in Table 16 on the basis of seasons. The aerial factors of air temperature, wind velocity, evaporation rate, and relative humidity as determined in the three stations during the period of the seasonal and day-night studies (November 4, 1937 to April 8, 1939) are graphically presented in Fig. 11, and the factors of precipitation, soil moisture, and soil temperature for the same period in Figs. 10, 13 and 14, respectively. Comparative values of air temperature, relative humidity, rainfall, and wind velocity in the three stations during the period of the pitfall studies (April 8 to November 4, 1939) are given in Figure 12.

It will be noted that slight differences in seasonal means of air temperature occurred in the three stations, the autumnal means of Stations 1 and 3 showing the greatest seasonal variance, 3.3°F., the hiemal means of the three stations falling within the seasonal minimum range of 1.2°F. Perhaps of greater significance are the differences in seasonal mean ranges of air temperatures that occurred in these three situations. Here the greatest variance is shown in the prevernal-vernal season, the postclimax deciduous shrub station producing a mean range of 7.6° in excess of that in the subseral true prairie, while in the postclimax tall-grass station the annual mean range is 9.4° over that in the true prairie subsere station. Seasonal means of air temperature in the shrub station are somewhat below those in the other two stations in the estival and autumnal periods, slightly above the mean in the tall-grass station in the hiemal; but notably above the other two stations in the prevernal-vernal. Figures 11 and 12 show the air temperature of the three vegetational units maintaining closely approximate patterns as calculated and plotted on the basis of two-week periods.

Seasonal means of relative humidity in the shrub station are consistently above those in the less protected situations studied. The annual mean variation in relative humidity is also least here, a condition likewise exhibited in the estival and autumnal periods. The other two seasons, however, produce greater mean ranges of relative humidity in the shrub station than in the true prairie subsere station (humidity records for Station 2 secured for autumnal period only, Table 6). This is in apparent correlation with the air temperature values in these stations.

The most striking differences in measurable meteorological factors shown by the three vegetational units investigated in this study are those exhibited by the seasonal and yearly mean wind velocities (Table 16). Because of the direct and biologically important correlation of wind with evaporation stress, these differences are worthy of particular note. Air movement values were at all seasons greatest in the true prairie subsere station, with the postclimax deciduous shrub station consistently showing the lowest values. While air movement values in the tall grass station at all times fell between those for the other two stations, they were markedly closer to those for the shrub (Figs. 11, 12), the steeper gradient maintaining between the true prairie subsere and the tall grass. The lowest seasonal mean wind velocity for Station 3 appeared in the estival period; the greatest discrepancy relative to Station 1 occurred in the prevernal-vernal. The annual mean wind velocity determined for Station 3 was 10.7% that for Station 1 and 45.6% that for Station 2; these values attest the greater efficiency of the shrubs in checking air movement at all seasons. The topographic differences of the stations, i.e., northwest slope of Station 3 and southwest exposure of Station 2, may have introduced complicating compensations which can not be evaluated.

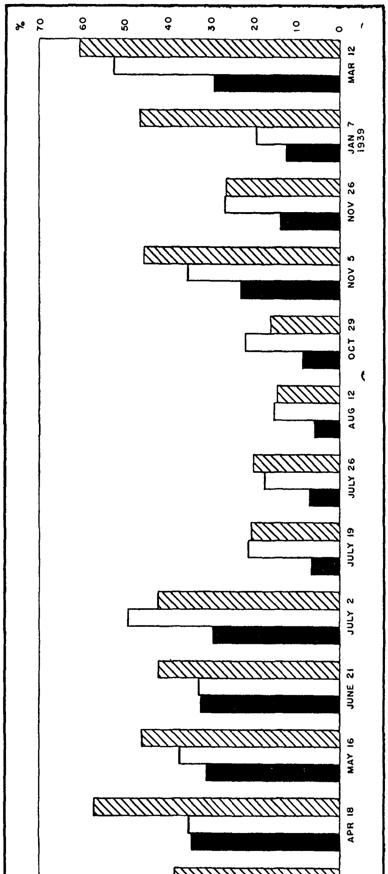
Sunset-sunrise readings on air movement were taken at various times during the estival and autumnal seasons of 1938. Total air movement values as low as 0.01 miles per night were recorded in the shrub station. During the same night 0.03 of a mile of wind was recorded in the tall-grass station, with 3.15 miles the total in the true prairie subsere station. Such a low, occurring between sunset of July 21 and sunrise of July 22, was an average of approximately 2 feet per hour. This may have been solely cold air drainage. Often on summer evenings, shortly after sunset, when the anemometer in the prairie subsere station would be motionless, the instrument in the shrub station would be turning slowly under the force of the cool air flowing down the ravine.

Probably no day passes when the prairie is without wind. Short periods of calm often occur during the day before approaching thunderstorms and their accompanying and often violent wind shifts.

Evaporation rates as measured by porous cup atmometers at 0.35 meters in the three situations show the expected gradient (Table 13). The estival mean for the tall-grass station is 58.8%, and that for the shrub station 46.5% of the mean for the true prairie subsere station. The rate at the 2 meter level in the shrub station (shrub stratum) approaches that of the prairie subsere station, being 86.2% of the latter. These meager data on evaporation rates show (Fig. 11) that a definite peak occurred during the two-week period ending August 15 in 1938, a time that showed one of the three recorded lows in relative humidity for that year, and, interestingly, corresponded with the period of highest mean temperature.

Heavy dews were common in the prairie during the summer of 1938. Only on nights when wind values were high was it possible to make sweep collections without the net becoming completely saturated with water.

Seasonal means of moisture content of the soil, expressed as per cent in excess of the hygroscopic coefficient, were consistently highest in the shrub station except in the autumnal period when that of the tall-grass station was slightly in excess of the shrub (Table 9; Fig. 13). Soil moisture values reached their lowest seasonal mean, 5.9%, in the true prairie subsere station during the autumnal season and the high of 47.3% in the shrub station during the prevernal-vernal period (Table 16).



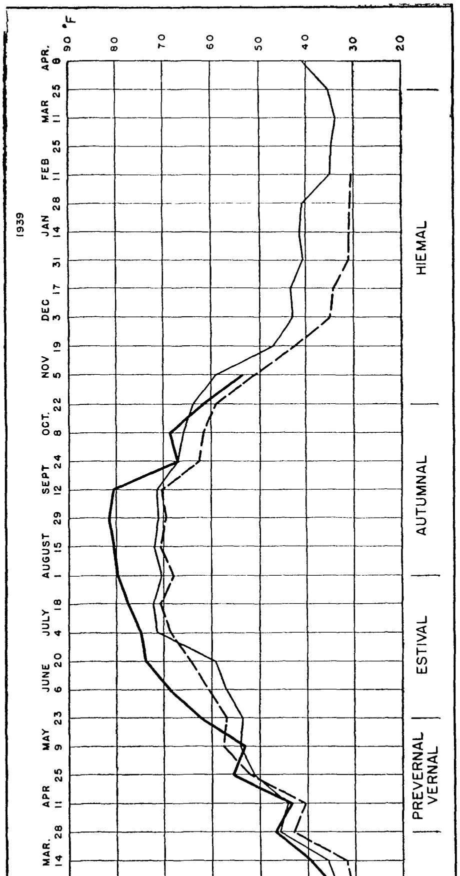


Fig. 13. (left).—Water content of soil, expressed as per cent in excess of the hygroscopic coefficient at a depth of 0 to 0.1 meter, on the dates indicated: Subseral true prairie (black bar); Postclimax tall grass (unshaded bar); Postclimax deciduous shrub (hatched bar).

Fig. 14 (right).—Temperature of the soil at 0.1 meter below the soil surface, expressed as mean °F. per two-week period, November 2, 1937 to April 8, 1939: Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

The estival mean soil temperature in Station 1 was 9.1°F. and 8.6° above that in Stations 2 and 3, respectively (Fig. 14). Station 3 produced the low mean soil temperature during the autumnal and hiemal periods but again exceeded Station 2 in the prevernal-vernal at which season it also exhibited its greatest mean range in soil temperature. These soil temperature phenomena are apparently in correlation with the amount of cover and the resultant decrease in insolation, the low annual mean of the shrub station further illustrating this feature. The fact that seasonal maximums in range of soil temperature are greater in the shrub station than in the tall-grass station for the hiemal and prevernal-vernal periods suggests that the vegetational cover of the tall-grass situation has a greater insulative effect upon the soil than that in the shrubs during these seasons. The situation is reversed, however, in the autumnal period, the differences in maximum range in soil temperature within these two stations then reaching 15.5°, while their maximum ranges are identical in the estival.

Inadequate but carefully secured information on light intensities in foot candles at the surface of the ground in the three stations (Table 14) shows that in full sunlight at midday the light intensity in the deciduous shrub station was approximately 20% of that in the subseral true prairie, while the intensity in the tall-grass area was slightly more than 30% of the intensity in the subseral true prairie (July 1, 1938).

On the basis of the environmental data gathered (albeit sometimes discontinuous or meager) and briefly reviewed here, general and comparative characterizations of the three habitats studied may be made in summary:

1. The true prairie subsere, the postclimax tall-grass, and the postclimax shrub stations showed, in the herb stratum, inconsistent and probably nonsignificant differences in mean air temperature values; the latter two stations showed, however, greater temperature ranges (maximum, mean maximum, and mean), with the widest ranges occurring in the tall-grass station, probably due to its southwest slope and consequent greater insolation.

2. Relative humidity was usually somewhat higher in the postclimax stations, although unexplained inversions of this gradient occurred.

3. The reduction of wind velocity at the herb level by the cover in both the shrub and the tall-grass station gave the most striking gradient of aerial factors.

4. Insolation was apparently greatest in the prairie subsere, least in the shrub station.

5. Evaporation stress, as measured in the herb stratum (late estival and early autumnal, 1938) was greatest in the true prairie subsere, least under the shrubs; evaporation rate values in the shrub stratum of the shrub station approached (once slightly exceeded) those recorded for the herb stratum of the prairie subsere. This environmental factor, being considered as a function (and index) of all other climatic factors to which terrestrial animals are subject (Blake 1926:48[412], Fichter 1939:197) furnished horizontal and vertical gradients which, in general, indicate the quantitative distribution of physical factors of the atmosphere through the three communities studied.

6. Correlative with the other environmental factors mentioned, available soil moisture was generally greatest in the shrub station, least in the prairie subsere.

Population Studies

Invertebrate animals in terrestrial habitats occupy places in time and space which are more or less inherent in the realization of their annual cycle of life processes. This ecological grouping, implemented by organic responses to conditions of the habitat in attempted fulfilment of the environmental needs of each species present, results in population structure. The differences in specific requirements, the changes in requirements of any given species as its life history unfolds, the responses to shifts in environmental optima, the motivations of innate behavior, the expressions of annuation and phenology—all these and probably many undiscovered forces—keep the structure of a community of active terrestrial invertebrates exceedingly fluid. Such a dynamic organization literally moves through time and space. This fluctuating chronological and spatial distribution is expressed in seasonal or aspect societies, horizontal differentiation and movement, and vertical groupings called stratal or layer societies which show both seasonal and diurnal changes, even in hibernation (Blake 1926:98[462]). These complex interrelationships of never-static forces and responses function to produce population phenomena which, albeit highly dynamic, are subject to both quantitative and qualitative analysis. The degree and fruitfulness of analysis depends, in part, upon cognizance of all environmental variables impinging upon the biota which is being subjected to examination. The known variables in any habitat are many; there are possibly as many unknown. Unfortunately, when the investigator enters a habitat to attempt his analysis of the animal community, he introduces another variable, a disturbing factor which he probably cannot measure; his presence and passing may alter the structure of the population in that given volume of space.

Despite the obvious overlaps of environmental factors and organic cycles, responses, and distributions, it is necessary to break down the time, the space, the forces, and the animal population into units suitable for measurement, analysis, and expression. This breakdown is an attempt to harmonize natural sequences and groupings with the expediencies of investigation and report. Any expression of the findings relative to one unit will, however, in some degree point out certain conditions in some or all of the other units of the breakdown, so integrated are the measurable phenomena. Thus, remarks on aspection will indicate some feature of annuation, certain stratal relationships, and horizontal groupings and re-groupings. Reports on stratification show seasonal and daily succession and *vice versa*. It is intended that the descriptive sections that follow, regardless of their headings, will present a generalized picture of the animal ecology of drought disturbed true prairie and its postclimax inclusions.

Considering, briefly, certain general characteristics of the invertebrate fauna of the three contacting vegetational complexes as studied from November 2, 1937, to April 8, 1939, it is evident that Homoptera constituted the numerically superior order of invertebrates studied, ranking first in the herb stratum of the true prairie subsere (Station 1), second in that stratum in the postclimax areas of tall grasses (Station 2) and deciduous shrub (Station 3), and third in the shrub stratum of the latter. The order Diptera ranked second numerically in the area investigated, being the most abundant order in the tall-grass and shrub stations, while ranking fourth in the true prairie. The third most abundant order taken in sweep samples was Coleoptera, ranking second in the subseral true prairie, sixth in the tall grass and in the herb stratum of the shrub, and fourth in the shrub stratum of the latter station. Ants of the family Formicidae showed population values which ranked them in fourth place in the sweep collections, being third most abundant in the herb stratum of the shrub station, fifth in the true prairie, seventh in the tall grass, and fifth in the shrub stratum. In fifth place among all groups taken throughout all stations was the Orthoptera, including families Phasmidae, Acrididae, Tettigoniidae, and Gryllidae. Orthopterans ranked third in the herb population of true prairie and postclimax tall grass and eighth in both herb and shrub stratum of the shrub station. Bees and wasps, here considered as a group, were seventh in numerical importance in Station 1 herb collections, fifth in these collections in both Stations 2 and 3, but second in importance only to the Diptera in the shrub stratum. In the herb stratum of subseral true prairie, tall grass, and deciduous shrub, the order Hemiptera ranked eighth, fourth, and fourth, respectively, and occupied ninth place in the shrub stratum. Eighth in the series of major groups was Araneida, spiders ranking fifth in Station 1 herb, eighth in Station 2 herb, and seventh in both herb and shrub stratum of Station 3.

It is seen that Homoptera and Coleoptera were the numerically prominent groups in the herb stratum of subseral true prairie, stratal prevalents and subprevalents being in these two orders. Among the tall grasses, Orthoptera, Hemiptera, and Diptera were largely contributory to population trends, with ants assuming a brief, minor importance; prevalents here were a grasshopper and a plant bug, the subprevalent an ant. Under the shrubs Homoptera and Diptera combined to furnish the majority numbers; a leafhopper and an aphid assumed prevalent rank; two species of flies became subprevalent. It should be noted here that although large numbers of flies were taken in the postclimax shrub station, the number of species remained so high that prevalent values were never attained by any single species.

Comparing the findings for the herb stratum in the true prairie subsere with those for the same stratum in postclimax tall grass and postclimax deciduous shrub (Table 22; Figs. 15, 19, 23, 25), it is immediately apparent that (1) the total population curves for the two grassland stations are generally similar, but that the tall-grass population maintained a more uniform population level, especially as regards the major (early estival) peak, and (2) the total population curve for the shrub station is remarkably different than for either of the prairie stations; the extremely high autumnal peak in the herb stratum of the shrub community is one of the most striking features reported here. Relatively uniform throughout the estival and first half of the autumnal aspect, with a tendency to build up in the early autumn, it shows a marked decrease in late September, followed by the sudden and dramatic upsurge to the short-lived October high.

The two grassland habitats showed some similarities in ground surface population patterns (Figs. 22, 23). There were two peaks of total population (estival and autumnal) albeit not coincident; the autumnal peak was the greater in the tall-grass, the estival the greater in subseral true prairie. Ants and beetles furnished the numerical majorities in both stations, the prevalents and subprevalents being members of these two groups.

The ground surface population in the shrub station also showed two peaks, but the second and autumnal high was nearly as striking as that for the herb stratum in the same station. Beetles and ants again figured to some extent in shaping the total population pattern.

ASPECTION

It has been shown (Carpenter 1937) that species of insects which hibernate as adults or late instars are active in the early spring "in the habitat where they spend the winter." Sweep collections made in the herb stratum of true prairie subsere, of postclimax tall grass, and of postclimax deciduous shrub on November 19, 1938, January 2 and 7, February 6, and March 12, 18 and 20, 1939, showed over-wintering insects active upon the dry winter vegetation on days when the maximum temperatures ranged from 43.0°F. to 68.0°F. McClure (1938:507) has reported that aerial collecting done "by means of a net attached to the front fender of an automobile" driven many times over a specified route near Danville, Illinois, during the period November 1, 1934 to May 1, 1935, took insects "when the temperature was 40°F. or above." General field observations on March 7 and 21, 1938, and on March 12, 1939, with maximum day temperatures of 53.0°, 82.5° and 61.0°, respectively, in the prairie, noted arthropods active in the air and on the vegetation, especially on south slopes and ravines with southward drainage. Flies, microhymenoptera, true bugs, grasshoppers, and beetles were in evidence, with many spiders

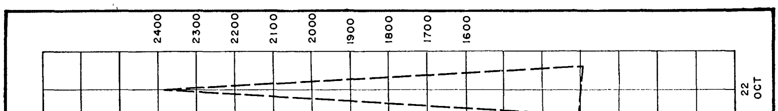


Fig. 15.—Trends of total populations of invertebrates (arthropods) in all aerial strata studied, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. *Herb stratum:* Subseral true prairie (line A); Postclimax tall grass (line B); Postclimax deciduous shrub (line C). *Shrub stratum:* Postclimax deciduous shrub (line D). (No collections in the shrub station during the two-week period ending September 12—see Tables 22 and 23.)

active on the surface of the ground. On the last date soil inhabiting larvae and earthworms were active at the surface of the soil. Dowdy (1944) found that soil invertebrates were influenced to move deeper into the soil in the fall at a temperature usually about 42°F. and that this same temperature caused their upward movement in the spring. Insects and spiders, finding hibernacula in the litter and the crowns of bunch grasses, such as the bluestems (Whelan 1927), and quickly responding to relatively brief daily peaks of air temperature as low as 43.0°, provide intervals of invertebrate activity above the surface of the soil at a time when plant life "except for fruits and seeds, is found almost entirely within the protecting soil and scarcely at all above it" (Weaver and Fitzpatrick 1934), and that in a dormant condition. Thus, with the advance of temperature values in the late hiemal period, characteristic prevernal activity begins before "the reappearance of young shoots from the awakening perennials" which has been characterized by Weaver and Fitzpatrick (1934) as the "only" organic process with which the new season is initiated. The prevernal aspect is first expressed faunistically.

Carpenter (1937), studying biotic communities in a large cattle range in central Oklahoma which was selected "as representative of the south-central mixed-grass prairies," found that "aspection . . . began earlier in the year in lower and sloping areas than in the high prairie, but proceeded more rapidly in the latter once activity had begun. Prevernal activity in the wooded ravines began as early as March 10 (1934) while the prairie itself showed little change in aspect until three weeks alter." Some agreement with this pattern of invertebrate activity is shown in the upland true prairie subsere and adjacent postclimax areas in eastern Nebraska. Sample collections made in the herb stratum during the two-week period ending March 28, 1938, showed population values of the shrub station to be in excess of those in the tall-grass and true prairie (Fig. 15), with values in the latter two being nearly identical. Illustrating the close correlation of temperature patterns and aspection as expressed by the invertebrate fauna, the shrub and prairie subsere curves of invertebrate populations show a distinct decrease in the two-week period following this initial rise, while the curve for the tall-grass station remains nearly constant. It will be noted (Fig. 11) that temperature curves show a decided low for this period, following which both temperature and invertebrate population curves tend consistently upward (Fig. 15). Greater protection from the high winds recorded during the two-week period ending April 11 (Fig. 11) in the tall-grass station, due to topographic position in relation to wind direction, may account for the maintenance of population levels in that station. Carpenter also noted the effect of protection from winds as a factor in initiating aspection in the prevernal period.

With the advent of the flowering period of *Prunus americanus* in late April and early May, the population values for the shrub stratum in the postclimax deciduous shrub station suddenly climb from nearly nil to the yearly high for that stratum (Fig. 15). As suddenly, near the middle of May, this population falls off, then renews its ascent with the initiation of the estival aspect and the period of anthesis of *Cornus stolonifera* to a not too distinct tertiary annual peak for the two-week period ending June 20.

Coincident with this poorly defined early estival peak in the shrub stratum are (1) the second of the four minor peaks of the herb stratum in the same vegetational complex and (2) the yearly high for the true prairie subsere invertebrate population. This latter high is apparently correlated with the period of anthesis of most of the true prairie plants; Steiger (1934) states that the "high prairie has the greatest number of species flowering in June." At this time the population of the herb stratum of the prairie subsere exceeded that in the same stratum of the postclimax tall grass as well as the populations in both herb and shrub stratum of the postclimax shrub area. The population value for the tall grass had at this time markedly decreased, possibly indicating a movement of insect forms out of this situation where maximum flower production was to occur later (Steiger 1934) into the true prairie subsere where the maximum of anthesis had already been reached—a movement that may have in part accounted for the estival peak in the prairie subsere.

The most notable features regarding total populations of invertebrates above the ground surface in the three stations studied following the first week of July (1938) are (1) the secondary peak of abundance in the shrub stratum of Station 3 during the last two weeks of July, followed by a rather rapid decline to practically nil near the end of September, (2) the extremely high population values exhibited by the herb stratum in the deciduous shrub area during the middle of October (late autumnal period), and (3) the marked decline of populations in all aerial (epiphytic) strata subsequent thereto toward the low values characteristic of the hiemal. The almost total disappearance of invertebrates from the shrub stratum coincides with and apparently results from the unusually early loss of leaves by *Prunus, Cornus* and other shrubs already mentioned. Population curves for all aerial strata considered show coincident and definite declines of various magnitudes for the two-week period ending August 15, 1938, the period marked by (1) the estival-autumnal temperature peak, (2) a recognizable low in fortnightly mean values of relative humidity, (3) a distinct peak of evaporation rate, and (4) a minor high in wind velocity values (Fig. 11). Epiphytic strata in the shrub and tall-grass stations showed gains in the invertebrate populations in the following two-week period whereas the population in the herb stratum of the true prairie subsere continued its decline. Haying operations beginning on August 13 probably accounted for the latter decrease, since sweep collections were made in both mowed and unmowed areas. During the next three to four weeks the herb stratum populations in the tall-grass and shrub communities again declined while that of the true prairie subsere tended upward, possibly in response to renewed growth of grasses following mowing. Subsequent to this time (September 4, 1938) the true prairie subsere curve tends downward to the hiemal low, the tall grass shows a late autumnal peak, and the curve that represents population values in the herb stratum of the shrub station soars to the remarkable autumnal high of 2,382 specimens per unit collection, a value 315% that of the estival high of the herb stratum in true prairie subsere (second highest peak) as determined in this study. This autumnal high thence gives way rapidly to the low hiemal values.

The quantitative relationships of litter (Table 24) and soil (Table 25) populations to aerial populations are illustrated in Figure 16 on a seasonal basis. It is principally notable that litter values are high during seasons when aerial populations are low, i.e., hiemal and prevernal-vernal, and low when aerial activity is in the ascendancy. Pearse (1946) has stated that in decidu-

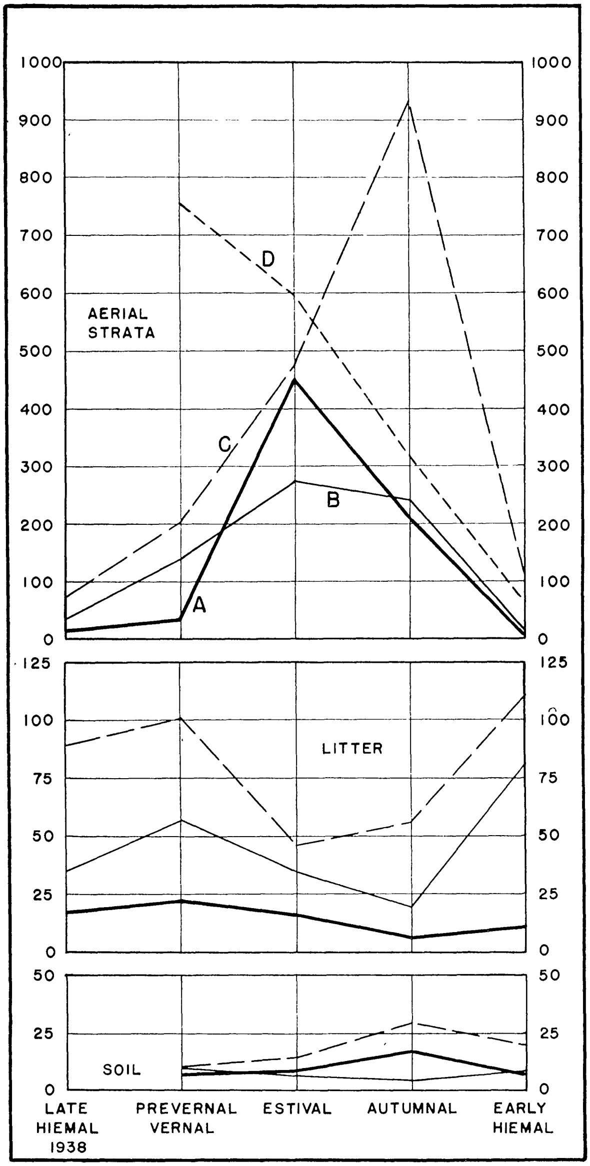


Fig. 16.—Seasonal trends of invertebrate populations expressed as average numbers per unit collection per seasonal period, late hiemal to early hiemal inclusive, 1938. *Aerial strata:* Herb stratum of subseral true prarie (line A); Herb stratum of postclimax tall grass (line B); Herb stratum of postclimax deciduous shrub (line C); Shrub stratum of postclimax deciduous shrub (line D). *Litter and soil strata:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

ous forest "soil moisture appeared to be more effective in controlling numbers of animals present than variation in temperature," a condition also described by Blake (1931:526).

Studies by means of alcohol pitfalls on the invertebrates inhabiting the surface of the ground, carried on between April 8 and November 4, 1939, show seasonal population curves (Table 26; Fig. 18) closely comparable to those of epiphytic strata just reviewed. Here, however, the population peak in Station 1 occurred during the first half of July (Fig. 17) rather than during mid-June as in the herb stratum in the preceding year, the Station 2 autumnal peak was two weeks earlier than in the herb stratum of that station in 1938, and the Station 3 autumnal peak occurred during early September rather than late October, the latter period being marked by the outstanding shrub station high previously noted. These discrepancies were possibly, if not probably, due to unmeasured differences in the habitats under the influence of aberrant climatic conditions, principally drought.

The most striking single feature regarding all total populations so far considered is the high autumnal peak in the postclimax deciduous shrub community.

Seasonal averages of invertebrates per unit collection in the herb stratum (Table 23; Fig. 16) show (1) a distinct estival high in the subseral true prairie station, (2) a much less marked estival high in the tall-grass station with an autumnal peak of slightly less value, (3) the strikingly high autumnal peak in the deciduous shrub area, and (4) in the shrub stratum of this station the suddenly attained prevernal-vernal peak of abundance.

Collection averages of Homoptera in the herb stratum of true prairie subsere, i.e., Station 1 and substations, show the advent of this order in considerable numbers during the two-week period ending May 9 (1938), the middle of the prevernal-vernal period (Table 22). Two peaks of abundance are attained, a mid-estival peak during the two-week period ending June 20, and a lesser mid-autumnal peak during the twelve-day period ending September 12 (Fig. 19). The Homoptera do not show a definite peak of abundance in the postclimax tall grass (Station 2 and substation) although prevernal-vernal activity appears closely comparable to that in Station 1. In the postclimax deciduous shrub complex (Station 3 and substations) two well defined peaks of abundance occurred in the herb stratum, the first during the two-week period ending August 29, the second between October 8 and 22 (Fig. 25). In this station Homoptera appeared in the sweeps about two weeks earlier

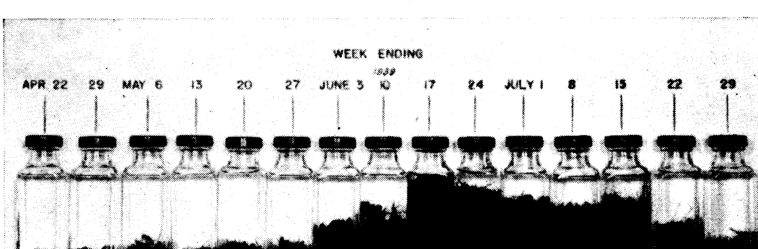


Fig. 17.—Bottles of invertebrates taken by the alcohol pitfall in the true prairie subsere station showing the early estival increase in numbers and volume, with a subsequent decrease, the peak in volume preceding the peak in numbers by two weeks.

than in the other communiites studied, showing, in fact, recognizable epiphytic population values during relatively warm winter days. In the shrub stratum of the shrub station (Table 23) prevernal activity of Homoptera began during the two weeks ending April 25, a population high being attained near the close of the estival period, July 18 to August 1 (Fig. 27). Homoptera were taken in very small numbers in the litter samples of all stations, were not in

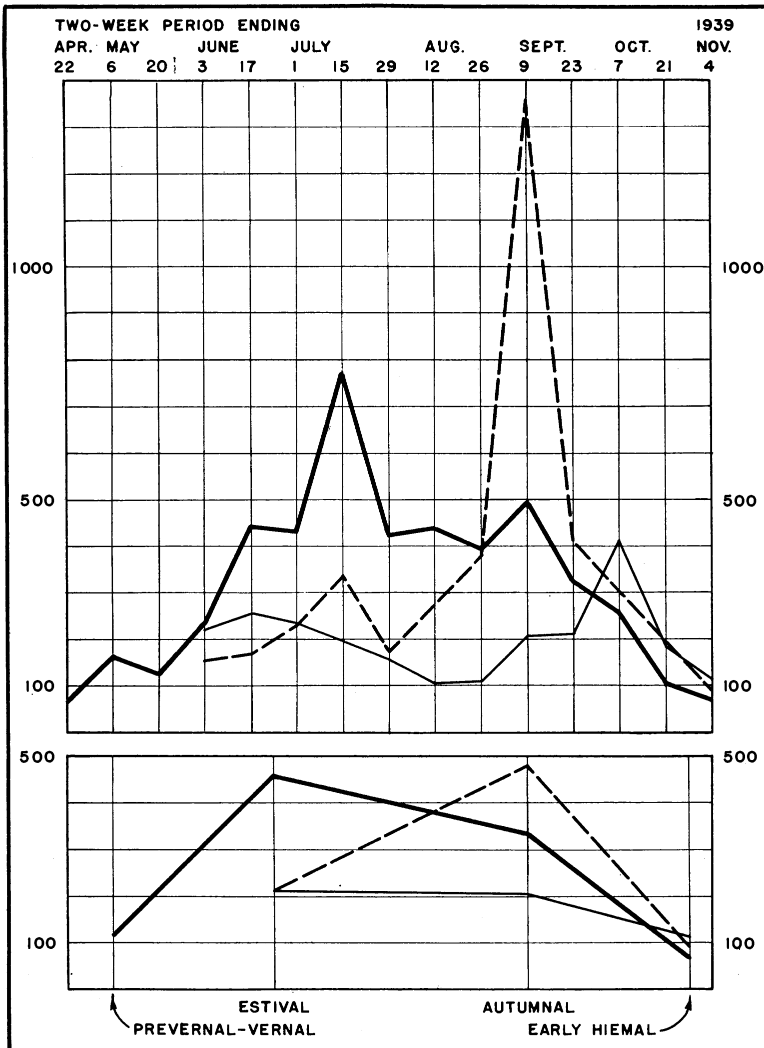


Fig. 18.—Population trends of invertebrates in the soil surface stratum, as indicated by alcohol pitfall collections, expressed as total numbers taken per two-week period (upper section) and as seasonal averages per unit collection (lower section). *Total population:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

any case retrieved by the soil washer, and were not considered as soil surface forms in the pitfall studies.

Diptera showed year-round activity (Table 22). Sweep collections made in the herb stratum on winter days when the temperature was at 43.0°F. or

Fig. 19.—Population trends of invertebrates (arthropods) in the herb stratum of subseral true prairie, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (line A); Homoptera: leafhoppers, etc. (line B); *Balclutha abdominalis,* a leafhopper (line C); *Delphacodes* sp., a leafhopper (line D).

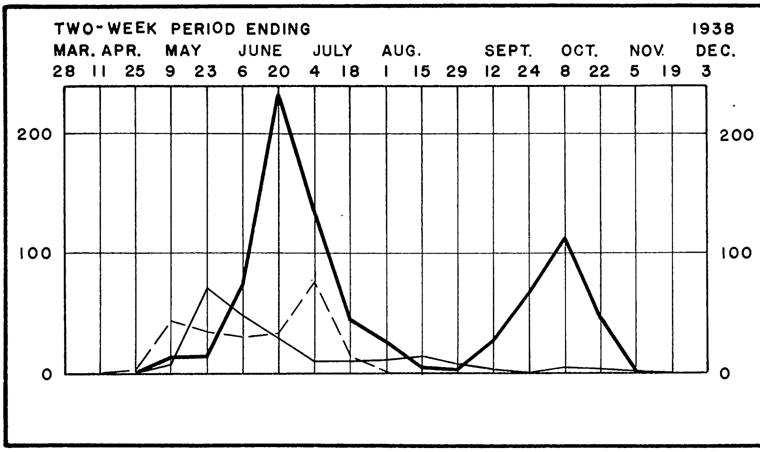


Fig. 20.—Population trends of *Balclutha abdominalis,* a cicadellid leafhopper, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. *Herb stratum:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

above, usually secured flies. Their numbers consequently built up rather suddenly in the prevernal-vernal aspect, producing an early estival peak in the herb community of true prairie subsere during the fortnight ending June 20, with a second and lesser mid-autumnal peak in this situation during the first half of September. Three poorly defined peaks are shown by flies in the herb stratum of the postclimax tall grass. In the postclimax shrub area Diptera presented important quantitative values, showing a more or less distinct high during the two weeks ending July 18 with a marked low late in September, thence producing a population peak which surpassed that of all other orders in all other communities studied, a population value largely responsible for the important autumnal peak of total populations already pointed out (Fig. 25). Flies were abundant among the flowers of *Prunus,* producing a prevernal-vernal high for the order in the shrub stratum during the two weeks ending May 9 (Fig. 27). Two lesser estival peaks appeared in mid-June and late in July. No flies were taken in the shrub stratum in September or in March. Diptera were rarely found in litter collections, none at all in soil samples, and are not here included in the pitfall studies.

Beetles (Table 22) played little or no part in the prevernal-vernal herb society in true prairie subsere, but with the advent of the estival season near the end of May climbed rapidly to a marked population high during the two-week period ending June 20 (Fig. 21). A second and very minor late autumnal peak appeared between October 8 and 22. Prevernal-vernal activity of Coleoptera in the herb stratum began considerably earlier in the ravine stations (2 and 3). Early estival highs appeared in these stations coinciding with that in Station 1, although being much less distinct. An autumnal high occurred in the latter half of August. In the shrub station an early estival peak was also produced, followed by a low and a second high of nearly equal magnitude during the two weeks ending July 18. In the shrub stratum of this station (Table 23) the year's peak of beetle population came at the time of anthesis of the wild plum during the fortnight ending April 25, maintaining nearly equal values until the end of the blossoming period at the advent of the estival aspect (Fig. 27). Conforming to the general population picture,

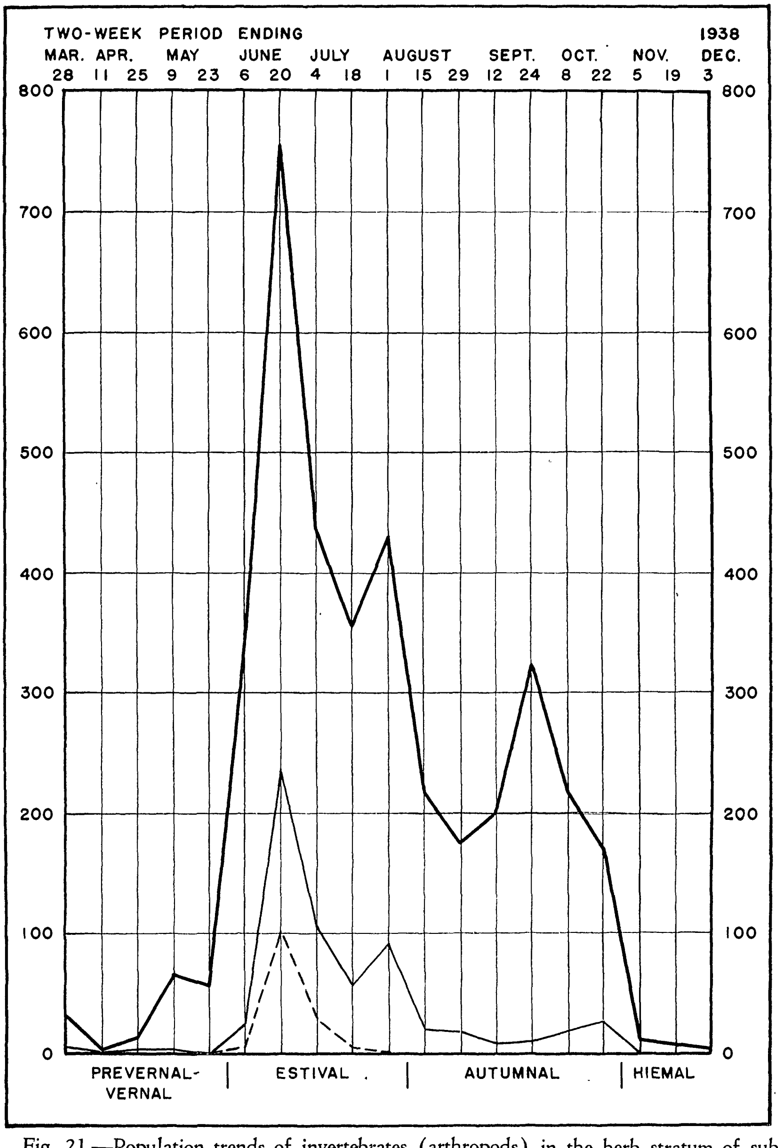


Fig. 21.—Population trends of invertebrates (arthropods) in the herb stratum of subseral true prairie, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (heavy solid line); Coleoptera: beetles (light solid line); *Pachybrachys litigiosus,* a chrysomellid beetle (broken line).

however, the beetles produced a second though lesser peak during the two weeks ending June 20. No beetles were taken in the shrub stratum in September. Beetles occurred in important numbers in the pitfall collections in all three stations. More numerous in these collections of ground surface forms in the shrub site than in the other stations, the group here reached its maximum of abundance in early autumn, July 29 to August 12, 1939 (Fig. 28). In the true prairie subsere where they were next most abundant the beetles showed a marked population peak in the ground surface stratum during the fortnight ending June 17 (Fig. 22) at which early estival period they also reached their greatest peak of abundance in the tall-grass station (Fig. 24).

Ants (Table 22) appeared in the herb sweeps in the true prairie subsere

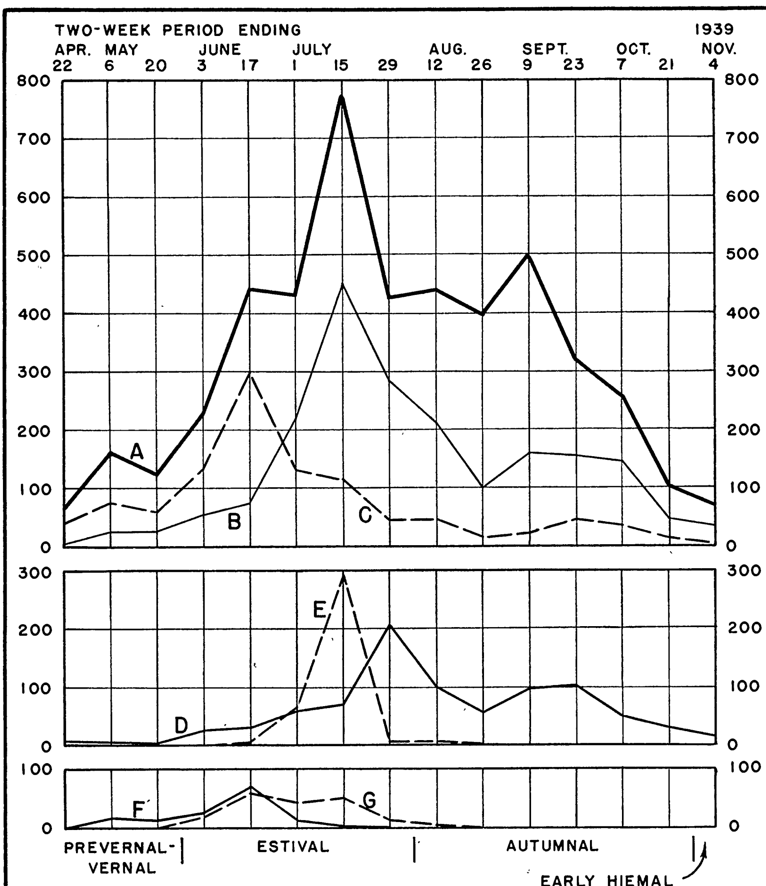


Fig. 22.—Population trends of soil surface invertebrates in subseral true prairie as indicated by alcohol pitfall collections expressed in total numbers taken per two-week period from April 8 to November 4, 1939. Total population (line A); Hymenoptera: ants and velvet ants (line B); Coleoptera: beetles (line C); *Crematogaster lineolata,* an ant (line D); *Dorymyrmex pyramicus,* an ant (line E); *Amara* sp., a carabid beetle (line F); *Eleodes opaca,* a tenebrionid beetle (line G).

and postclimax tall grass late in April and about two weeks earlier in that stratum in the shrub area. Significant peaks appeared in Station 2 in late August (Fig. 23) and in Station 3 in late October. In the shrub stratum (Table 23) ants produced a prevernal-vernal peak in late April and early May and a second peak during the fortnight ending June 6. The reasons for these peaks are not clear. Ants showed relatively important values in litter collections with prevernal-vernal highs occurring in Stations 1 and 2, and a late hiemal-perevernal-vernal high in Station 3. It must be remembered, however, that "the population of the ground is in patches and not uniform" (Shackleford and Brown 1929), and that all data based on litter samples is, therefore, subject to distortion. Unimportant numbers of ants occurred in soil samples. In the pitfall studies more ants were taken than were specimens of any other major group of invertebrates, the greatest number in the shrub station collections. In the true prairie subsere a definite peak of abundance occurred during a two-week period ending July 15 (Fig. 22), sharp peaks not appearing in the other two stations until the two weeks ending October 7 (Figs. 24 and 28).

Certain of the grasshoppers, wintering over in late instars, were usually in evidence on warm winter days. These species, however, appeared to be much less abundant than those which passed the hiemal period in the egg stage, thence emerging as small nymphs with the coming of spring. Significant numbers of young grasshoppers (family Acrididae) appeared simultaneously in all stations during the fortnight ending May 9 (Table 22). Newly hatched walking sticks (family Phasmidae) appeared in the upland true prairie subsere on May 16. The orthopteran population, composed chiefly of these two families until mid-August, with the tettigoniids assuming important numbers from mid-June till the advent of winter, produced early estival and late estival peaks in the herb stratum of the prairie subsere, a fairly well defined late vernal peak and a secondary autumnal peak in the tall-grass station (Fig. 23), and a single, weakly expressed, late vernal high in the shrub station. Orthopterans were most abundant in the shrub stratum during the two weeks ending July 18 (Table 23). Significant numbers of orthopterans were not taken in litter or soil samples, and takes in the pitfalls were relatively low though consistent. Because of the saltatory abilities of grasshoppers the takes in sweep net collections are undoubtedly subject to discrepancies which alter the true picture of the order's population values.

The winged forms of the order Hymenoptera are often active on warm winter days in protected situations. In this study they appeared in large numbers in the shrub station in late April and early May, in the tall-grass station about two weeks later, and in the upland true prairie subsere station during the two weeks ending June 6, at which time their yearly peaks for that society were reached (Table 22). Bees and wasps produced no observable peak in the Station 2 herb stratum, but exhibited a relatively enormous late autumnal population in that stratum in the shrub station during the two weeks ending October 22. Two marked peaks of abundance of winged Hymenoptera appear in the shrub stratum (Table 23), the first from April 25 to May 9, the second and somewhat higher from July 4 to 18 (Fig. 27), these highs corresponding to the periods of blossoming of *Prunus* and *Cornus* respectively, giving quantitative expression to the already well known affinities of these insects for flowers.

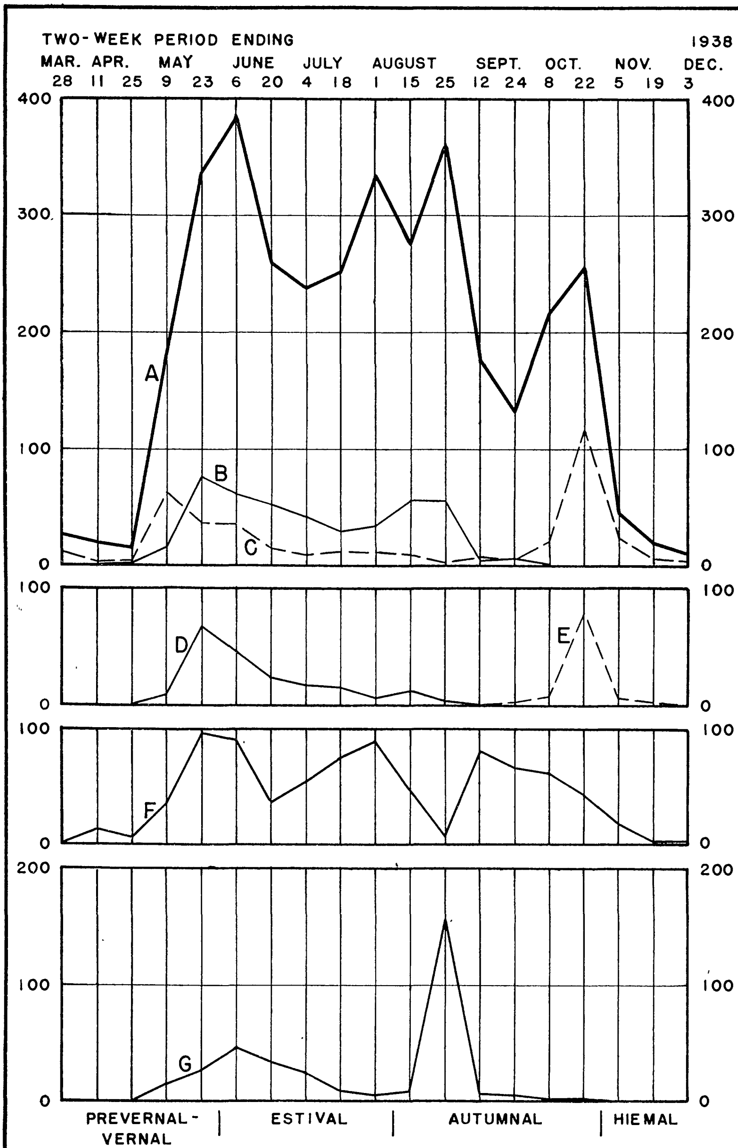


Fig. 23.—Population trends of invertebrates in the herb stratum of postclimax tall grass (ravine site), expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (line A); Orthoptera: grasshoppers (line B); Hemiptera: bugs (line C); *Melanoplus bivittatus*, a grasshopper (line D); *Lygus pratensis*, a bug (line E); Diptera: flies (line F); Formicidae: ants (line G). The early autumnal peak in ant numbers was forced by a single winged species, *Pheidole bicarinata* (see Table 28).

The order Hemiptera has often been pointed out as importantly abundant in the true prairie. Clements and Shelford (1939) state that "an abundance of Hemiptera characterizes the prairie." In this study these bugs (Tables 22, 23) were usually in evidence, although not in numbers which would conform to such a characterization. Sharply defined high peaks of abundance appeared in the herb sweeps in the tall-grass (Fig. 23) and shrub stations during the

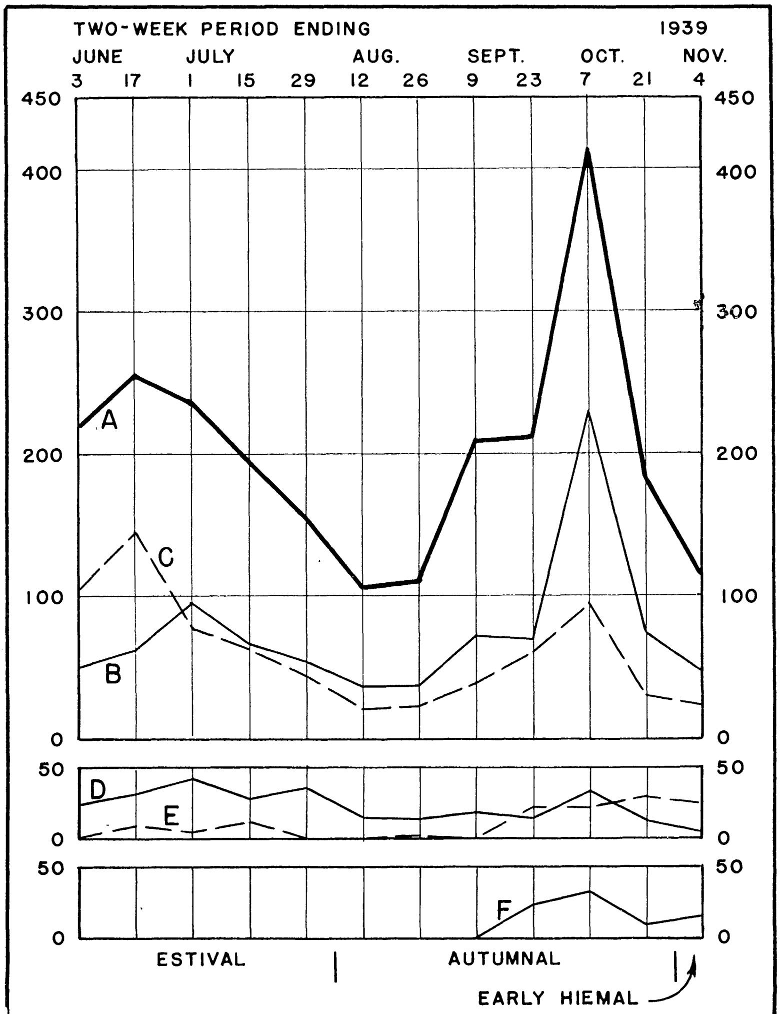


Fig. 24.—Population trends of invertebrates of the soil surface stratum in postclimax tall grass (ravine site) as indicated by alcohol pitfall collections and expressed in total numbers taken per two-week period, May 20 to November 4, 1939. Total population (line A); Hymenoptera: ants and velvet ants (line B); Coleoptera: beetles (line C); *Crematogaster lineolata,* an ant (line D); *Prenolepis imparis,* an ant (line E); *Agonoderus pallipes,* a carabid beetle (line F).

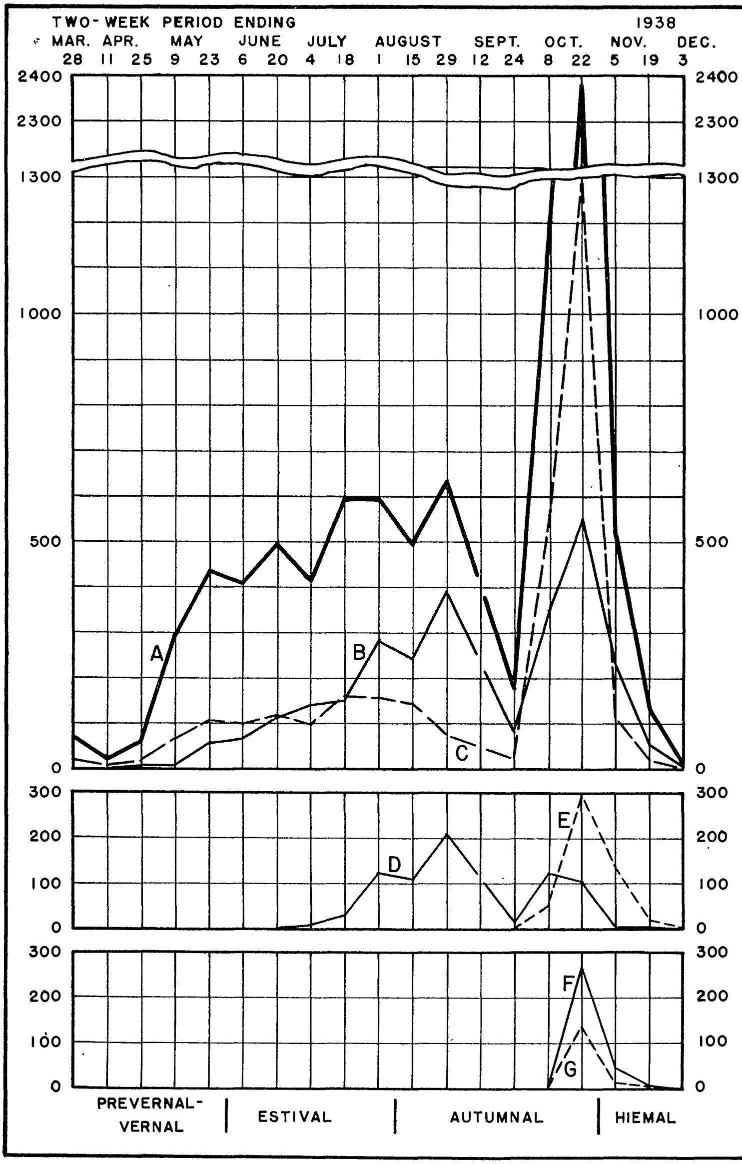


Fig. 25.—Population trends of invertebrates in the herb stratum of postclimax deciduous shrub (ravine site), expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (line A); Homoptera: leaf hoppers, etc. (line B); Diptera: flies (line C); *Dikraneura abnormis*, a leafhopper (line D); *Anoecia graminis*, an aphid (line E); *Oscinella coxendix*, a chloropid fly (line F); *Elachiptera costata*, a chloropid fly (line G). (No collections during the two-week period ending September 12—see Table 22.)

two-week period ending October 22, followed by a marked increase of bugs in the litter samples in the fortnight following. Here is presented probably the most convincing example offered by this study of the horizontal movement of grassland insects into forest margin conditions and their subsequent descent

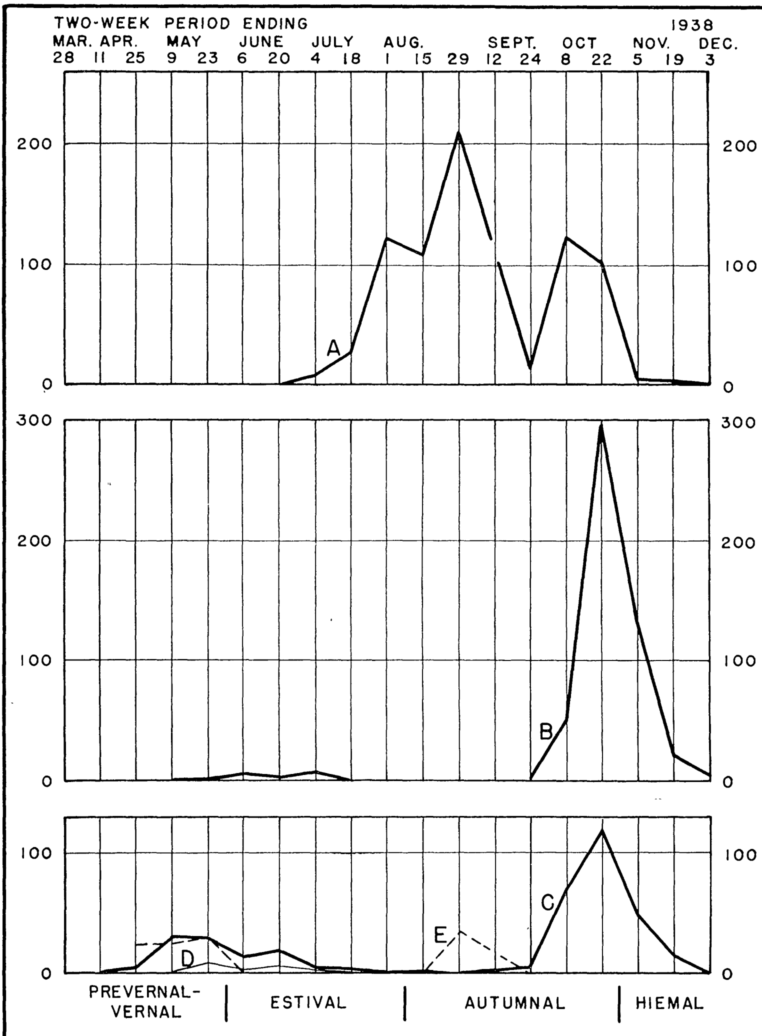


Fig. 26.—Population trends of three prevalent species, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. *Dikraneura abnormis,* a leafhopper, in the herb stratum of the postclimax shrub station (line A); *Anoecia graminis,* an aphid, in the herb stratum of the postclimax shrub station (line B); *Prenolepis imparis,* an ant: In the herb stratum of the postclimax shrub station (line C), in the herb stratum of the postclimax tall-grass station (line D), in the shrub stratum of the postclimax shrub station (line E). (No collections in the shrub station during the two-week period ending September 12—see Tables 22 and 23.)

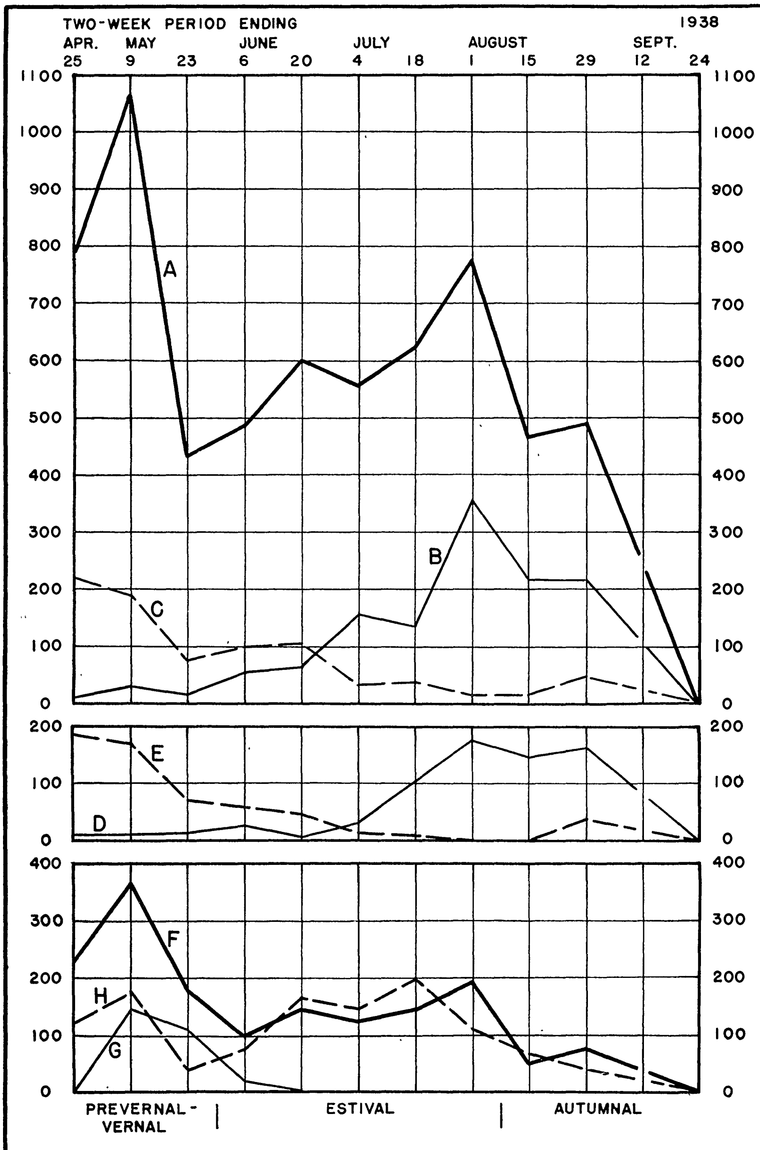


Fig. 27.—Population trends of invertebrates (arthropods) in the shrub stratum of postclimax deciduous shrub, expressed as average numbers per unit collection (day sweeps) per two-week period, April 11 to September 24, 1938. Total population (line A), Homoptera: leafhoppers, etc. (line B), Coleoptera: beetles (line C), *Erythroneura* sp., a leafhopper (line D), *Chalcoides fulvicornis,* a chrysomelid beetle (line E), Diptera: flies (line F), *Tachydromia maculipennis,* an empidid fly (line G), Hymenoptera (winged): bees and wasps (line H). (No collections during the two-week period ending September 12—see Table 23.)

into hibernating cover at the close of the autumnal aspect, as pointed out by Weese (1924) and others. Very low numbers of hemipterans were taken in the alcohol pitfall in the true prairie subsere during the entire period of that study, and in the tall-grass site until late October, when somewhat larger numbers appeared. In the shrub station pitfall, however, a very high hemipteran population was recorded during the two weeks ending September 9, 1939. This high is comparable to the late autumnal peak just described for the herb stratum of the preceding year, resulting from the high values produced by a single species of cydnid bug, to be discussed later. Such marked high points on the curve of total population have been pointed out by Blake (1926) to be apparently "due to the presence of certain particular species whose numbers attain a maximum, rather than to any general increase of any considerable number of species making up the population." Fichter (1939) noted population characteristics of this type in Wyoming spruce-fir forest, a condition that lends significance to the determination and scrutiny of prevalent species.

Spiders (Tables 22, 23) of several species appeared in all but one of the hiemal sweep collections in the herb stratum of the deciduous shrub station, and in this community their prevernal activity was much in advance of that in the tall grass and the true prairie subsere, producing a peak of abundance during the fortnight ending May 23. A second peak in this community coincided with the only peak of spider abundance occurring in the tall-grass station, that of August 15 to 29. The population of Araneida in the tall grass thence decreased rapidly while the population in the herb stratum of the shrub station dwindled rather slowly. In the true prairie subsere maximum abundance occurred during mid-September. The curve then tended sharply downward. Recognizable population peaks were not produced by spiders in the shrub stratum. Spiders were notably numerous in the litter collections in the hiemal period only. Values in the pitfall collections exhibited a marked uniformity throughout, a single, possibly significant peak occurring in the prairie subsere in the two-week period ending August 26.

Larval forms of Coleoptera, Lepidoptera, and Neuroptera, which must be arbitrarily considered here as a single group (Tables 22, 23), produced their highest combined population values in the herb stratum of Station 1 during the fortnight ending July 4 and in Station 2 during the preceding two weeks, while in Station 3 two well defined and much higher peaks were attained during the two-week periods ending May 23 and July 4. In the shrub stratum the maximum of population was reached between May 9 and 23. Litter values of this group are particularly high in the shrub station with the greater numbers occurring in the hiemal period. In the tall-grass litter samples, highs are shown in the prevernal-vernal and hiemal periods, while only the prevernal-vernal collections from the true prairie subsere yielded significant numbers of larvae. Pitfall values were, however, highest for larvae in this latter station, with a distinct peak occurring for the two-week period ending September 9.

Lepidoptera (Tables 31, 41), while commonly observed as apparently abundant in restricted areas of the prairie tract, such as over the alternes of western wheat-grass during its period of anthesis, appeared in all collections in insignificant numbers.

Seasonal aspects in grassland "are determined primarily by the seasonal march of habitat factors, of which temperature and length of day are the most important. So far as the palnts themselves are concerned, they may be in evidence throughout the entire growing season, but they give character to the matrix of vegetation only during the period of flowering" (Weaver and Clements 1939).

"The culmination of fruition and maturity of the autumnal blooming forms and late maturing grasses occur in September and October. After this time there is a gradual deterioration of the vegetation, which is hastened by repeated frosts. . . . The leaves of the grasses dry in place on the erect stems" . . . and plant life "is found almost entirely within the protecting soil. . . . In late winter and spring many mosses and numerous lichens are to be found on the damp soil between the tufts of sod" (Weaver and Fitzpatrick 1934).

The prevernal-vernal aspect.—Late March introduced the prevernal-vernal aspect in the true prairie subsere and the adjacent and contacting areas of tall grass and deciduous shrub. Insect and arachnid species which had spent the winter in the adult or late instar stages furnished a sudden surge of visible life during the warm days of this awakening period. Spiders, carabid beetles, and nymphal grasshoppers in late stages of development were especially evident on the surface of the ground. Although sweep net collections in the dry herbage of upland true prairie subsere during this period in 1938 revealed superior numbers of Diptera, the number of species of flies was so great that among the lesser, but at this time rapidly ascending numbers of Homoptera, occurred the prevernal-vernal prevalent in this stratum. The leafhopper *Balclutha abdominalis* (V.D.) (Tables 27, 29), did not, however, attain this rank until late in the aspect, and was at no time as conspicuous to casual observation as other and less abundant forms. In the litter the carabid beetle, *Amara* sp. (Tables 27, 30) was prevalent. Soil and pitfall collections* showed this beetle to be the prevalent species in the shallow layers of the soil and upon the ground surface. In the ravines within the postclimax tall-grass complex the dipterans were even more abundant than in the high prairie. Hemipterans, especially *Piesma cinerea* Say (Tables 27, 30) and *Lygus pratensis* (Linn.) (Tables 27, 30), stirring from their hibernacula, showed much activity among the old grass stems, the former giving subprevalent numbers. The cicadellid, *Balclutha abdominalis,* exhibited subprevalent values and other homopterans were here in marked abundance, but nymphs of *Melanoplus bivittatus* (Say) (Tables 27, 30), the two-lined locust, assumed prevalent rank. The chinch bug, *Blissus leucopterus* (Say) (Tables 27, 30), showing some low values in the sweep collections, was subprevalent in the litter stratum where the enchytraeid worms of the genus *Fridericia* (Tables 27, 30) prevailed at this season, while *Amara* sp. showed prevalent numbers in the soil.

Invertebrate species were even more abundant in the postclimax deciduous shrub areas of the ravines, with prevernal activity beginning in this complex well in advance of that in both true prairie subsere and tall grass. Flies were likewise here the most abundant order at this season, the chloropid, *Madiza* sp. (Table 28), showing subprevalent numbers. With ants and homopterans showing approximately equal population values in the herb stratum, *Balclutha abdominalis* assumed the prevalent role in this community as well as in the

* All pitfall records taken in 1939.

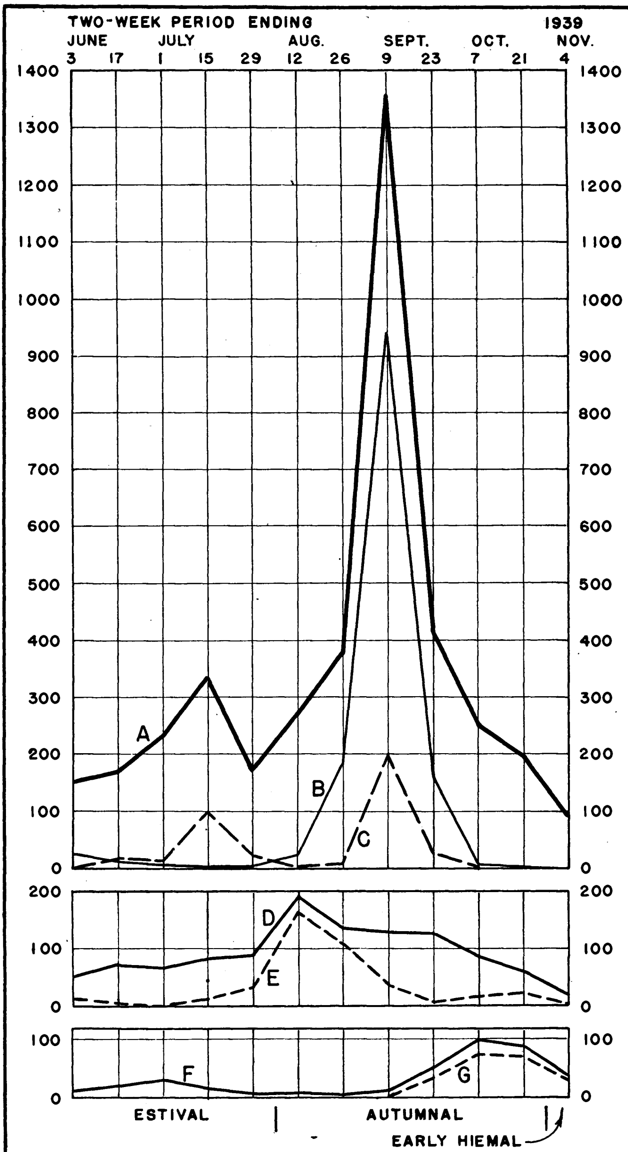


Fig. 28.—Population trends of invertebrates of the ground surface stratum in postclimax deciduous shrub, as indicated by alcohol pitfall collections and expressed in total numbers taken per two-week period, May 20 to November 4, 1939. Total population (line A); *Geotomus robustus,* a cydnid bug (line B); *Leiobunum* sp., a phalangid (line C); Coleoptera: beetles (line D); *Ataenius cognatus,* a scarabeid beetle (line E); Hymenoptera: ants and velvet ants (line F); *Prenolepis imparis,* an ant (line G).

subseral true prairie herb stratum. The typically woodland fly, *Tachydromia maculipennis* Walker (Table 28), attained subprevalent rank. The prevernal-vernal season constituted the high total population period for the shrub stratum. Here among the flowers of *Prunus americanus,* adults of Diptera, Coleoptera, and Hymenoptera were especially abundant, as were larvae of numerous species of insects. The chrysomelid beetle, *Chalcoides fulvicornis* (Fabr.) (Tables 27, 31), although less conspicuous, was here the prevalent species. In the deep litter beneath the shrubs *Fridericia* was active in prevailing abundance. In the soil small numbers of the pupoid snail, *Gastrocopta armifera* (Say), were found; more thorough studies of this stratum might have showed this small gastropod to be prevalent.

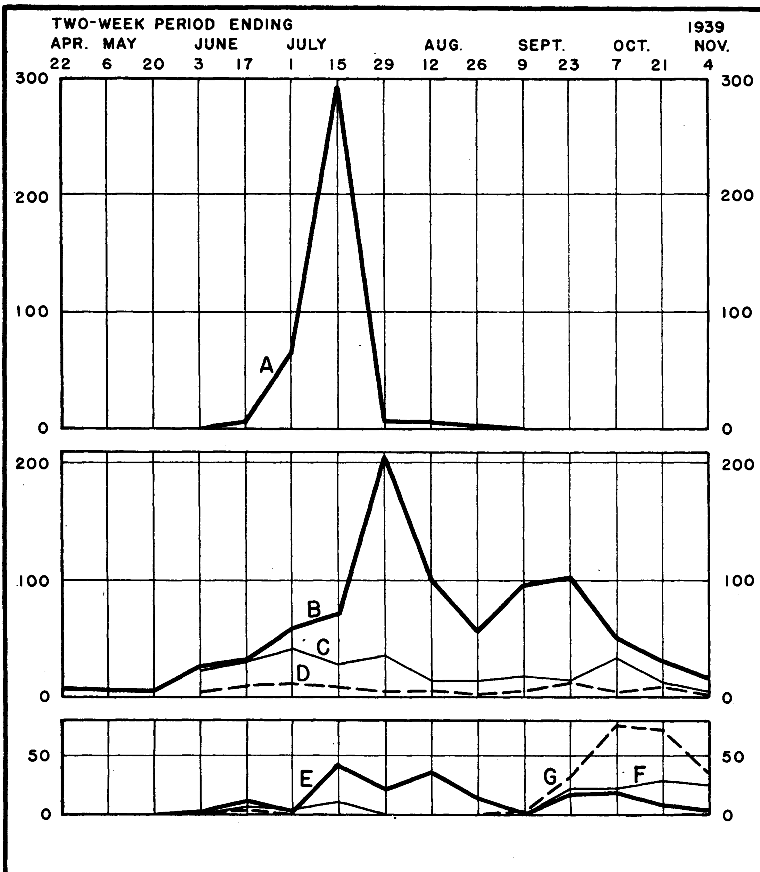


Fig. 29.—Population trends of three prevalent species of ants (Formicidae) in the ground surface stratum, as indicated by alcohol pitfall collections and expressed in total numbers taken per two-week period, May 20 to November 4, 1939. *Dorymyrmex pyramicus:* Subseral true prairie (line A). *Crematogaster lineolata:* Subseral true prairie (line B), postclimax tall grass (line C), postclimax deciduous shrub (line D). *Prenolepis imparis:* Subseral true prairie (line E), postclimax tall grass (line F), postclimax deciduous shrub (line G).

The estival aspect.—During the last week of May, with the spikes of June grass beginning to open, needle grass in full bloom and the wild alfalfa characterizing the subdominant vegetation, the estival period witnessed a rapid increase in the total population of invertebrates in the herb stratum and on the surface of the ground in the true prairie subsere. Homoptera and Coleoptera characterized this fauna in the herb layer, with Diptera and Orthoptera present in marked abundance. Prevailing was the leafhopper, *Balclutha abdominalis,* with the psyllid, *Aphalarea veaziei* Patch, the fulgorid, *Delphacodes* sp., the chrysomellid beetle, *Pachybrachys litigiosus* Suffr. and *Orthocis* sp., a cioid beetle, showing subprevalent numbers (Tables 27, 28, 29). Conspicuous in the first half of this aspect was *Pachybrachys luridus* Fabr., the walking stick, *Diapheromera veliei* Walsh, and the May beetle, *Phyllophaga lanceolata* (Say), the latter abundant on the wild alfalfa. *Delphacodes* became markedly abundant after mid-July (Tables 27, 29), at a time when *Pachybrachys litigiosus, P. luridus* and *Phyllophaga lanceolata* were showing marked decreases. Invertebrate numbers were low in the litter and soil strata in the estival period, with *Fridericia* prevailing, while the ant, *Dorymyrmex pyramicus* Roger (Tables 27, 29), characterized the ground surface population in company with the subprevalent tenebrionid beetle, *Eleodes opaca* (Say) (Table 28).

Balclutha abdominalis attained the rank of estival prevalent in the herb stratum of the postclimax tall-grass areas, although the Diptera presented the greatest abundance of all invertebrate orders, especially those flies of the family *Muscidae.* The cicadellid, *Macrosteles divisus* (Uhl.) (Table 28), showed subprevalent values along with *Delphacodes* sp. and *Pachybrachys litigiosus.* In the soil the carabid, *Amara* sp., still prevailed, sharing subprevalent rank with the ant, *Crematogaster lineolata* Say (Tables 27 and 29) in the litter where the annelid, *Fridericia,* had attained prevalent rank. On the surface of the ground *Crematogaster lineolata* produced distinctly prevailing numbers during the estival period in 1939.

Within the shrub station *Balclutha abdominalis* still held prevalence in the herb layer, with the cicadellids, *Empoasca* sp. and *Dikraneura* sp., and the empid fly, *Rhamphomyia* sp., in subprevalent rank (Table 28). Adding distinction to this society, and indeed to the forest margin character of the postclimax deciduous shrub, was the typically woodland fly genus, *Dolichopus,* and the woodtick, *Dermocenter variabilis* Say. Producing prevalent numbers in the shrub stratum was *Erythroneura* sp., a cicadellid which was confined to this society (Tables 27, 31).

Fridericia still prevailed in the litter, with the ant, *Ponera coarctata pennsylvanica* Buckley, subprevalent (Table 28). *Gastrocopta armifera* continued to be present in small numbers in the shallow layers of the soil. Vividly characterizing the estival invertebrate fauna of the soil surface in the deciduous shrub station was the phalangid, *Leiobunum* sp. (Tables 27, 31). This harvestman came into prominence in mid-July and again in early September, being superseded in the latter instance, however, by the hemipteran, *Geotomus robustus* (Uhler) (Tables 27, 31), thereby attaining a prevalent rank only in the estival. Accompanying *Leiobunum* sp. was the dung beetle, *Ataenius cognatus* Lec. (Tables 27, 31), as a subprevalent.

The autumnal aspect.—Early August and the advent of the autumnal period in the grassland and its associated postclimax areas, was marked by the gradual end of anthesis of the estival plants, the beginning of flowering of the coarse composites, and the loss of much of the green color in the grasses. With this distinct change came a decrease in populations of the invertebrate fauna of the true prairie subsere. Characteristic of the August decline was the walking-stick, *Diapheromera veliei.* Still prevalent in the herb stratum of true prairie was *Balclutha abdominalis,* with the minute brown scavenger beetle, *Corticaria* sp., the chloropid fly, *Oscinella minor* Adams, the gryllid, *Oecanthus niveus* (DeG.), and the ants, *Tapinoma sessile* Say, *Aphaenogaster fulva aguia* Buckley, and *Pheidole bicarinata* Mays, ranking as subprevalents (Table 28). The ground beetle, *Amara* sp., in this season assumed prevalent rank in both soil and litter and the ant, *Crematogaster lineolata,* was now prevailing upon the surface of the soil.

The tarnished plant bug, *Lygus pratensis,* attained autumnal prevalence in the tall-grass sites where the subdominant *Aster multiflorus* was conspicuously in flower and characterizing the herb stratum. *Delphacodes* sp. acquired subprevalence in this community at this season, sharing this rank with an undetermined species of cecidomyiid fly.

The downward movement of the Hemiptera into the litter began in the autumnal aspect. The tingid bug, *Piesma cinerea,* became prevalent in the litter during this season while the tarnished plant bug showed subprevalent values. *Amara* sp. and *Crematogaster lineolata* still prevailed beneath the surface and on the surface of the soil, respectively, while a second carabid, *Agonoderus pallipes* Fabr. (Table 28), acquired subprevalence at the soil surface.

Homoptera and Diptera thoroughly dominated the picture of the markedly high autumnal invertebrate population in the herb stratum of the postclimax deciduous shrub area. With *Dikraneura abnormis* (Walsh) (Tables 27, 31) in the prevalent role, the fly, *Oscinella coxendix* (Fitch), the cicadellid, *Empoasca* sp., the fulgorid, *Delphacodes* sp. (Table 28), the aphid, *Anoecia graminis* Gillette and Palmer (Tables 27, 31), and an undetermined fly, produced subprevalent populations. The high October peak of total population produced by the arthropods in this community, already recounted, is largely the result of increases in these six species populations. *Ataenius cognatus* continued its subprevalence upon the surface of the soil, a rank which it shared with the ant, *Prenolepis imparis* Say (Tables 27, 31), while *Geotomus robustus* was also prevailing in the soil stratum.

The hiemal aspect.—The acquisition of prevalence by an invertebrate in aerial strata during the hiemal aspect is, of course, intermittent and dependent upon temperature conditions. The high frequency values of the fulgorid, *Delphacodes* sp., in herb sweep collections in the true prairie during the winter and its superior though low numbers accord it hiemal prevalence in this community. *Piesma cinerea* prevailed in the litter in the true prairie, while *Amara* sp. retained its prevalence in the soil. *Crematogaster lineolata* maintained its autumnal prevalent rank at the soil surface into the early hiemal period (1939).

Hemiptera characterized both the herb and litter stratum in the tall grass during the hiemal aspect. Among the grasses during early November *Lygus pratensis* showed prevalent values, with the pentatomid, *Thyanta custator* Fabr., a conspicuous subprevalent. *Nabis ferus* Linn. was in evidence. Chinch bugs, *Blissus leucopterus,* moved into the litter in such numbers as to accord this species prevalent rank in that stratum where *Piesma cinerea* and the coccinellid beetle, *Hippodamia convergens* Guer., were present at subprevalent values (Table 28). The soil surface invertebrate fauna of early winter was characterized by *Prenolepis imparis,* and *Amara* sp. continued as soil prevalent.

Retaining a considerable portion of the subprevalent values which it built up in the late autumn, *Anoecia graminis,* an aphid, assumed the prevalent role in the herb stratum of the deciduous shrub area during the early hiemal. *Empoasca* sp. and *Delphacodes* sp. retained their subprevalent values acquired in the late autumn, and *Lygus pratensis* here became a subprevalent. Prevailing in the litter of the shrub station in this aspect was the enchytraeid worm, *Fridericia* sp., with the hemipterans, *Piesma cinerea, Blissus leucopterus, Orius insidiosus* Say, the staphylinid beetle, *Oxypoda* sp., and the ant, *Leptothorax curvispinosus ambiguus* Emery, exhibiting subprevalent values. At this season the soil harbored prevalent numbers of *Ataenius cognatus* and subprevalent numbers of *Geotomus robustus,* while *Prenolepis imparis* prevailed upon the surface of the ground during the post-autumnal transition.

STRATIFICATION AND DIURNATION

Stratal relationships of invertebrate animals have been investigated and reported upon for pine-hemlock forest in Maine and deciduous forest (winter) in Illinois by Blake (1926), for the "tree layer" of maple-red oak forest in Illinois by Davidson (1930), for spruce-fir forest in Wyoming by Fichter (1939), for "young elm-maple stage" of deciduous forest in Tennessee by Dowdy (1941), and for oak-hickory forest in Missouri by Dowdy (1947). The concensus of these authors is, in general, that stratal distribution of invertebrates occurs rather regularly in forest in response to vertical gradients of physical factors which probably operate together with certain biological factors, with seasonal and diurnal changes in strata and stratal composition being evident.

In the herbaceous cover of open grassland, obviously much shallower than forest cover, any aerial strata resulting from factor gradients are probably by comparison also much shallower. Stratification of physical factors in prairie veegtation can be discerned and measured, but is studied faunistically with greater difficulty than in forest, or even shrubby cover. Don B. Whelan conducted certain ecological studies within the prairie tract reported on here, and he has kindly furnished me with unpublished data which is helpful in this consideration of stratification. Whelan took 699 readings with a hand anemometer from March 10, 1928 to September 14, 1929, inclusive. His three sets of readings were made in feet-per-minute at five feet above the ground surface, at 14 inches above the ground surface, and at the ground surface in high and low prairie. Considering his readings at the five foot level (which was above the tops of the herbs) as base value (i.e., 100%), the wind movement values at the 14 inch level in high prairie through the late hiemal, prevernal-vernal, estival and autumnal aspects were 75%, 70%, 58%, and 53% respectively; at the ground surface 46%, 37%, 11%, and 5% respectively; at the 14 inch level in the low prairie, 71%, 76%, 60%, and 53% respectively, and at the ground surface 29%, 31%, 13%, and 4% respectively. Yearly mean averages of Whelan's data show air movement values at the 14 inch and ground surface levels to be 63% and 23%, respectively, of that at five feet above the ground in the high prairie, and 65% and

20% in the low prairie. It is apparent that the gradient became steeper as the growing season progressed, the greatest differences occurring in the autumnal aspect. Readings were taken several times when the anemometer registered 0 feet per minute at the ground level (which is actually about 0-6 inches above the ground surface) while the other two levels showed considerable movement. For example, on August 8, 1929, in the high prairie (corresponding to Station 1 of this study) the reading at the ground surface, 14 inch, and five foot levels were, respectively, 0, 310, and 856 feet per minute.

Whelan gathered further data which indicate recognizable stratification of physical factors in prairie. He exposed porous cup atmometers at ground level and at 12 inches above the ground surface. The values which he secured throughout the estival and autumnal season (May 24 to October 11) show evaporation rates at the ground level to have averaged 72% of those at the 12 inch level. It is not known whether these data on evaporation were gathered in 1928 or 1929, or whether the values furnished me were standardized; the general indication is to be considered reliable, however.

In the present study the entire depth of the herbaceous cover in the three stations was treated as a single stratum. Inasmuch as this is primarily a study of grassland invertebrates, and since the herb stratum received the most attention, a more or less detailed analysis of the physical factors and invertebrate populations of that stratum in the true prairie subsere is appropriate. Phenomena of aspection and horizontal distribution will be further illustrated as well. The conditions and processes of stratification and diurnation will, of course, be more strikingly shown in studies made in the deciduous shrub habitat.

Fortnightly means of air temperature (as determined for the purposes of this study) rose to above 40°F. in the herb stratum of true prairie subsere during the two-week period ending March 28 and fell below this level during the comparable period ending December 3 in 1938 (Fig. 11). The two weeks ending August 15 produced the annual temperature peak, with a fortnightly mean of 83.7° and an absolute maximum of 112.0°. Two rather well defined depressions appear in the temperature curve, the first for the two-week period ending April 11, the second for the 12-day period ending September 24. Accompanying the April depression in temperature was the year's greatest fortnightly peak of mean wind velocity, and one of three fairly well defined lows in relative humidity. Accompanying the September depression was one of three well expressed lows in wind velocity. During this approximately 250 day period with fortnightly means of temperature above 40°F., absolute temperatures ranged from 21.5° to 112° (a range of 90.5°), fortnightly maximum ranges varying from 34.5° to 62.0°.

Fortnightly means of relative humidity for this period appear quite constant, varying from 54.1% to 79.6%, with a maximum range, however, of over 80% (16.5% to nearly 100%), with this range occurring in the two-week period ending March 28. The lowest range of humidity values, 44.5%, was recorded during the fortnight ending June 20.

Sweep collections in the herb stratum of this drought disturbed true prairie during the hiemal period yielded arachnids and insects when temperatures were above 40°F. for even short periods. Spiders, short-horned grasshoppers, hemipterans such as plant bugs, damsel bugs, and stink bugs, homopterans, especially *Delphacodes* sp., coleopterans (principally flea beetles), dipterans (principally an undetermined ephydrid in March), and very few winged Hymenoptera were taken. Unit collections (50 sweeps) in the hiemal season took from 0 to 47 specimens, the latter number appearing in the collection for March 21, 1938; 55.3% of this population was composed of the undetermined ephydrid fly. The average population value per unit collection for the fortnight ending March 28 (end of hiemal aspect) was 31 (Table 22); that for the following two-week period (beginning of prevernal aspect) was 2.5. This low coincided with the depressed temperature and relative humidity values and the annual peak in wind velocity. From this marked low at the onset of the prevernal aspect in the true prairie subsere, the population of invertebrates in the herb stratum built up to the annual (estival) peak for the two weeks ending June 20 (Fig. 15) with a collection average of 756. Homoptera and Coleoptera, constituting 67.7% of the total numbers (36.4% and 31.3%, respectively) were likewise at their annual population peaks (Figs. 19, 21). These two orders continued to contribute the greatest numbers to the population, in part forcing two subsequent lesser peaks, one for the fortnight ending August 1, the other for the 12-day interval ending September 24. This third and autumnal peak is perhaps the more noteworthy of the lesser two, with Homoptera contributing 42.4% of the average collection value 323. Diptera had reached its peak in the preceding two-week period and was at this autumnal high forming 16.4% of the total population. Spiders were at their peak in this stratum and station, comprising 11.8% of the total numbers collected. Orthoptera were of some importance in the late July peak. Within six weeks following the autumnal high all group populations had fallen off to typical hiemal low value levels. There is some possibility that these two lesser peaks may have resulted from a rather deep "notch" in what would have been a single autumnal high, as a result of immediate and lagging effect of the August 1-15 high temperatures and wind velocities and low relative humidity (Figs. 11, 15).

Into this picture of strato-seasonal activity prevalent species, as determined in this study, fit with comparable patterns. Figures 19 and 21 show the population curves of two homopteran prevalents and coleopteran subprevalents which forced the peaks of population for their respective orders, and also forced or contributed largely (so far as species are concerned) to the total population peaks. Figure 20 compares the population curves of *Balclutha abdominalis* (Homoptera, Cicadellidae) in the only stratum in which it was taken—the herb stratum of the three stations studied; its superiority in this stratum of the true prairie subsere is marked; its preference for this stratum is obvious.

Much more conspicuous in this situation than *Balclutha abdominalis* were the walking stick, *Diapheromera veliei,* the chrysomelid beetles, *Pachybrachys litigiosus* (Table 28), and *P. luridus,* and the scarabeid, *Phyllophaga lanceolata.* Yet only *Pachybrachys litigiosus* attained even subprevalence. The top day collections of both *Balclutha abdominalis* and *Pachybrachys litigiosus* were made in the afternoon of June 17; 103 of the beetles were taken in this sample, a number only 23.6% of the homopteran prevalent's value.

This partial description of the invertebrate population of the herb stratum in true prairie subsere through the various seasonal aspects has so far been based upon daytime samplings. Collections designed to sample the populations during (1) comparatively low temperature and high relative humidity values in the presence of light, (2) high temperature and low relative humidity values in the presence of light, (3) comparatively high temperature and low relative humidity values in the absence of light, and (4) low temperature values and high relative humidity values in the absence of light, were made at irregular intervals from June 12 to October 29, inclusive, in 1938. Tables 32 and 33 and Figures 30 to 35, inclusive, indicate the time limits in which these collections were made, which for convenience in the text will be called day A.M., day P.M., night P.M., and night A.M., respectively. Table 17 to 21, inclusive, present the physical factor data relative to these collection periods, and Figures 30 to 35, inclusive, graphically show certain of these values. The first week of the hiemal period as previously delimited is included with the autumnal in these studies on diurnation.

Through the period June 12 to October 29, 1938, total population values as determined by sweep net collections in the herb stratum of true prairie subsere averaged highest in the night P.M. collections when temperature and relative humidity values averaged more or less intermediate in their ranges and wind values averaged a marked low; mean population values were lowest in the night A.M. collections, when temperature values were lowest, relative humidity values at a marked high and wind values intermediate (Fig. 30). It must be noted, however, that (1) the temperature averages for day A.M., night P.M., and night A.M. show relatively little range (about 4.6°F.), while the day P.M. temperatures averaged from about 15° to 20° above the others, (2) relative humidity means for the day A.M. and the night P.M. periods approach each other while those for day P.M. (low) and night A.M. (high) are nearly 38% apart, and (3) that the night P.M. values of wind velocity show a well defined low. Obvious shifts in physical factors occurred in the herb stratum; coincident with them were fluctuations in the total numbers of invertebrates taken by a standardized sampling method. On the basis of averages, the early part of the night, when (of the four periods considered) temperature and humidity conditions were intermediate but wind values quite low, produced a population high in the herbs; late in the night when temperature values were slgihtly lower than during the preceding period, but when wind values were again building up and relative humidity reached its daily (*diel* of Carpenter 1938:80) peak, the population dropped in a rather steep gradient to the daily low.

Determining and graphing these values (as available) separately for the estival and autumnal seasons, mean temperature and relative humidity are seen to retain much the same patterns, except that day P.M. relative humidity values were notably lower in the autumnal period. On the contrary, population patterns did not remain the same for the two seasons; the population decrease from a night P.M. high to a night A.M. low is even more striking (the loss amounting to 45.4%) than in the two-season averages. In the autumn the night P.M. total population retains its ascendancy, but is only slightly greater than that for the night A.M.; the two day population averages are likewise nearly identical but notably less than those for the night. In other words, the daily high and low are both produced in the night during the estival period, and a plateau high is produced in the night in the autumn (Fig. 30).

The average values used in this consideration, as based on relatively long periods (seasons), are compared with the same environmental and population values as ascertained and graphed (1) for the four-week period ending July 4, 1938 (mean collection values), and (2) for four unit collections within a 51-hour period, 8:00 A.M. June 17 to 11:00 A.M. June 19 (actual collection values). These temperature, humidity, and total population curves retain

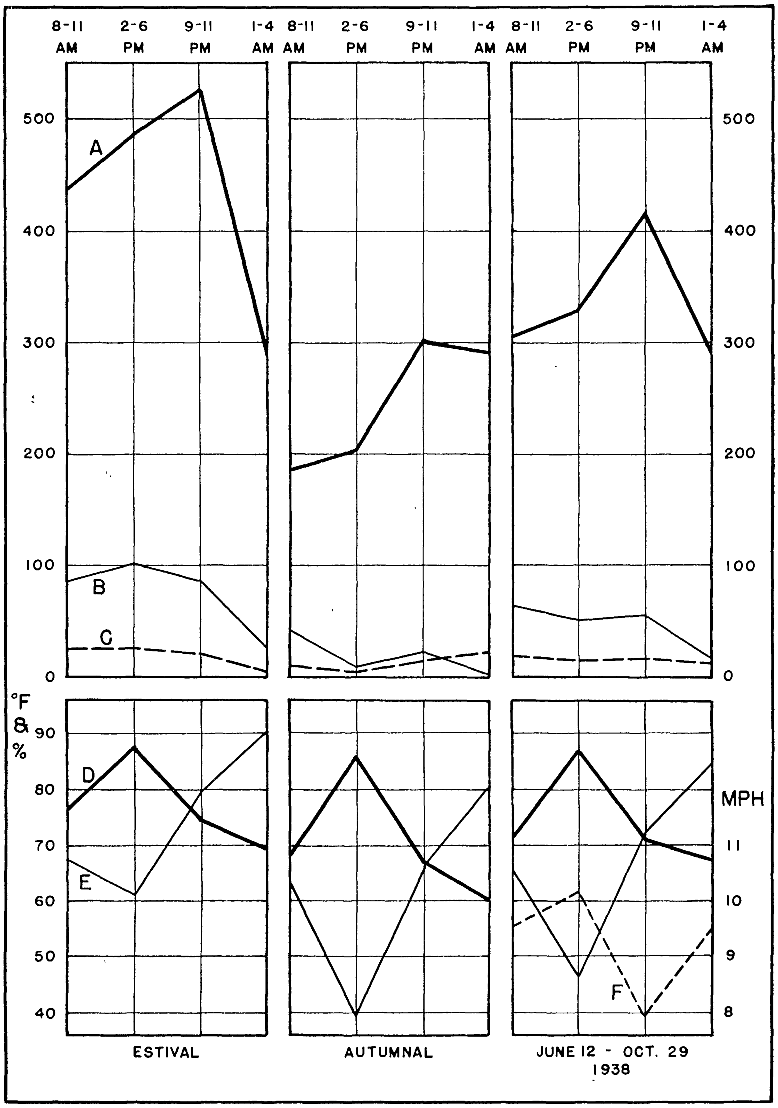


Fig. 30.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of subseral true prairie, and of wind at Lincoln, Nebraska, expressed as means for the periods indicated. Total population (line A); *Balclutha abdominalis*, a leafhopper (line B); *Delphacodes* sp., a leafhopper (line C); Temperature (line D); Relative humidity (line E); Wind velocity (line F).

essentially the same pattern as those for the season that encompassed these short periods (Fig. 31).

Such apparent fluctuations in quantitative structure of invertebrate groupings within a daily cycle suggest the probability of changes in qualitative structure, expressed through (1) variations in relative numbers of the many kinds of community components, and (2) sojourns by certain species into this stratum only during certain periods of the 24-hour cycle. Indications of such community phenomena are offered by prevalent and subprevalent species. For example, during the estival aspect the fulgorid, *Delphacodes* sp. (presumably a single species), retained a population ranging from 24.1% to 30.2% that of the cicadellid, *Balclutha abdominalis,* in the day A.M. and P.M. and night P.M. collection periods (Fig. 30); in the night A.M. period, although both *Delphacodes* and *Balclutha* declined, the former lost in relation to the latter, showing population values 18.5% those of *Balclutha.* Still more striking ratios were found in the values representing the entire period of study, including both seasons, *Delphacodes* maintaining values from 28.0% to 35.8% those of *Balclutha* through the day and first half of the night, but, despite slight decreases, showing values 70.6% those of *Balclutha* in the night A.M. samples. In the autumnal period inversions of these two species populations occurred within the daily cycle, and *Delphocodes* held ascendency over *Balclutha* in the night A.M. collections by a ratio of about 10:1. These population values are admittedly small; they might not be considered statistically valid; they do, however, show population trends and are indicative of changes in community structure during the daily cycle. Further indications are offered by comparison of the population values of *Balclutha abdominalis* and the subprevalent chrysomelid beetle, *Pachybrachys litigiosus* (Fig. 31), in which case higher population values were available for consideration. Comparable ratios of these two species are seen in the average-per-collection values for a four-week period and the actual collection values in a 51-hour period; most striking are the latter. The numbers of the subprevalent beetle taken in the day A.M., day P.M., and night P.M. samples were 43.7%, 23.6%, and 22.1%, respectively, those of the prevalent leafhopper. But in the night A.M. collection an inverse ratio appears and the leafhopper's abundance in the herb stratum was 44.3% that of the beetle.

Some comparisons of findings in this stratum with those of other strata in the same station are in order.

Data on the litter and soil populations in the true prairie subsere station are too meager to warrant any reliable comparative analysis. It may be briefly stated that litter populations exhibit lows during the estival and autumnal aspects and highs in the hiemal, with some buildup over the hiemal level during the early hiemal and prevernal periods, though this was not strikingly so in the true prairie subsere (Fig. 16). Soil populations appeared to attain a peak in the autumnal aspect; the values secured are probably too low to be reliable. Those conditions are probably the function of movements into and out of hibernacula, inadequately measured in this investigation.

Although the data were gathered in the following year, elucidating population values were determined for the ground surface stratum in the prairie subsere station. That the herb and ground surface strata were not studied simultaneously is unfortunate (resulting from belated employment of the alcohol pitfall method) and introduces a weakness in the examination of

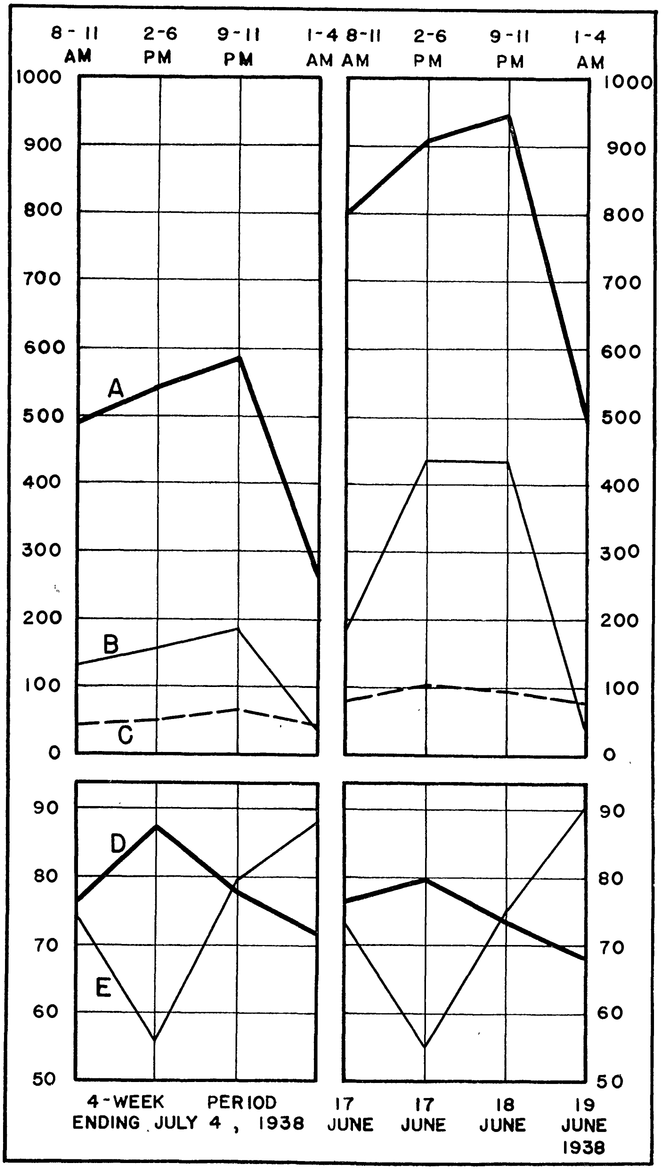


Fig. 31.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of subseral true prairie, expressed as means for the intervals indicated within the four-week period ending July 4, 1938, and (for the animals) as actual numbers taken in four unit collections within a 51-hour period, June 17 to 19, inclusive, 1938. Total population (line A); *Balclutha abdominalis,* a leafhopper (line B); *Pachybrachys litigiosus,* a chrysomelid beetle (line C); Temperature (line D); Relative humidity (line E).

stratal behavior attempted here. Any expressions of annuation that might have existed are hidden, but none the less complicating.

In 1939 the ground surface population of the true prairie subsere as measured in this study attained a distinct peak in the two-week period ending July 15 (Fig. 18). This high shows a lag of approximately four weeks behind the 1938 population high of the herb stratum of the same station. This comparison cannot, of course, be conclusive, being based on the records for two different albeit consecutive years. That both strata show an estival peak of population does seem significant, however; the time difference may be actual in any year, or may in this instance have been the function of the rapidly changing nature of the prairie vegetation and aberrant weather picture already outlined. It is of interest to note that the ground surface population here shows a second lesser and autumnal peak somewhat in keeping with a lesser peak in the herbs in the preceding year.

Ants and beetles were largely responsible, as groups, for the estival peak, less so for the autumnal peak (Fig. 22). Coleoptera forced the total population up during the vernal and early estival period to a "peak within a peak" for the two weeks ending June 17 (Fig. 22). Then, as ants were coming into prominence, beetle population values fell off. At their June 17 peak of abundance beetles comprised 67.6% of the take, ants 17.2%. A month later ants were obviously forcing the total population peak (estival), comprising now 58.1% of the total collection value, beetles making up 15.0%.

The species which forced these trends were the prevalent ants, *Dorymyrmex pyramicus* and *Crematogaster lineolata,* the prevalent ground beetle, *Amara* sp., and the subprevalent tenebrionid beetle, *Eleodes opaca* (Fig. 22). At the estival peak *Dorymyrmex pyramicus* contributed 65.1% of the ant population and 37.9% of the total population. In the two-week period following this species' numbers fell to nearly nil, but the ground surface ant population was bolstered by a sudden increase of *Crematogaster lineolata* which produced its major peak in this period; *C. lineolata* also contributed materially to the lesser, autumnal peak.

These two species of ants show some interesting stratal relationships. *Crematogaster lineolata* was regularly taken in the sweep collections in the herb stratum of the true prairie subsere, in both day and night samplings. In contrast *Dorymyrmex pyramicus* was never taken in the herbs. The carabid and tenebrionid beetles, *Amara* sp. and *Eleodes opaca,* show comparable stratal relationship. *Amara* was taken frequently in soil and litter samples and in considerable numbers in pitfall collections during the estival aspect in subseral true prairie, but was never found in the sweep net collections in the herb stratum. *Eleodes opaca* was at no time secured by sweeping the herbs during the day but appeared in noteworthy numbers in the night sweeps.

Inasmuch as most studies of stratification and inter-stratal movement of invertebrate animals have been made in forest habitats, a consideration of these phenomena in the postclimax shrub station is of special interest here. Such vertical behavior is more easily recognized and measured in this essentially forest margin habitat than in the grassland, the plant cover being higher and thereby offering deeper and more divergent, if not more strata as regards both biotic factors and physical factors as they are modified by the vegetation. Comparable and simultaneous sampling methods in the herb and shrub strata of this station offer special scrutiny of these two strata.

Considered as an entity the postclimax shrub community produced two relatively enormous population peaks in its aerial strata in 1938, the first a vernal peak in the shrub stratum, the second a late autumnal peak in the herb stratum (Figs. 25, 27). The early autumnal high which occurred in the ground surface population in the following year (Fig. 28) may or may not be related to the autumnal high of the herb stratum; the six weeks difference in time of occurrence (as the findings for the two consecutive years are compared) may have been actual, or the product of a disturbed phenology and aspection under the influence of drought. A second marked peak in the shrub stratum, contributed to in considerable measure by the homopteran

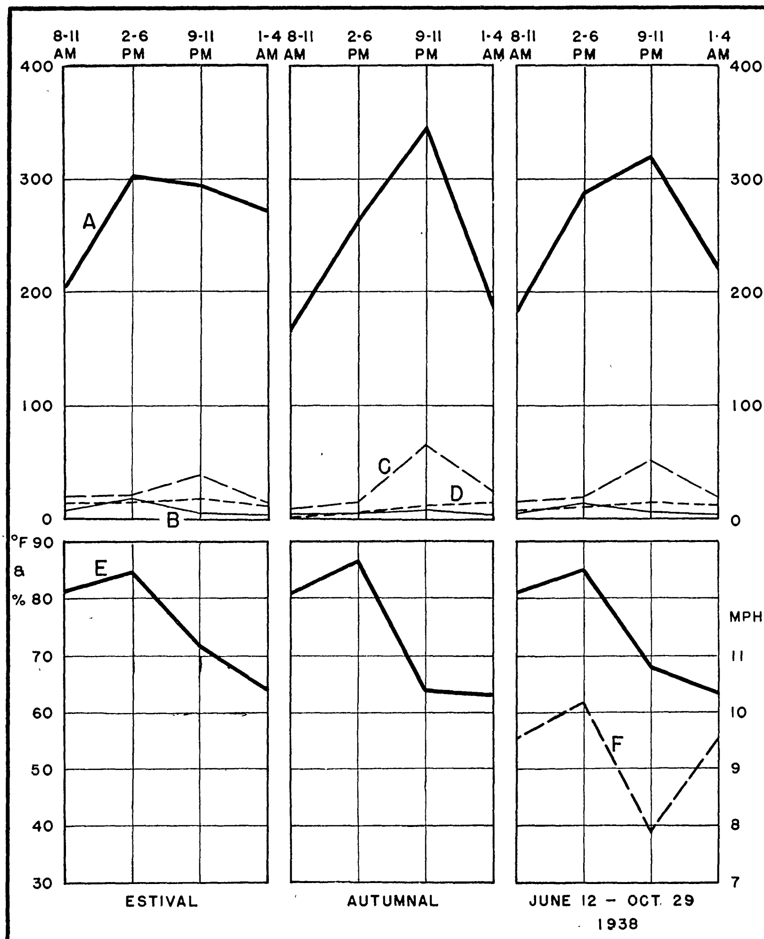


Fig. 32.—Diurnal and nocturnal values of invertebrate populations and temperature in the herb stratum of postclimax tall grass, and of wind at Lincoln, Nebraska, expressed as means for the periods indicated. Total population (line A); *Balclutha abdominalis,* a leafhopper (line B); *Delphacodes* sp., a leafhopper (line C); *Melanoplus bivittatus,* a grasshopper (line D); Temperature °F. (line E); Wind velocity (line F).

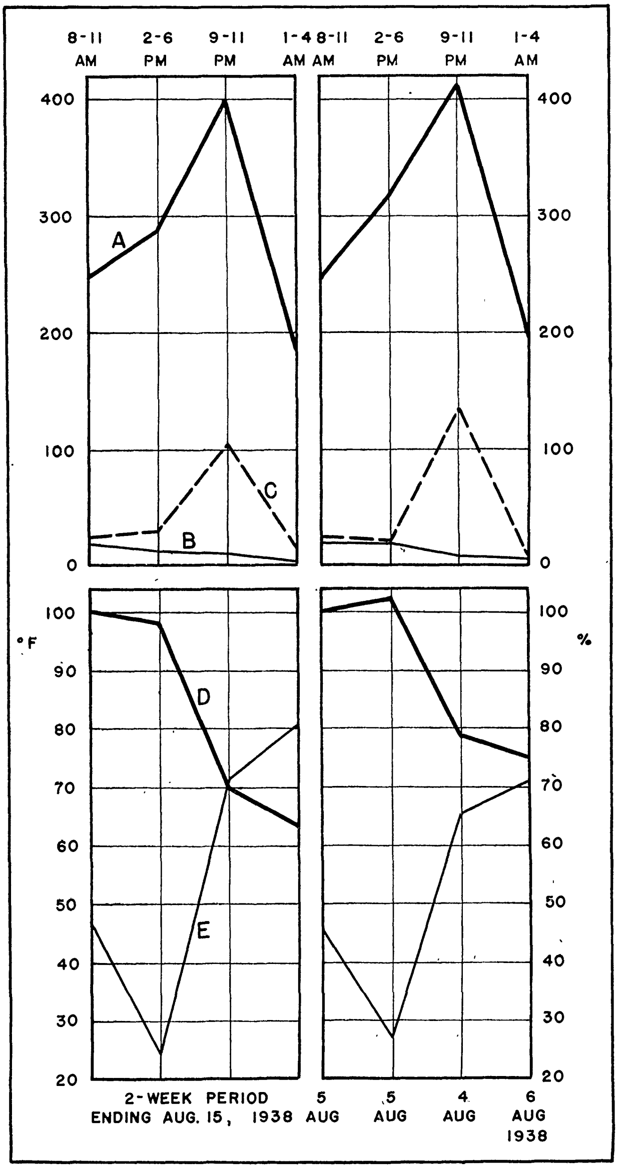


Fig. 33.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of postclimax tall grass, expressed as means for the intervals indicated within the two-week period ending August 15, 1938, and as actual values and collection averages within a 31-hour period, August 4 to 6, inclusive, 1938. Total population (line A); *Balclutha abdominalis*, a leafhopper (line B); *Delphacodes* sp., a leafhopper (line C); Temperature (line D); Relative humidity (line E).

Erythroneura sp., appeared at the end of the estival aspect. The first of these two major shrub peaks was coincident with the vernal blooming of wild plum. A rather poorly defined tertiary peak of shrub stratum population was produced principally by many species of flies and micro-hymenoptera six weeks later during the anthesis of the dogwood. Following the late estival peak the total population of the shrub layer as measured in this study fell off rather abruptly, being somewhat bolstered, however, in the latter half of August by *Erythroneura,* the beetle, *Chalcoides fulvicornis,* and the order Diptera. This decline in shrub layer population was coincident with the loss of leaves suffered by *Prunus* and *Cornus* in this situation which may have in part resulted from injury by *Erythroneura.* There is little or no evidence of downward migration into the herb stratum in this instance—the total population of the herb was likewise decreasing. Values for the 12-day period ending September 24, 1938, show the shrub stratum population at zero, and the herb stratum population at the lowest point since late in the vernal aspect. At this point the remarkable autumnal high of the herb stratum begins to form, reaching its zenith in the next four weeks thence to fall off within six weeks to hiemal levels.

The compositions of the peaks in these two aerial strata are interesting. The vernal peak in the shrub stratum coming at the time when *Prunus* was flowering was made up of many species. Even the insect groups contributing most heavily to this high, namely Diptera, Coleoptera, and winged Hymenoptera comprised only 34.3%, 17.7%, and 16.5%, respectively, of the total numbers of invertebrates; the prevalent, *Chalcoides fulvicornis,* a flea beetle, was on the decline and comprised but 15.7% of the peak population. Here is indicated (1) the presence of many species and (2) the formation of a total population peak independent of a single species pattern.

The late autumnal peak in the herb stratum of the same station (a high more than twice the magnitude of the vernal peak in the shrub stratum) was largely the function of populations of Diptera and Homoptera, these orders comprising, respectively, 53.8% and 23.0% of the total population. However, the two prevalents, *Dikraneura abnormis* (Homoptera, Cicadellidae) and *Anoecia graminis* (Homoptera, Aphididae), and the two subprevalents whose population peaks occurred in this period, namely, the flies, *Oscinella coxendix* and *Elachyptera costata,* jointly contributed only 35.9% to the total peak. *Dikraneura abnormis* was in decline; the most abundant fly, *Oscinella coxendix,* comprised but 21.0% of its order and 11.3% of the entire population of the herb stratum. Single species appear to contribute only lightly to the formation of this autumnal peak.

It is of especial significance to note that *Anoecia graminis,* the aphid which as a single species contributed the greatest population values to this peak in the herb stratum of the shrub station, was confined to this stratum and this station. *Dikraneura abnormis,* a cicadellid leafhopper, which had forced a previous lesser peak by forming 32.9% of the total population during the fortnight ending August 29, was likewise confined to this stratum and station, so far as the methods of study ascertained. The leafhopper, *Erythroneura* sp., was taken only in the shrub stratum of this station, and the chrysomelid beetle, *Chalcoides fulvicornis,* was confined to the shrub station and largely to the shrub stratum.

On the surface of the ground under the shrubs the cydnid bug, *Geotomus robustus,* and the dung beetle, *Ataenius cognatus,* were omnipresent throughout the period of the pitfall studies in that station (May 28 to November 4, 1939); the harvestman, *Leiobunum* sp., was also continuously in evidence until early October. The outstanding autumnal peak in this situation was almost entirely the function of *Geotomus robustus* and *Leiobunum* sp., the bug contributing 69.3% of the total numbers, the phalangid 14.6%—together 83.9% of this total ground surface population as measured. *Geotomus robustus* was taken only in the shrub station in ground surface or litter collections, with the exception of a single specimen taken in the alcohol pitfall in the true prairie subsere during the week ending September 23, 1939.

Certain of these prevalents, representing, to be sure, relatively few species, were apparently subject to vertical limits of distribution in the deciduous shrub habitat. The cydnid bug, *Geotomus robustus,* and the dung beetle, *Ataenius cognatus,* were taken commonly and in considerable numbers in the ground surface collections, sparingly in the litter collections; the harvestman, *Leiobunum,* commonly, and briefly in large numbers, in ground surface collections, in small numbers in the herbs. The leafhopper, *Dikraneura abnormis,* and the aphid, *Anoecia graminis,* were taken only in the herb stratum. *Erythroneura* sp., another leafhopper, was taken solely in the shrub collections, sharing prevalent values here with the flea beetle, *Chalcoides fulvicornis,* which was taken only sparingly in the herb stratum. On the other hand, the ant, *Prenolepis imparis,* was found in important numbers on the surface of the ground, in the herbs, and in the shrub stratum.

Data on daily fluctuations of arthropod numbers in the shrub station are not as complete as desired, but the curves derived show the pattern of daily movements (if the fluctuations in take indicate movements) in the herb stratum to be somewhat different from those in the prairie habitats (Figs. 30, 32, 34). For the June 12 to October 15 period the daily high (mean) occurred in the day A.M. period with the low in the night A.M. This before-dawn low agrees with the grassland pattern; likewise a build-up from day P.M. to night P.M. is simiiar. But the sudden eruption from the night A.M. daily low to the day A.M. daily high is strikingly different. The temperature-relative humidity pictures are comparable except that in the shrub station (ravine) the night P.M. temperatures dropped faster and humidity values built up faster than in the grassland. This may be a function of the cold air drainage described earlier and a phenomenon known to all who have traveled country roads in rolling country on summer nights. The striking wind velocity differences must also be remembered in this instance.

These curves largely reflect those for the autumnal aspect, data from the estival being incomplete. It will be noted that slight temperature increases are indicated for the night A.M. over the level for the night P.M., and that on the two temperature rises, whether great or small, smaller numbers of invertebrates were taken in the sweep net. In the true prairie subsere, however, the greatest numbers of animals were taken in the night P.M. when temperature values were below those for the day (Fig. 30).

The curve of the herb population in the shrub station (Figs. 34, 35) tends downward (instead of upward as in the prairie station) from a day A.M. high, while the curve of the shrub population is tending upward. This might indicate that the herb stratum was losing its population to the shrub stratum above it during the day, the shrub peak being reached in the day P.M. With the coming of darkness, and its lowering temperature, increasing relative humidity, and low wind values, the shrub curve tends downward and the herb population shows a marked increase, apparently indicating that the shrub day popu-

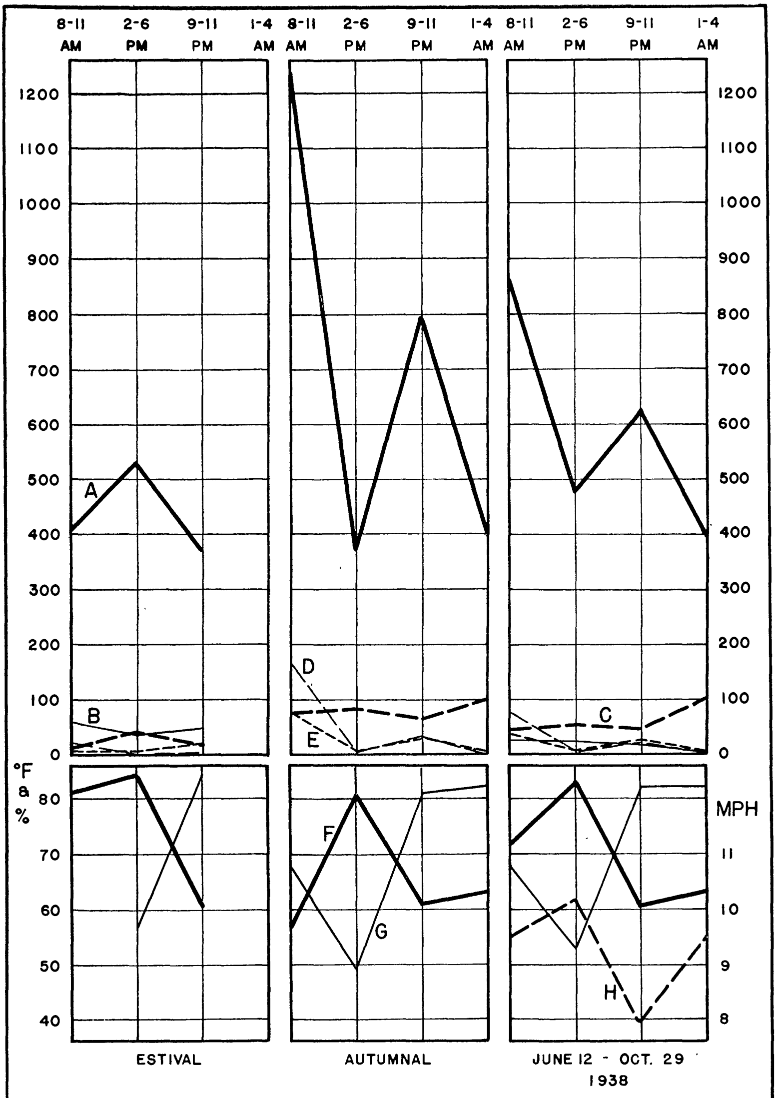


Fig. 34.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of postclimax deciduous shrub, and of wind at Lincoln, Nebraska, expressed as means for the periods indicated. Total population (line A); *Balclutha abdominalis,* a leafhopper (line B); *Dikraneura abnormis,* a leafhopper (line C); *Anoecia graminis,* an aphid (line D); *Prenolepis imparis,* an ant (line E); Temperature (line F); Relative humidity (line G); Wind velocity (line H). No 1-4 AM collections in this habitat during the estival period—see Table 32.)

lation is in part gathering in the lower stratum. The night A.M. low for both strata shown by the continued fall of both curves would indicate a telescoping of both populations in the lowest vegetational levels. The seemingly incongruous high in the herb day A.M. population is apparently the result of a returning vertical movement, aerial or epiphytic populations now moving upward somewhat simultaneously toward the maximum vertical spread which is reached in the afternoon when the temperatures are highest, humidity lowest, and wind velocity at its normal daily maximum.

The curves representing daily fluctuations of invertebrates in the two aerial strata studied in the shrub station show strikingly different patterns from those

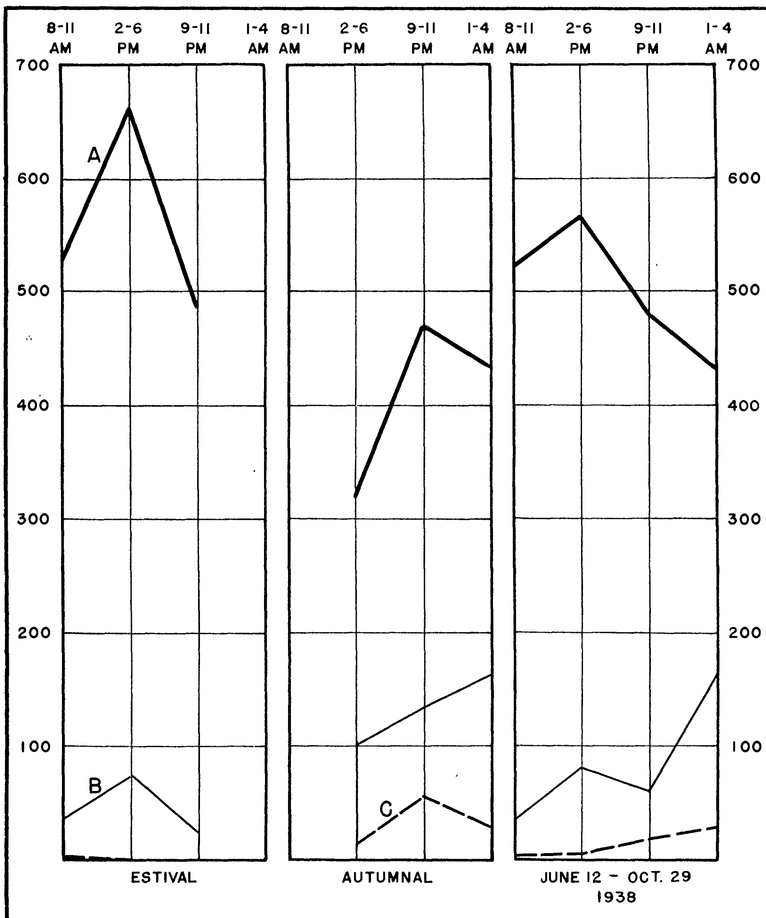


Fig. 35.—Diurnal and nocturnal values of invertebrate populations in the shrub stratum of postclimax deciduous shrub, expressed as average numbers per collection for the intervals indicated. Total population (line A); *Erythroneura* sp., a leafhopper (line B); *Crematogaster lineolata,* an ant (line C). (No. 1-4 AM collections in this habitat during the estival period—see Table 32.)

in the grasslands, but appear to express, in general, the same responses to physical factors.

Accounts of Prevalents

Delphacodes sp. (Tables 27, 29, 33; Figs. 19, 30, 32, 33).—If it is ecologically valid to consider that an invertebrate species can attain prevalence in an aerial or epiphytic stratum during the hiemal aspect, this member of the homopteran family Fulgoridae became the hiemal prevalent in the herb stratum of the drought-disturbed true prairie, where it was taken in every month excepting April and December. However, it should be noted that six sweep collections made in both the tall-grass and subseral true prairie during the winter of 1937-38 yielded no specimens of this form, all of the hiemal specimens being taken during the next winter, 10 out of 14 samples containing *Delphacodes* in the true prairie subsere, and 7 out of 17 producing in the tall grass. Temperature differences were not present to account for this discrepancy. If one of the objectives of this study had been the naming of communities, and data from the second winter only had been available, this hiemal society could have been accorded a name based on an animal that was absent from the society in the previous year.

Delphacodes was confined to the two prairie stations, first appearing in the tall-grass (ravine) herb stratum collections on April 25 (1938), in the prairie subsere (upland) sweeps on May 30. This five-week lag is illustrative of the aspectional sequence shown by ravine and upland sites in early spring, discussed earlier in this paper.

In the true prairie subsere where it occurred in 66.6% of the herb stratum collections and produced 4.8% of the total annual population figure, it showed an abundance peak for the two-week period ending July 18, 1938, its collection average during this interval being 47, and forming 13.3% of the total take (Fig. 19). Its peak of abundance in the tall grass came in the fortnight following, during which time it constituted 16.3% of the total population and averaged 83 specimens per sample.

Balclutha abdominalis (V.D.) (Tables 27, 29, 33; Figs. 19, 20, 30-34).—This cicadellid leafhopper was the most important species taken on the basis of numbers, frequency, and distribution, being the prevernal-vernal, estival, and autumnal prevalent in the herb stratum of subseral true prairie, the estival prevalent in the herb stratum of postclimax tall grass, and the prevernal-vernal prevalent in the herb stratum of postclimax deciduous shrub. Its greatest abundance occurred in the true prairie subsere (Fig. 20), producing here a daytime collection frequency of 69.3% and comprising 17.4% of the total numbers taken. In the tall grass its day collection frequency was 50.8%, its percentage of total numbers taken only 5.8%; under the shrubs it constituted 4.4% of the total take and occurred in 46.0% of the samples.

Balclutha abdominalis was first taken on March 19, 1938 in the postclimax shrub station, and appeared nearly a month later, April 25, in the prairie habitats. It was last collected in the prairie stations on October 29 but lingered awhile under the shrubs, being last taken there on November 11 although no specimens were collected there during the autumnal season. An early hiemal movement of this cicadellid into the shrub habitat may be indicated by these data.

During its period of aerial or epiphytic activity its collection frequency in

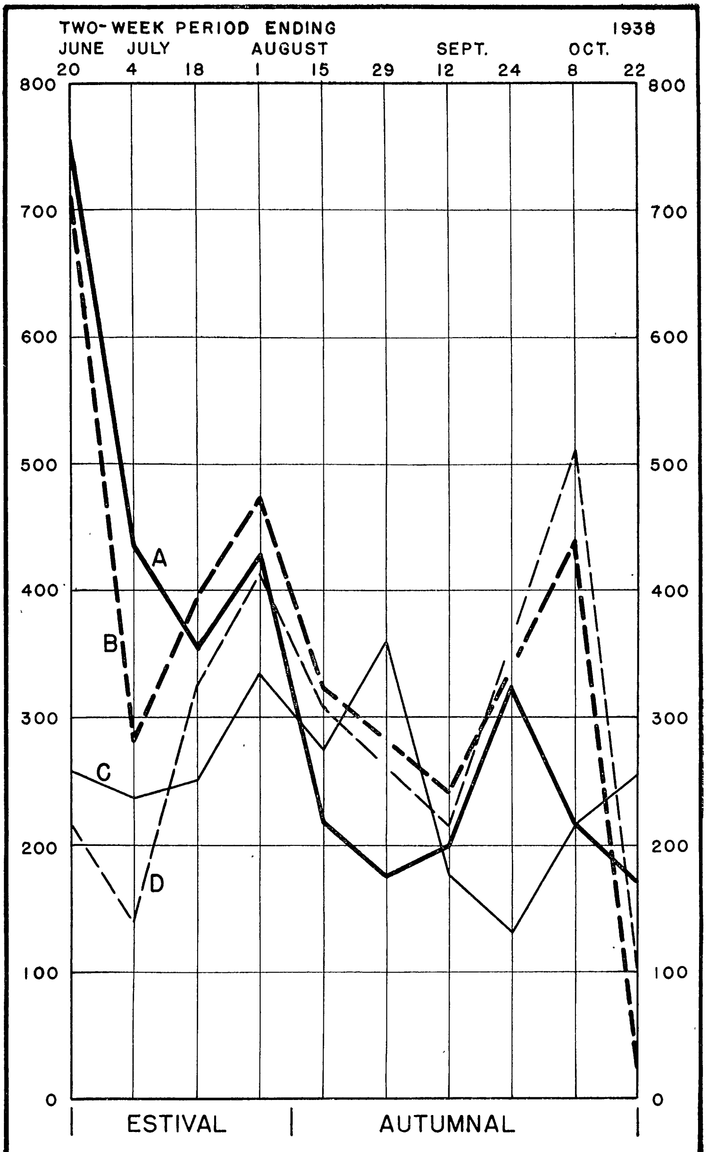


Fig. 36.—Diurnal and nocturnal trends of total populations of invertebrates (arthropods) in the herb stratum of grassland, expressed as average numbers per unit collection (sweeps) per two-week period, June 6 to October 22, 1938. Subseral true prairie: day (line A) and night (line B); Postclimax tall grass: day (line C) and night (line D). (No night collections during the two-week periods ending August 29 and September 24—see Table 32.)

Stations 1, 2, and 3 was 96.3%, 86.1%, and 63.3%, respectively. Its collection frequency in the true prairie subsere and tall grass for the estival aspect was 100%, the average collection numbers for these two stations being 89 and 17, respectively.

Two population peaks were produced in the true prairie subsere by this cicadellid (Figs. 19, 20), the first an estival high for the two-week period ending June 20, 1938, with a collection average of 235 individuals comprising 10.4% of the total population, the second an autumnal peak for the fortnight ending October 8 with a collection average of 113 specimens constituting 52.1% of the total numbers taken in that period. In the two weeks ending July 4 it produced peak values in the two postclimax stations, forming during this interval 29.4% of the herb stratum population in the tall grass with a collection average of 61 and 18.5% of the total herb population in the shrub habitat with a collection average of 77.

Dorymyrmex pyramicus Roger (Tables 27, 29; Figs. 22, 29).—This small ant is common, nesting in the ground and preferring open, sunny spots. The workers feed mainly upon other insects, but are also fond of "honey dew" from aphids. Although found in all kinds of soils, it seems to prefer light, dry soils (Bare, unpublished manuscript and personal communication).

Dorymyrmex pyramicus is chiefly notable here for its almost complete confinement to the upland subseral true prairie as determined by pitfall collections, and its apparently complete absence from the shrub station, a distribution in keeping with Bare's observation that it seems to prefer light, dry soils. It was taken only in ground surface collections, first appearing in them in subseral prairie in the fortnight ending June 17, building up to a rather high peak for the two weeks ending July 15, thence disappearing from the collections following August 26 (Table 29; Figs. 22, 29).

Crematogaster lineolata Say (Tables 27, 29, 33; Figs. 22, 24, 29, 35).—O. S. Bare (unpublished manuscript and personal communication) states that *Crematogaster lineolata* is a very abundant ant in this region, nesting under stones and logs, in dead wood, beneath the bark of trees, and often in the soil. Its food habits vary; it feeds to considerable extent on animal matter, mainly insects, but is also fond of sweets and may often be found attending aphids.

This ant was the autumnal and early hiemal prevalent in the ground surface stratum of subseral true prairie and the estival prevalent in that stratum of postclimax tall grass. It occurred in the herb, litter, and ground surface collections of all three stations and in the shrub layer of Station 3. Dowdy (1947) reports this ant abundant and distributed "through all five strata" in oak-hickory forest. Its numbers were never remarkably great, although its peak of population in the subseral prairie ground surface stratum showed a two-weeks pitfall take of 207 specimens which comprised 48.8% of the total take (Figs. 22, 29). It appeared somewhat earlier and disappeared slightly later in the herb layer collections in the shrub habitat than in the other two stations.

Piesma cinerea Say (Tables 27, 30, 33).—Rather unrestricted in its spatial distribution within the area studied, this tingid bug was the hiemal prevalent in the litter stratum of the two prairie stations. It was important in the hiemal litter collections in all stations, however, and produced its highest values in the shrub habitat where a collection average of 38 individuals accounted for 32.5% of the sample. One of the shrub litter collections in this period yielded 67 specimens of this bug which was 38.0% of the total number of invertebrates present. This was undoubtedly a massed group of hibernating *Piesma cinerea*, the finding of such aggregations being common in litter samples. The coccinellid beetle, *Hippodamia convergens*, was frequently found in this manner, further exemplifying the spotty distribution of certain hibernating insects.

Piesma cinerea was taken in low though noteworthy numbers in the herb stratum of the two postclimax stations in April and May of 1938, first appearing in the shrub habitat in sweeps made on April 18, in the tall grass on May 2. Its appearance in relatively large numbers in the herb stratum of the tall-grass station was sudden, the May 2 collection taking 67 specimens, the largest number taken in any sample at any time. On this same date a light peak of vernal abundance was evident in shrub station sweeps. The bug's numbers in the herbs of both habitats declined rather quickly, last appearing in the tall-grass sweeps on May 23, in the shrub station on June 12. In this latter site it reappeared in low numbers in mid-October. There are no indications of its whereabouts during the balance of the estival and autumnal periods.

These data seem to indicate, however, a vernal-early estival emergence of hibernating adults of *Piesma cinerea* from hibernacula in the shrub and tall-grass habitats, activity beginning earliest in the shrub station, and a return to these sites in the late autumn—illustrating the horizontal-vertical prehibernation movements pointed out by Weese (1924).

It must be remembered that hibernating individuals of *Piesma cinerea* were also taken in the litter in the upland true prairie subsere. It should further be noted that this bug was taken in the shrub stratum in 25.0% of the collections, albeit in very low numbers.

Fridericia spp. (Tables 27, 30).—Confined to the litter and soil of all stations studied, this little annelid proved to be the prevernal-vernal-estival prevalent in the litter stratum of subseral true prairie and postclimax deciduous shrub and the estival prevalent in the litter of the postclimax tall-grass habitat. Data concerning it are considered quite inadequate here, and it figures but little in this analysis. However, it is noteworthy that this genus of enchytraeid worm exhibited peaks of abundance in the litter stratum of the two postclimax vegetational units—in the shrub station for the two weeks ending April 5, 1938, where it comprised 55.1% of the litter population as sampled and averaged 117 individuals per collection (square foot), and in the tall-grass station from June 20 to July 4 where a unit collection average of 47 specimens comprised 88.5% of the total number of invertebrates taken.

It occurred in winter samples of litter in these two stations, but with much less regularity than during the warmer seasons.

Amara sp. (Tables 27, 29, 30; Fig. 22).—The carabid, *Amara* sp., was taken in those strata which would be expected of a ground beetle—namely, the soil, the litter, and the ground surface. It occurred in all three stations, but principally in the grassland stations. Its most important numbers appeared in the soil stratum of the tall grass where it comprised 44.0% of the total population as sampled, occurring in 68.4% of the collections; here it was the annual prevalent. It likewise proved to be the annual prevalent in the soil stratum of the true prairie subsere, where it was also the autumnal prevalent in the litter stratum and the prevernal-vernal prevalent of the ground surface stratum. Its only noteworthy peak of abundance occurred in the ground surface stratum of the subseral prairie station during the fortnight ending June 17, 1939 (Fig. 22). In this cumulative two-weeks collection this ground beetle formed 14.9% of the total take. It first appeared in the pitfall collections in this site between April 22 and May 6 and was last taken in the collection for July 29 to August 12. Its litter collection frequency was greatest in the tall-grass station where it was taken in greatest abundance from mid-April to early July. Its soil values were also highest in the tall grass, producing a collection frequency of 68.4% and 44.0% of the total population secured.

Melanoplus bivittatus (Say) (Tables 27, 30, 33; Figs. 23, 32).—The two-lined locust is listed by Peairs (1940) among what he terms the five important species of grasshoppers which are widespread as well as destructive. This conspicuous member of the prairie fauna overwinters in the egg stage in the ground, hatches in the spring, and appears as adults in midsummer. It continues feeding until cold weather kills it. Grass is the normal food for grasshoppers, but this species will feed on nearly any kind of vegetation. Dry conditions probably favor hatching.

Remarks on grasshoppers as a group or as species in this study should be prefaced with the note that it is probable that sweep collection records do not furnish data which truly reflect grasshopper populations. The life habits, especially the alertness and escape responses of grasshoppers are thought to make it impossible to take completely reliable sweep net samples of grasshopper populations in daylight and in warm weather. It is felt that night sweeps might give a more accurate picture of grasshopper numbers, presuming, of course, that darkness covering the activities of the investigator leaves the grasshopper comparatively little disturbed until taken.

Melanoplus bivittatus made its earliest appearance as nymphs in the southwesterly sloping (ravine) tall-grass station, in a sample of the herb populations taken on April 25, 1938. A week later the species was present in all stations, but produced its greatest numbers in the tall-grass habitat, where it appeared in 49.2% of all day sweep samples and comprised 5.7% of the entire (annual) population. It showed peaks of abundance in both postclimax stations for the two weeks ending May 23; in the tall grass its collection average was 67 during this fortnight and it made up 19.9% of the population (Fig. 23); in the deciduous shrub station it yielded 30 specimens per collection and furnished 6.8% of total numbers.

Melanoplus bivittatus was taken in 16.6% of the daytime collections in the shrub stratum, but comprised only 0.14% of the specimens taken. The species apparently disappeared first in the true prairie subsere, although mowing undoubtedly confused the picture here, and was last taken in the postclimax vegetation in mid-October.

Lygus pratensis (Linn.) (Tables 27, 30, 33; Fig. 23).—After wintering in trash and debris of all kinds, adults of *Lygus pratensis* appear with the first warm days of spring. Older nymphs and eggs may also survive winter. After their spring emergence bugs of this species feed for awhile in grassy fields and on weeds. There may be several generations per year; in the autumn the life cycle occupies 30-35 days (in Missouri), probably less in the earlier, warmer part of the year (Herrick 1925, Fernald and Shepard 1942).

Blake (1926) found the tarnished plant bug appearing "in considerable but varying numbers throughout" the period of his study on the animal ecology of deciduous forest in winter in Illinois. He found it in increasing numbers on the shrub and herb strata during the fall; it then disappeared from these epiphytic strata and "became abundant in the leaf stratum" (on forest floor) . . . indicating "an inward migration from the forest border, followed by a downward migration into the leaves, similar to that described by Weese for several species of forest-border beetles in this same habitat." Adams (1941) likewise found *Lygus pratensis* to be a "hibernating species which occurred in the ground stratum during the winter." Both authors report it on the herbs and bare shrubs on "warm" winter days.

The tarnished plant bug was taken in all of the habitats studied, its greatest numbers occurring in the tall-grass and shrub stations where its annual collection frequencies were 31.1% and 36.0% respectively, comprising 14.0% and 15.1% of the respective populations. Its classic late autumnal and early hiemal behavior in the herb stratum of hibernation cover was evident in both postclimax stations. In the tall-grass habitat it showed such high values that it became the autumnal prevalent of the herb stratum in that station (Fig. 23). There, during the two-week period ending October 22 its average sweep sample number was 80, making up 31.3% of the total specimens taken. One collection during that period, made during the forenoon of October 15, contained 232 specimens of *Lygus pratensis,* a value 60.6% of the total sample. Its autumnal peak in the herb stratum of the shrub habitat occurred two weeks later than that for the tall grass, in both 1937 and 1938. This possibly suggests a movement from tall-grass situations to shrubby cover following an earlier concentration in the tall grass, or a movement of at least a part of the tall-grass concentration. This is further suggested by the fact that collections from the litter stratum taken throughout the hiemal period showed *Lygus pratensis* to be hibernating in that stratum in both postclimax stations, but in much greater abundance in the shrub area. Only 3.3% of the litter collections in the tall grass produced bugs of this species, while a third of those from under the shrubs contained the species. The bug was present in low numbers in the grassland stations throughout the prevernal-vernal, estival, and early autumnal aspects, but in low numbers infrequently taken. During the month of May in 1938, large numbers of hemipteran nymphs were present in the shrub station; they may have been and probably were nymphs of *Lygus pratensis.* Unfortunately, they were not reared to adults or identified as juveniles.

Prenolepis imparis (Say) (Tables 27, 31, 33; Figs. 24, 26, 28, 29, 34).—The ant, *Prenolepis imparis,* was the early hiemal prevalent in the ground surface stratum of postclimax tall grass and deciduous shrub, as determined by pitfall studies during 1939. During the two weeks ending October 7 this species exhibited a population peak constituting 30.5% of the total ground surface population values for the same period; its annual collection frequency in this site was 45.8% and it comprised 5.5% of the annual population (Fig. 29). In the tall grass its peak of abundance occurred in the following fortnight with an average colletcion value of 15, making up 15.8% of all specimens taken. It likewise produced a peak of abundance in the subseral true prairie, during the fortnight ending July 15 with a take average of 21 and a total population percentage of 2.7. Despite these lower values for the grassland stations during the period of its population peak, its annual collection frequencies in these habitats exceeded those for the shrub, being 60.0% in the upland prairie and 66.6% in the tall grass, its proportion of total populations in these two stations 3.8% and 5.1%, respectively.

Prenolepis imparis, according to Bare (unpublished manuscript and personal communication) is a very common ant throughout eastern Nebraska, where it nests in the ground, preferring heavy clay soils in moist locations, particularly in woodlands. It is active mainly in moist, cool weather, inactive through the hot, dry portion of the summer. The workers attend aphids and feed on "honey dew."

The cosmopolitan horizontal distribution of *Prenolepis imparis* in the prairie tract studied has already been indicated; it showed deep distribution vertically, as well. Dowdy (1947) found *P. imparis* one of the most abundant species of ants in oak-hickory forest, and distributed "through all five strata." It was present in 29.2% of the shrub stratum collections, but formed only 1.8% of the total population taken. It showed a peak of abundance in this stratum for the two-week period ending May 9, 1938, averaging 40 specimens per collection and making up 3.5% of the total numbers. Under the shrubs it was showing a peak in the herb stratum for the same period, averaging 30 specimens per sample here and yielding 10.0% of the total take.

A second peak of abundance in the herb stratum of the shrub station which occurred in the fortnight ending October 22 sents its collection average up to 120; its total population proportion was, however, down to 5.0%. It is of special interest to note that the aphid, *Anoecia graminis,* produced its population peak in this same situation, to which it was confined, and in the same period (Fig. 26). The "tending" relationship with *Anoecia graminis* is further illustrated in the daily curves for the two species as presented in Figure 34, those for the autumnal period being especially clear.

Prenolepis imparis was taken in 100.0% of the night collections made in the herb stratum of the shrub station (June 18 to October 21, 1938), yet yielded only 3.6% of the total take. Its night collection numbers showed a peak corresponding with that for day collections for the two weeks ending October 22, its collection average being less than that for the day sweeps, but comprising slightly more of the total population. Its night population in the herb stratum also showed a high for the fortnight ending June 20; *Anoecia graminis* was also present in the herbs at this time but in much smaller numbers than at its remarkable late autumnal peak (Fig. 26).

Blissus leucopterus (Tables 27, 30, 33).—The chinch bug has been labeled as one of the most injurious insect pests of cereal crops in the United States (Swenk and Tate 1941:3). That this important crop pest maintains itself from year to year in grassland has been pointed out by Osborn (1939:174), being also injurious to grasses (Herrick 1925:366), feeding on all the grasses (Fernald and Shepard 1942). Although it hibernates in many situations, such as "leaves and litter under borders of woodlots," its favorite and most successful wintering place in the plains states is in the dense tufts of bunch grasses, especially the blue stems (Whelan 1927, Swenk and Tate 1941:5).

Emergence of the hibernating population of chinch bugs is gradual, and the spring dispersal to small grains and grasses usually begins when temperatures attain 70°F. or more for a few days in succession. In Nebraska this usually takes place in early April through May. Egg deposition is irregular also, taking place at or just below the surface of the ground from late April to late June. The first generation appears in about 45 days, and in the middlewest young of a second generation appear in August and early September. *Blissus leucopterus* is particularly affected by weather conditions, apparently being favored by dry weather. Heavy spring rains during the hatching period are said to be suppressive (Herrick 1925:320, Osborn 1939:175, Swenk and Tate 1941).

Blissus leucopterus, reported as an original inhabitant of true prairie (Clements and Shelford 1939:275), was the prevernal-vernal and hiemal prevalent in the litter of postclimax tall grass. In this habitat it was taken in 46.7% of all litter collections. In eight collections made here from May 9 to October 8, inclusive, a period encompassing the entire estival aspect, no chinch bugs were found. Out of 18 prevernal-vernal, autumnal, and hiemal samples from the litter stratum of the tall-grass habitat, 14 contained chinch bugs, the numbers ranging from 1 to 102 per square foot sample. This bug was also taken with approximately the same frequency in litter collections under the shrubs but averaged less than one-third as many individuals per collection. Its autumnal appearance in the litter stratum was discovered in collections made on October 15 in both ravine stations. Out of 23 prevernal-vernal, estival, and autumnal collections of litter in the true prairie subsere, only one contained chinch bugs, and that only two specimens.

Sweep collections took chinch bugs in the herb layer only in March, April, May, late September, and October, and these in greatest abundance in the tall-grass habitat. This suggests its virtual absence from the prairie tract during the estival and early autumnal aspects.

Chalcoides fulvicornis (Fabr.) (Tables 27, 31, 33; Fig. 27).—This flea beetle was the prevernal-vernal prevalent in the shrub stratum of postclimax deciduous shrub. Occurring in 79.2% of all shrub layer collections, it attained its peak during the fortnight ending April 25, averaging 185 specimens per unit sample and comprising 23.5% of the total numbers. It was also taken in the herbs of this station but in numbers so low as to suggest that it was in this stratum accidentally.

Erythroneura sp. (Tables 27, 31, 33; Figs. 27, 35).—Population values determined for this leafhopper show it to have been the estival-autumnal prevalent in the shrub stratum of the postclimax deciduous shrub station. In this situation it appeared in 79.2% of all day time collections, and in 100.0% of all night collections. It made up 8.3% of the day time population, 22.4% of the night population. In the fortnight ending August 1, 1938, *Erythroneura* produced its population peak, showing 175 specimens per unit daytime collection and comprising 22.6% of the total population. In the following two weeks it showed a peak in the night sweeps, averaging somewhat fewer specimens per collection, 155, but forming a greater percentage of the animals present, 33.3%. These data suggest that either (1) in the event this invertebrate population thinned out of the shrub layer under the impact of night conditions, the population of *Erythroneura* was less affected, or (2) night conditions increased the susceptibility of this leafhopper to capture by the sweep net to a greater degree than it did the remainder of the animals present. However, autumnal averages show the night P.M. and night A.M. collection values of *Erythroneura* in ascendancy, and an upward movement into the shrub stratum during the cooler and more moist portion of the daily cycle is suggested (Table 33; Fig. 35).

Peairs (1941) lists six species of *Erythroneura* as grape leafhoppers. "There seems to be little important difference in the biology of the various species," Peairs says. They winter as adults, feed on plants other than grape before grape foliage becomes plentiful, and produce two broods per season. Adults of the second brood go into hibernation when forced by lack of food and occurrence of frosts. Early season rainfall seems to be unfavorable to these leafhoppers. Defoliation of infested trees may be several weeks earlier than that of trees free of the insects.

Adams (1941) found three species of *Erythroneura* the "most common species of leafhoppers in the tree stratum" in the "young elm-maple stage of a deciduous forest climax" in Tennessee, where they were "occasionally taken from the herb and shrub strata at noon and in the late afternoon" in small numbers. Blake (1926:95[459]) listed *Erythroneura obliqua* as one of five "predominants from the summer shrub societies" of deciduous forest in Illinois.

In the postclimax deciduous shrub station *Erythroneura* sp. was taken only in the shrub stratum.

Dikraneura abnormis (Walsh) (Tables 27, 31, 33; Figs. 25, 26, 34).—The distribution of this autumnal prevalent in the herb stratum of postclimax deciduous shrub illustrates rather sharply defined habitat preference. It was taken only in collections from that situation, in which it was prevalent. Present in these sweeps from June 12 to November 11, 1938, it apparently produced two peaks of abundance—the first in the two-week period ending August 29 when it formed 31.2% of the population of the herb stratum, the second and lesser peak for the two weeks ending October 8 when it comprised 10.2% of the numbers collected.

Anoecia graminis Gillette and Palmer (Tables 27, 31, 33; Figs. 25, 26, 34).—Making its autumnal appearance in the herb stratum of the postclimax shrub habitat in sweeps made on September 18, 1938, this aphid produced its population peak by the middle of the fortnight ending October 22, and attained the rank of early hiemal prevalent in this society. It shared confinement to this habitat with the leafhopper, *Dikraneura abnormis,* and was responsible for 12.4% of the dramatic total population peak in this stratum and station for the two-week period ending October 22 (Fig. 25).

Patch (1938:60) lists *Anoecia graminis* as feeding on grasses of the genus *Hordeum*. Steiger (1930:188) lists two species of *Hordeum* growing on "disturbed areas" within this prairie tract. Whether this genus of grasses was present among the herbaceous growth of the shrub station in 1938 is not known. Osborn (1939:165) states that *Anoecia corni* (Fabr.) and *A. querci* (Fitch) alternate between grass and dogwood, being found on the latter in the autumn, and that *A. querci* is largely dependent upon ants. Indications of this aphid's relationship to ants as shown by this study have been reviewed in the account of the ant, *Prenolepis imparis* (Fig. 34).

Geotomus robustus (Uhler) (Tables 27, 31; Fig. 28).—According to Comstock (1940) members of the hemipteran family Cydnidae burrow in sandy places, or are found on the surface of the ground under sticks and stones, or at the roots of grass or other herbage.

This bug was almost wholly confined to the shrub habitat where it was taken in soil, litter, and ground surface collections. In the latter stratum it was present in 76.0% of the collections, comprised 33.7% of the total number of invertebrates taken, and during the two weeks ending September 9, 1939, appeared in such numbers as to force a striking population peak (Fig. 28), 470 specimens comprising 69.3% of the total two-week take. Its numbers in the soil built up perceptibly toward late autumn. It thus became the autumnal prevalent in the soil and ground surface strata of postclimax deciduous shrub.

Also noteworthy is the complete absence of this burrowing bug from the pitfall collections in the shrub habitat during the two weeks ending July 22, before which it declined rather steadily from its early summer level, and following which it built up to its remarkable autumnal high.

Leiobunum sp. (Tables 27, 31; Fig. 28).—The harvestman, identified here only to genus but apparently conspecific, showed two periods of marked abundance in the ground surface stratum of postclimax deciduous shrub where it was the estival prevalent. Although the phalangid was taken in 75.0% of the pitfall collections in this situation, both highs had the appearance of eruptions. During the week ending July 8, 1939, a single specimen was taken in the week-long gather of the alcohol pitfall; in the following week 98 were collected. In similar manner, no specimens were taken during the week ending August 19, 7 were taken in the next, and 117 in the next, ending September 2. This seemingly eruptive behavior may have been more apparent than real due to the nature of the pitfall, which is subject to appraisal in another part of this paper. Very small numbers of this arachnid were taken in the pitfall in the tall-grass station.

Ataenius cognatus Lec. (Tables 27, 31; Fig. 28).—Confined to the postclimax deciduous shrub habitat, this dung beetle was the hiemal prevalent in the soil stratum of that station, its litter values being negligible. The little scarab's presence and activity under the shrubs throughout the vernal, estival, and autumnal aspects was evidenced by its frequency of 80.0% in the ground surface (pitfall, 1939) collections in which it comprised 10.1% of the numbers taken. In the collection for the two-week period ending August 12 its population peak was realized, a take of 163 comprising 85.3% of the beetle population and 59.9% of the total.

Discussion

The horizontal distribution of physical environmental factors through the three habitat complexes studied, *viz.*, upland true prairie (in subsere due to recurrent drought), postclimax tall grass, and postclimax deciduous shrub, was apparently somewhat comparable to their vertical distribution within the shrub community. These measurable factors would not, of course, present a graded horizontal series such as those pointed out by several workers for the vertical gradients of physical conditions in forests. Although the data presented here regarding evaporation, an environmental force now established as a fairly reliable index of the combined operation of other physical factors of the atmosphere, are inadequate, measurements of this force in the three vegetational units point to this analogy. Of the three habitats, the upland true prairie exerted the greatest evaporation stress upon its herb inhabitants, the deciduous shrub the least, but the inhabitants of the shrub stratum in the latter community were subjected to rates which approached those in the herb layer of the prairie. The analogy is especially clear when the grouping of wind velocity values is considered, this environmental factor and that of evaporation apparently being closely related. The picture of physical conditions in the soil is somewhat less conclusive, yet even in this stratum the differences show a discernibly consistent pattern of distribution through the three habitats. Because of the agreement of life form of the vegetation in the upland true prairie and the included areas of postclimax tall-grass, conditions in these two habitats might be expected to approach each other rather closely, with both at considerable variance with those of the shrub area. This is not always shown, however, especially as regards soil temperature values and wind velocities. Indeed, individual factors exhibited gradients of their own, presenting a complexity of physical conditions which can be thoroughly understood only after measurements of micro-climatic phenomena more detailed and minute than were carried out in this investigation have been made.

The faunal gradient, if the distribution of the invertebrates through these three habitats may be so characterized, was probably in part correlative to this pattern of environmental factors, but due to inter-specific relationships of the animal species, would be less susceptible to analysis. Comparative analysis has disclosed that the communities of invertebrates occupying these three vegetational complexes showed recognizably different though related structure. The population patterns of subseral true prairie and postclimax tall grass, whether considered quantitatively or qualitatively or on the basis of seasons, strata, or daily fluctuations, showed the closest relationship; those of the postclimax deciduous shrub were markedly different from either of the grassland habitats, although certainly related to them. This suggests that the life form of the vegetation, dominating the habitat, is of primary importance in determining the animal communities; the closer relationship of the grass habitats would, of course, be expected. Blake (1926:95-96[459-460]), in his comparison of animal communities of coniferous and deciduous forests, concluded that ecologically it was "the forest cover, that is, the biotic association as a whole," that was "the determining factor for the presence of a typical forest animal community"—that the "nature of the trees" was of secondary importance. The postclimax deciduous shrub habitat studied here closely approaches forest margin conditions although geographically at some distance from deciduous forest as such; the animal communities of the shrub station appear more closely related to deciduous forest communities than to those of the contacting and surrounding grassland. This picture strongly suggests the important bearing of biotic differences (or similarities) of habitats upon horizontal distribution of animals, acting in combination with, but somewhat precedent over the differences (or similarities) in physical factors. Because of topography and farming operations shrub areas such as this are often discontinuous and without connection with the deciduous forests of stream valleys; they present islands of forest margin communities that are interesting ecologically and readily subject to detailed investigations.

In the ground surface stratum ants were precedent (on the basis of numbers) in the two grassland stations, while Hemiptera ranked first in the shrub habitat. Coleoptera maintained a close second in all three situations. The two prairie habitats were characterized in the ground surface stratum by (1) the same two insect groups, namely the order Coleoptera and the family Formicidae, (2) prevalents and subprevalents in the same insect family, namely Carabidae and (3) by the prevalent ant, *Crematogaster lineolata*. Beetles and ants were prominent, though less so, in the shrub station. Species of beetles which showed prevalent and subprevalent values at the ground surface in the shrub station and the upland prairie represented families of little or no prominence in the tall grass. Distribution of animals and the consequent variation in community structure are, of course, the result of responses to a maze of environmental factors which operate in an effort to satisfy many and changing physiological needs—a complex phenomenon that is reflected in *habitat preference.* Probably more reliable than group differences in this comparison of structure are the habitat choices evidenced by certain species, that is, degree of faunal relationships of the three habitats is probably best expressed by species distribution. For example, the beetle, *Pachybrachys litigiosus,* was an estival subprevalent in both of the grassland stations, but was at all times absent in the shrub complex. The scarabaeid, *Ataenius cognatus,* was confined to the soil and ground surface strata of the shrub area, and the cicadellid, *Erythroneura* sp., was taken in no other sweeps than those made in the shrub stratum of that station. These latter two illustrate, as well, the integrity of stratal societies. On the other hand, *Balclutha abdominalis* was the estival prevalent in the herb stratum of all three stations. A comparison of the distribution of prevalence shown by the 18 prevalent species is interesting in this connection: Two prevalents prevailed in only Station 1, three in only Station 2, three in only Stations 1 and 2, one in only Stations 2 and 3, two in all three stations, and *seven* in only Station 3. These habitat relationships of the prevalents further indicate the faunal correlation of the two grassland stations, and will be considered somewhat further in discussion of prevalents. The greater diversity of animal population structure in the shrub habitat suggested here is probably in part due to the greater internal diversity of habitat, as suggested by Dowdy (1944a:220).

The structural differences in invertebrate communities in the three habitats studied are reflected in the relative rankings attained by major groups within the habitats. The Homoptera, the most abundant group (insect order) found in the aerial strata (as determined on the basis of day sweep collections), composed 33% of the invertebrate population of the herb stratum in the true prairie, an order population 15% greater than that of the second-ranking Coleoptera. In the herb stratum of the postclimax areas, however, the Homoptera were numerically subordinate to the Diptera, and in the shrub stratum, to both Diptera and the winged Hymenoptera. Diptera in first rank in the postclimax stations was relegated to fourth rank in the upland true prairie, with the winged Hymenoptera taking relatively low rank in all societies other than the shrub. The population values of Coleoptera approached each other in the herb of true prairie and the shrub stratum of the shrub complex, tending toward a common but much lower value in the herb stratum of the tall-grass and shrub stations. These are hard-bodied insects and are considered as less affected by evaporation stress than such forms as the Diptera and Homoptera. The Orthoptera showed more striking values, ranking third in both the true prairie and the tall-grass areas, i.e., possessing approximately equal population values in the two grassland communities, while attaining rather low rank in both epiphytic strata of the shrub complex.

Shackleford (1934) has mentioned "the integrity of the seasonal societies" as a striking feature in mixed prairie populations, stating that "no forms were abundant throughout several consecutive seasonal societies." This study has borne out that conclusion, although it was found that certain species, such as *Balclutha abdominalis* showed population peaks in consecutive seasons and tended to characterize the populations of those two seasons. The combination of abundant species characteristic of one season did not carry over into a following aspect, however, the faunistic composition appearing to change continuously and at times at a rate discernible from day to day. This would be expected, of course, in view of the known variance in emergence and maturity characteristics of insects.

Expression of the prevernal aspect faunistically preceded its expression floristically. Prevernal activity of invertebrates above the surface of the soil began in the shrub community well in advance of that in the other two communities. Such aerial and epiphytic activity, even in the hiemal aspect, appeared generally to be initiated when ascending temperatures reached about 40°F., and was indulged in by relatively very few species.

Definite peaks of total populations occurred in all communities, those of the aerial and ground surface strata being most convincing, possibly because of more reliable collecting methods in these strata. Populations of single species, relatively few in number, appeared largely responsible for population peaks in their respective orders, and contributed in considerable proportion to total population peaks. This relationship has been brought out in earlier community studies. In some instances, group (order) population peaks and, in turn, total population peaks were forced by single species (prevalent and subprevalent) populations. In the herb stratum of subseral true prairie Homoptera and Coleoptera attained their annual (estival) peaks simultaneously. Both the herb and ground surface strata in this station produced estival peaks of population, although in this study the two strata were studied in different years and the chronological relationships of the peaks are not clear. Prevernal-vernal and estival population peaks of certain arthropods were coincident with periods of anthesis of certain plants or groups of plants. Autumnal peaks of total abundance in the herb and ground surface strata, of much greater magnitude than any other highs in their respective strata, were produced in the postclimax deciduous shrub habitat.

The spectacular autumnal highs in the shrub station might indicate an inward and downward movement of grassland species showing pre-hibernation activity. This cannot be considered categorical, however, since the ground surface peaks, as determined in this study, were forced almost exclusively by two species largely confined to this situation. The picture of the autumnal high in the herb stratum is not so clear, but likewise appears to be in considerable measure the function of endemic (although many) species, especially flies. The "inward and downward" movement of arthropods seeking hibernacula, pointed out by Weese (1924) and Blake (1926), did occur, however, most convincingly evidenced by three species of Hemiptera, in both postclimax tall grass and deciduous shrub.

Population peaks may or may not reflect maturity. According to Dr. Martin Muma, Citrus Experiment Station, Lake Alfred, Florida, bugs of the family Nabidae, for example, cannot be swept in any appreciable numbers while still nymphal, but seem to erupt at maturity in a given vegetational unit. Unfortunately, no maturity studies were made in this investigation.

Just as a species tends to have a center of abundance in its horizontal distribution, so its population values will tend to remain highest at its stratal optimum, thinning out above and below the optimum. The dimensions of stratal limits are probably not identical for any two species. Thus, in any given habitat, there may be many degrees of overlapping by many species. Stratal limits, dictated by the habitat requirements of the species, the general meteorological conditions, the vegetation, and the time of day, may be shallow at one time, deep at another. So may the vertical distribution or layering of the animal fluctuate. A species with deep distribution may occur commonly in two or more levels that have been arbitrarily selected for study and may, thereby, be pointed out as occupying more than one stratum. Arbitrary aerial strata primarily reflect the apparent and well defined layering of vegetation; the gradient factors of the atmosphere, measurable but usually without definite limits, are secondary in determining choice of strata to be examined. It is further conceivable that some species of invertebrates might be distributed through all of the strata chosen, named, and studied as expedience demanded, appearing thereby to conform to no stratal organization as conceived by the investigators.

Stratification of physical factors is precedent over stratification of animals, i.e., vertical distribution of physical environmental factors is not dependent upon animal distribution, at least not directly. The stratal organization of a biota is, on the other hand, in part a response to the vertical gradients of such forces as light, wind, temperature, humidity, and the comprehensive factor, evaporating power of the air—"in part" because such response to physical factors produces a stratification of biological factors which, in turn, exert pressures on and lead to further stratification of other members of the community. These biological pressures are exerted through the requirements for food, shelter, and reproductive activity. Invertebrate animals feeding as adults on, through the surface of, or within roots, stems, leaves, flowers, or fruits become stratified according to their needs just as those biological sources of food are stratified. Blake (1926:65[429]) has pointed out that "a very large number of phytophaga indicate by their vertical distribution that the stratum in which they are found is determined by the presence of the host plant." These same animals may require different sets of conditions at different stages of their life histories, or, as adults, while they are quiescent, resulting in a regrouped but nevertheless defined stratal distribution. Physical factors must remain within certain limits to allow an organism or a group of organisms to successfully respond to the biological factors in a given habitat. Physical shifts may occur beyond these limits forcing still other regroupings that ignore biological pressures. It becomes more nearly accurate to state, therefore, that stratification of both environmental forces and invertebrate animals exists subject to continuous fluctuations of both limits and composition. The very dynamics of stratal distribution may be verification rather than refutation of the concept of such community organization.

Evidence of (1) stratal choice by groups and by species, so well defined in such species as *Chalcoides fulvicornis* and *Anoecia graminis* as to result in virtual stratal confinement, and (2) stratal shifts in physical factors and coincident shifts of groups or species of animals have been pointed out. The role of biological factors in determining stratal distribution is illustrated by the presence of *Chalcoides fulvicornis* almost exclusively in the shrub stratum during anthesis of the wild plum. That biological factors may shift with a daily rhythm is illustrated by the *Prenolepis imparis-Anoecia graminis* relationship. It is not known in this instance, however, which insect is primarily responsible for the shift; the relationship of physical factors to the movement is even more obscure.

Carpenter (1935) has reviewed the few studies which up to that time had been directed toward daily fluctuations of invertebrate populations in prairie-forest ecotone, pointing out the general conclusion that "periodic fluctuations in insect populations take place throughout the several periods of the day much as they do from season to season and year to year." "The importance of daily cycles is appreciated," Carpenter states, "when it is recalled that fluctuations of all kinds play a tremendous role in food chain relationships." Davidson and Shackleford (1929) studied this problem during the vernal aspect in a central Oklahoma prairie.

Adams (1941:214) concluded "that the animals of the forest are on the whole stratified" and that "while there was some diurnal movement from strata to strata on the part of some species, on the whole this was negligible."

Measurable daily fluctuations of total populations of invertebrates occurred in the herb and shrub strata as considered in this study. These population fluctuations appeared coincident with fluctuations in physical factors of the environment as measured, principally temperature of the air, relative humidity, and wind velocity, and were expressed both quantitatively and qualitatively. The behavior of prevalent and subprevalent species presents some evidence of qualitative changes in the invertebrate groupings within the daily cycle.

Seasonal changes in the structure of the invertebrate population in any given stratum, are inevitable under the influence of such phenomena as emergence, anthesis, breeding requirements, and death. For example, in the shrub stratum during the flowering period of *Prunus,* Diptera composed 34% of the total population, during the flowering of *Cornus* about 6 weeks later 24%, and for a two-week period at the end of the estival aspect, 25%. Homoptera built up from less than 1% of total population values in the *Prunus* period, to a value of 46% at the close of the estival, with a 10% value for the *Cornus* period. Such seasonal fluctuations in stratal structure do not obviate the concept of stratification. It becomes evident, however, that discernment of stratification of animals, if it does occur, is easier on the basis of short-time observations. Seasonal fluctuations, and even daily fluctuations tend to obscure the groupings. It is further suggested that the larger taxonomic groups (orders and families) may in many instances constitute a false premise on which to base recognition or evaluation of stratifiaction, at least in aerial strata. Innate life habits and the consequent habitat requirements within these groups are not sufficiently narrow to warrant such an attempt. The concept and analysis of stratification must be based primarily upon the vertical distribution of single species groups.

Considering first the daily patterns only for much of the estival aspect, it is seen that total populations in the herb stratum in true prairie subsere and postclimax tall-grass showed related but somewhat different diel curves. The night P.M. population produced the highest value in both of these stations; in the subseral prairie the night A.M. population was lowest, in the tall-grass the day A.M. population was lowest. On the basis of values gathered within shorter periods within the estival aspect, however, the daily curves for the two grassland stations more closely approach a common pattern (Figs. 31 and 33). This curve is at variance with the findings of Davidson and Shackleford (1929) who state that the herb population (in prairie in Oklahoma) "reached its daily maximum between midnight and three A.M., and had a second lesser peak between noon and three P.M." Differences in timing of collections in the two studies may in part account for these discrepancies in fluctuation patterns. These authors concluded that larger numbers of specimens were taken in their collections due to inactivity of the insects during the warmest and coldest portion of the 24 hour cycle. It is suggested here that unless the warm part of the cycle suffered extremely high air temperatures during the period of their study (April and May), inactivity would not characterize that part of the day. The curves shown here do not bear out this conclusion, since in this study the fewest individuals were taken during the coldest of the four divisions of the 24 hour cycle, the greatest during a period of intermediate temperatures; during the period of high temperature intermediate numbers were collected.

During the field operations it seemed that because of heavy dews and the consequent saturation of the sweep net while making night collections, considerable portions of the populations of such soft and minute forms as leafhoppers might not be retrieved from the net if, indeed, they were swept from the vegetation. Examination of Table 32 and of Figure 36 shows, however, that, though some specimens may have been lost, the night collections were much of the time taking higher numbers than were the day sweeps. In this connection it is also of interest to point out that night sweep values for *Balclutha abdominalis* in the estival and autumnal aspects were, respectively, 69.8% and 69.5% those of the day sweep values, in the upland station, although the estival abundance was four times the autumnal.

It is noteworthy that during the estival period and again in the late autumnal, the day sweeps produced more individuals than the night sweeps in the grassland stations, while during the interim the night sweeps were in the ascendancy. This would suggest either (1) the seasonal and transitory presence of night feeders in the popualtion which spent the day low on the grasses or on the ground surface, or (2) different daily fluctuation patterns due to changing patterns of factor shifts before and after the warmest part of the year.

The physiological responses producing the apparent downward movement of the invertebrate populations in the shrub area are not clear. Because of cold air drainage, so evident in ravines on still summer nights, it seems that temperatures would be lowest at the ground surface. It has often been pointed out that animals do migrate from situations of apparently unfavorable environmental conditions to those which appear more favorable, and this, with "the presence of an 'innate rhythm' " is suggested by Carpenter (1935) as possible causes of population fluctuations. Downward movement at night of animals occupying the shrub stratum during the daytime, where high afternoon temperatures presumably obtain during the summer and evaporation rates approach those in open grassland (Fig. 13), must result from altered physiological needs resulting possibly in the absence of the light factor. It is not impossible that many of the shrub stratum forms do not migrate downward in the usual sense, but literally fall to the herb stratum. The answer to this problem will be found in closer scrutiny of key species in these populations and their physiological life histories.

A reciprocal upward nocturnal movement of ground surface forms was shown by the appearance of certain spiders, and especially the tenebrionid beetle, *Eleodes opaca,* all of which occurred abundantly in pitfall collections, in night sweeps in the herb stratum of all three stations.

There are obviously four major problems posed by these data: (1) Were different numbers of invertebrates taken in the herb and shrub strata at different times of the daily cycle because of (a) fluctuations in animal numbers within those strata during that period, or (b) because different combinations of physical factors so affected collecting techniques and the response of the animals to those techniques that differentials in take indicate fluctuations that are more apparent than real; (2) if the animals were actually less numerous in one or the other of the strata during a given part of the 24 hours than at other periods studied, whence did they migrate; (3) what factor or combination of factors dictated their movements; and (4) what accounts for the differences in estival and autumnal diurnal patterns of total populations?

While the effects of changes in physical factors of the atmosphere upon invertebrate populations are probably most easily observed in vertical and recurrent daily fluctuations, responses of invertebrates to non-rhythmic shifts in aerial factors were also apparent. Population depressions occurred in all aerial strata coincidentally with the annual peak of temperature (in 1938) which was accompanied by a low in relative humidity values, a minor high in wind velocity, and a distinct peak of evaporation rates. As a matter of fact, this seeming extreme of environmental stress apparently "notched" total population peaks in these situations. Here, indeed, is suggested a period of inactivity produced in part by high temperatures, but it did not result in the capture of more insects—rather, fewer were taken indicating some movement out of the aerial (epiphytic) strata. This decline in invertebrate populations was especially marked in the more moist habitats, i.e., the tall grass and deciduous shrub, and might, as concluded by Davidson and Shackleford, indicate accelerated activity. Movement to more moist, cooler situations, probably downward, is most convincingly indicated, however.

Autumnal peaks of population tended to accompany or immediately follow a well defined secondary peak of temperature in September and October of 1938. The temperature depression of early April, 1938 was reflected in lowered epiphytic population values which had just begun building up.

On the basis of described aspection and horizontal and vertical distribution and fluctuation of invertebrate (mostly arthropod) populations, the significance of prevalent species, as determined in this study, should be discussed. It has been suggested that the population characteristics of prevalent species, which are more readily analyzed than those of total populations, *may* indicate (or at least illustrate) the conditions and processes of habitats, and possibly various phenomena of total populations. For practical purposes in field studies the rank of prevalence as defined here would probably need not be determined. In fact, weaknesses have appeared in the designation of prevalence as employed here. For example, a species may acquire prevalence in a season other than the one in which its highest values are shown.

It is emphasized that numbers as such cannot be categorically significant. Satisfying the requirements of statistical analysis may not necessarily reveal the complex relationships of habitat and organic needs and responses. It is conceivable that certain species of lesser abundance might more nearly indicate the environmental offerings of a given habitat and the general requirements of the habitat's total population than any numerically superior species. Apparently more significant in the determination of indicator values than mere numbers is the degree of confinement to a given society. It is, thereby, obvious that the physiological life history of a species must be known before indicator values can be definitely assigned. The fact that a single species may force a total population peak cannot be considered conclusive as regards indicator values. Such specific highs may be eruptive and short-lived, and reflect but little regarding the nature of the habitat or the total population. Predatory species, such as spiders, may leave a destroyed or disturbed habitat and move into another.

Despite these weaknesses, there is evidence that prevalent species do present some indicator values. However, it is probable that no single prevalent (or any one species) can possess indicator values for all ecological phenomena in any given terrestrial habitat, i.e., one may indicate integrity of a society, another horizontal movement, dependence on more than one habitat, and innate changes in environmental needs, another fluctuations of physical or biotic factors or both through vertical movements, etc. The ecologist must know more about an individual species than its numbers, absolute or relative, to realize and reliably take advantage of its peculiar values as an indicator. In short, a blanket statement of indicator values is probably not possible.

Three of seven prevalents determined for the subseral true prairie (Station 1) were also prevalent in the tall grass (Station 2), which produced eight prevalents. Station 1 had one prevalent prevailing in three strata. The shrub habitat (Station 3) had one prevalent prevailing in two strata, and Station 2 had no prevalents prevailing in more than one stratum. These data, showing a tendency for closer confinement of postclimax species to their respective strata, may on the basis of distribution (stratification) indicate deeper strata and greater diversity in stratal factors in the deeper vegetation, i.e., the shallower the vegetational cover the more telescoped the strata as recognized on the basis of factor gradients, and, therefore, perhaps weaker definition of stratal societies. This suggests that in shallow strata the "spilling over" of animals might obscure stratal responses—that integrity of stratal societies is mechanically easier to maintain in deeper strata.

Just as plant communities, the members of which are adapted to each other and to their common surroundings, are more reliable indicators than individual plants (Weaver and Clements 1938:454), it may be found that animal communities are more reliable as indicators of conditions and processes than are individual species. Plant ecologists have shown, also, that "the dominant species are the most important indicators, since they receive the full impact of the habitat usually year after year" (Weaver and Clements 1938:454). The significance of *dominance* in terrestrial habitats is, of course, well understood; the significance of *prevalence* (i.e., numerical superiority by whatever term it has been designated) is much less if at all evident. The role of a species in a community is determined by more criteria than its numerical rank. The pitfall studies reported here have suggested the importance of *volume* of each species population in its biological significance within its community (Fig. 17). A prevalent species may produce much less bulk than a numerically inferior species. On the other hand, a minute species if present in great abundance might produce a greater volume than several less abundant, larger, and conspicuous species.

The naming of communities (societies, etc.) on the basis of numerical superiority of a few animal species (predominance of Shelford) supposes biological significance or indicator value. This predication needs examination. It is apparent that the various prevalents as determined in this study may indicate different conditions and processes of habitat, but that they are not consistently or equally useful. Before the name of any animal in a terrestrial habitat can be assigned to its community with ecological honesty, the life history of that species, and especially its influence upon the habitat, termed *reaction,* must be known in detail. Its effects upon the other organisms of the community, called *coaction,* must likewise be known.

Prevalence, while it may serve as an indication of possession by the prevalent of significant biotic or diagnostic value, does not necessarily establish the role of the species in the economy of the community. "The importance of any organism in the household of nature is primarily a matter of food; on the one hand, the amount which the organism consumes, and on the other, the amount it supplies for other species. This, in turn, depends upon the abundance of the species and on its size and rate of metabolism" (Young 1938). Neither does prevalence, or by whatever term simple numerical superiority is designated, submit a valid criterion on which to base the naming of communities. It is suggested that the role of an animal species in the complex bio-ecological processes of reaction and coaction shall determine its qualification as a community constituent upon which to establish the name of the community. Such fundamental significance is not ascertained with the expediency afforded by the superficial counting of more or less individuals. The effect upon vegetation is of prime importance in the ecological evaluation of animal species and their place in the classification of terrestrial communities. The measurement of such effects by invertebrate species is faced with many difficulties.

This importance of relationship to vegetation, probably more specifically to the dominant species, suggests a possible significance in the consistent occurence of a species throughout a unit of vegetation whether climax or seral, and the concept of *paradominance.* For example, suppose that samples of invertebrate populations are made in large numbers of true prairie remnants showing climax structure, i.e., normal abundance of dominant grasses. The consistent presence of a certain species of insect is revealed. Comparable collections in prairie where drought or other disturbances have largely or entirely eliminated the dominants, show inconsistent occurrences or the complete absence of this species. The insect is indicated to be a concomitant of one or more of the dominant grasses, and could be assigned the role of *paradominant.* This would be an ecological designation based upon *frequency,* not upon abundance or influence. A species could, however, simultaneously be paradominant, prevalent, and influent. Weaver and Clements (1938) state that "the visible unity of the climax is due primarily to the dominants or controlling species." If the concept of paradominance is valid this statement might be reworded to say that "the visible unity of the climax is due primarily to the dominants and the paradominants, or the controlling plant species and their accompanying animal species."

These considerations of the volume and frequency values of a species population further suggest the possible ecological importance of those species presenting relatively low numerical values. Although the prairie studied was not in climax (due to recurrent drought) certain species which were either subprevalent or without designated rank may be exemplary. The walking stick, *Diapheromera veliei,* the chrysomelid beetles, *Pachybrachys luridus* and *P. litigiosus,* and the scarabeid, *Phyllophaga lanceolata,* because of their size or frequency, did much to characterize the apparent structure of the invertebrate fauna of the prairie tract studied. Their known predilections for prairie plants suggest further important relationships. Yet, of these four consistently conspicuous and certainly characteristic species only one attained even subprevalence.

The marked decrease or disappearance of a so-called paradominant in response to losses suffered by the dominants is, of course, hypothetical. It is probable that such responses would show considerable lag, that disappearance, if ever effected, would be gradual. It is of some interest to note in this connection that the three species of beetles which attained prevalent values and two species which showed subprevalent values in this study are not listed as having been taken by Whelan (1936) in the same tract during 1928-30. Differences in collecting methods may have accounted for their absence in Whelan's list, however.

Appraisal of Methods

A comprehensive appraisal of the field methods used in this investigation is probably not possible on the basis of this short-time study, nor desirable in this report. Certain weaknesses were outstanding, however, and, though probably already recognized by many workers, should be briefly mentioned.

The problems involved in sampling the invertebrate populations of the soil and litter have been ably discussed at length by King (1939). It is felt that in this study the soil and litter samples were too few in number to yield conclusive data, probably due to (1) the unequal horizontal distribution of the invertebrates in these two strata, also pointed out by Dowdy (1944a), Blake (1945), and others, (2) inefficiency of the washing technique used for securing invertebrates from the one-third cubic foot soil sample, and (3) limitations of the investigator in sorting the animals from the debris of the litter samples.

While the sweep net continues to be the best device for sampling epiphytic and aerial populations of invertebrates, it is probable that sweep samples do not secure the whole picture (see also Muma and Muma 1949). The possible inadequacy of sweeps in sampling grasshopper populations and the complicating effects of dew have already been mentioned. The sweep net obviously does not sample any populations concentrated at or very near the bases of herbs, a distribution thought possibly to have occurred in this study under the telescoping effect of lowered temperatures on stratification, and left undetermined. The physical difficulties and the inefficiency of sampling the invertebrate population in such head-high shrubby vegetation as wild plums with a sweep net is immediately and painfully evident to the investigator. Only the periphery of such cover can be sampled; the interior of the shrubby thickets were often "alive" with aerial activity of flies, a stratal society that defied sampling with a sweep net because of the nature of the woody cover. Even in cover which is readily sampled with the net continuous care must be exercised to maintain a standard. Wind, darkness, terrain, variations in height of the vegetation, and fatigue of the investigator all serve to operate against securing the desired standardization of samples. It is probable that in most community studies carried on to date sweep samples, although made and handled with relative care, have left some of the story of populations undiscovered because of too infrequent use. Only high frequency and hard work can in part compensate for the weaknesses inherent in the sweep net sampling technique.

While the alcohol pitfall method of collecting devised and used in this study is remarkably easy, it cannot be considered as a sampling method, at least not in the same sense as other methods. Its gather is continuous and dependent upon the movement of the individual animals. It may, thereby, be more efficient as a measure of activity than of population density, and as such may be most valuable in determining activity patterns in the ground surface populations of invertebrates thereby serving best as an adjunct to true sampling procedures. In this connection, Muma and Muma (1949) have pointed out the heavy preponderance of one sex or the other of certain prairie spiders in pitfall collections. The alcohol pitfall has the advantages of (1) operating in the absence of the investigator and thereby upon an undisturbed fauna, and (2) having its periods of take readily broken down into any subdivision of time that is desired. Its fixed position may result in thinning of the population in the immediate vicinity of gather, a possible weakness determinable by experimentation.

Finally, the following suggestions are offered toward possible improvements in studies designed merely or primarily for ascertaining population and community phenomena:

1. Thorough study can best be accomplished on one habitat at a time. Simultaneous comparative studies are fascinating and for many purposes desirable or indispensable, but the mimimal standards of sampling and the weight of data gathered can be beyond the limitations of the investigator.

2. A habitat that is distinctly uniform over a large area will yield the most reliable community information. Dowdy (1944a:220) has pointed out that "uniformity of habitat makes for a limited number of species but the number of specimens might be great." These conditions lend strongly to ease of operations as well as reliability of data gathered.

3. To base community (society) nomenclature upon short-time studies appears ill-advised (see also Blake 1931). The naming of ephemeral and possibly non-recurrent though striking groupings of invertebrates results only in "cluttering the literature." Any investigation carried on for less than three years, albeit continuously, must be considered "short-time."

4. In studies on stratification and daily fluctuations mean values may be misleading. Detailed, on-the-spot, simultaneous (in so far as possible) measurements of both populations and physical factors are probably more reliable.

5. Detailed life history studies on as many species as possible within the habitat will help complete the picture of habitat-fauna relationships. These key species may be initially indicated by any combination of three criteria—prevalence, paradominance, or endemicity.

6. Laboratory studies may be necessary in analyzing and evaluating the responses of key species to environmental shifts as measured in the field.

7. The need for perfecting and employing methods of sampling the invertebrate populations of more and shallower aerial or epiphytic strata within the many kinds of cover is evident; for example, this study could have profited from unadulterated samples of the animals present on the herbs from 0-6 inches above the surface of the ground, or even within 0-2 inches.

Summary

The invertebrate fauna and environmental factors of upland true prairie (subseral in response to recurrent drought) and associated units of postclimax tall grass and postclimax deciduous shrub were quantitatively studied from November 2, 1937, to November 4, 1939.

Attention was focused upon (a) the differences in the environmental complexes within the three habitats studied, (b) the faunal interrelationships of these three stations, (c) horizontal and vertical movements as exhibited by stratal, seasonal, and diel values of total populations as sampled, and (d) the strato-seasonal activities of prevalent species.

Prevalent species were determined on the basis of strato-seasonal abundance, i.e., that species which showed the highest seasonal population within a given stratum thereby attained the rank of prevalent for that season, a designation which indicates only that the species prevailed numerically in that stratum.

A species which exhibited a seasonal population less than that of the prevalent, and which may or may not have equalled the frequency values of the prevalent, but which exceeded the population values of the latter at one or more brief intervals, even in any one sample collection, was considered as possessing subprevalent rank.

Four strata were studied in the true prairie subsere and postclimax tall grass, namely (a) soil, (b) litter, (c) ground surface, and (d) herb, with the addition of (e) the shrub stratum in the postclimax deciduous shrub station. The soil stratum was sampled to a depth of 10 cm. (4 inches), always beneath the one square foot of litter collected for examination from the litter stratum. The ground surface invertebrate fauna was studied by use of an alcohol pitfall, an apparatus which does not measure any given unit of population at any given time, but which does appear to indicate population trends. The population of the herb and shrub strata were sampled by the sweep net method at 0-75 cm. above the ground surface in the herb and at the 1-2 meter level in the shrub.

Seasonal studies (sweeps, and litter and soil sampling) were carried on from November 2, 1937 to March 20, 1939, the day-night (diurnation) studies (sweeps only) from June 12 to October 21, 1938, and the pitfall (ground surface) studies from April 8 to November 4, 1939. This study is based upon the collection and examination of 81,811 specimens of invertebrates.

The term invertebrate as herein employed includes only the phyla Annelida and Mollusca and the classes Arachnida (excepting the Order Acarina) and Insects (excepting the orders Collembola, Thysanoptera, and Corrodentia).

This study was conducted within a continuous tract of native true prairie one-half section in extent (Township 10 N.—Range 5 E., Section 2, east half), which is located five and one-half miles west and three miles north of Lincoln, Nebraska. Haying operations have constituted the only cultural disturbance to which the vegetation has been subjected, with the exception of grazing by a small band of horses during one winter about 1933.

Severe drought had been in progress for about four years in the true prairie region when this investigation was initiated. The grassland studied was in a generally reverse though fluctuating succession from true prairie to mixed prairie—a subsere induced by drought and marked by great, rapid, and com-

plex changes in the vegetation. Postclimaxes were less affected by the drought.

The true prairie subsere station was placed slightly below the rounded top of the next to the highest hill of the tract, on a south-southeast slope. *Stipa spartea, Bouteloua curtipendula, Andropogon scoparius, Koeleria cristata,* and *Sporobolus heterolepis* were the most abundant grasses, much bare soil surface being evident with little or no litter. *Psoralea floribunda* was the most prominent forb. *Erigeron ramosus* was markedly abundant in the subseral true prairie substations.

Average conditions of postclimax tall-grass habitat were found in a ravine which was centrally located in the tract and which drained to the south-southwest. Station 2 was established here, where *Andropogon furcatus, Elymus canadensis, Panicum virgatum,* and *Poa pratensis* characterized the vegetation, forming a dense sod, with *Aster* the prominent forb.

Station 3 was located near the northeast corner of the tract. Here an area some 20 yards long and about 15 yards wide was rather densely covered by *Cornus stolonifera, Prunus americana, Rhus glabra,* and *Symphoricarpos occidentalis,* and presented an ecological "island."

Measurable environmental (micro-climatic) differences were found to exist in the three vegetational complexes, most conclusively shown for the aerial forces of wind and evaporation stress and for the soil moisture factor. The horizontal gradient of wind velocity was steepest between the subseral true prairie and the postclimax tall-grass stations, while the gradients of relative humidity, evaporation rate, and soil moisture showed their highest values in the shrub station, indicating an approach here to the environmental conditions of forest margin.

The invertebrate communities of these three habitats exhibited recognizable distinctness, the structure of those of the tall grass and subseral true prairie being much more closely related than that of either of these to the communities of the deciduous shrub habitat.

Faunistic expression of the prevernal aspect preceded floristic expression.

Seasonal societies of invertebrates showed well defined correlations with floristic aspects, affording an indication of biotic influences in chronological distribution as expressed in innate rhythms of life histories. The integrity of seasonal societies, as determined by analysis of prevalent and subprevalent species was evident, though not infallible.

A few species occupied important rank in all three vegetational complexes, showing that inherent activity patterns and physiological needs of key species must be known before evaluation of populations can be determined and the biotic valence of their component parts be established.

Key species may be indicated by prevalence. Endemicity and paradominance, the latter a concept of ecological significance based on frequency of occurrence, may also define key species.

Prevalence, attained in a given season or stratum, does not necessarily denote that the greatest yearly abundance of the species is reached in that society, i.e., fluctuations in composition of communities, either spatial or chronological, may bring into prevalence a species which has not significantly altered its absolute population value.

Extremes of high temperature, wind velocity, and evaporation seemed to have less effect upon the invertebrate population of the true prairie subsere than upon those of the postclimax habitats.

Horizontal movements of insects from one community to another were evident, especially by members of the order Hemiptera during the prevernal and late autumnal aspects. These may be interpreted as resulting from changes in food and cover requirements. Responses to food source produce a horizontal distribution characteristic of periods of heightened physiological rate, while responses to cover requirements result in a horizontal-vertical redistribution which characterizes periods of lowered physiological rate.

Stratification of physical factors was discernible even in the comparatively shallow herbaceous cover of the prairie.

Vertical movements, in part characterizing the daily pattern of invertebrate population activities, apparently occurred in response to daily shifts in physical factors, especially in the deeper cover of the shrub station. The relative importance of causative factors in this relationship is not clear.

Populations of invertebrates in the grassland stations displayed two high points—one in the estival aspect, another in the latter half of the autumnal aspect.

The herb population of the deciduous shrub, proportionately higher than that of the grassland, exhibited an enormous peak of abundance in late autumn. This appeared to be due largely to the emergence and increase of endemic and distinctly woodland or forest margin species at this time.

The shrub stratum showed its peak of invertebrate abundance in the prevernal-vernal period coincident with anthesis of *Prunus*.

Litter and soil populations reached their maxima in the hiemal aspect, while the invertebrates of the ground surface showed a pattern of population values similar to that of the herb stratum.

Invertebrate population peaks in all situations were for the most part due to the presence of one or a few species whose numbers build up, rather than to general and concurrent increases of the many species comprising the entire population.

Homoptera, Coleoptera, Orthoptera, Diptera, and Hymenoptera (Formicidae) generally characterized the invertebrate fauna of the upland true prairie (subseral) tract and its included postclimax areas during the period of the study. *Balclutha abdominalis* (Homoptera), *Oscinella coxendix* (Diptera), *Pachybrachys litigiosus* (Coleoptera), *Crematogaster lineolata* (Formicidae), and *Melanoplus bivittatus* (Orthoptera) constituted the most abundant species within each of these orders.

Balclutha abdominalis was the most important species taken on the basis of numbers, frequency, and distribution.

The subseral true prairie presented an invertebrate population (principally arthropods) which may be characterized as follows:

(a) The herb stratum population was comprised largely of Homoptera, Coleoptera, Orthoptera, Diptera, Formicidae, Araneida, winged Hymenoptera, and Hemiptera in that order of group abundance; that of the ground surface largely of Formicidae, Coleoptera, and Araneida in that order of group abundance; that of the litter stratum largely of Coleoptera, Formicidae, Araneida, and Annelida in that order of group abundance; and that of the soil stratum largely of Coleoptera and Annelida in that order of abundance.

(b) In the herb stratum the cicadellid leafhopper, *Balclutha abdominalis,* was the prevernal-vernal, estival, and autumnal prevalent, the fulgorid, *Delphacodes,* was the estival prevalent; in the soil surface stratum the carabid beetle, *Amara* sp., was the prevernal-vernal prevalent, the ant, *Dorymyrmex pyramicus,* was the estival prevalent, the ant, *Crematogaster lineolata,* was the autumnal and early hiemal prevalent; in the litter stratum the enchytraeid earthworm, *Fridericia* spp., was the preverna1-vernal and estival prevalent, *Amara* sp. the autumnal prevalent, and *Piesma cinerea,* a bug. the hiemal prevalent. *Amara* was the annual prevalent in the soil stratum.

(c) Subprevalent or conspicuous in the estival aspect was the psyllid, *Aphalara veazei,* the walking stick, *Diapheromera veliei,* the May beetle, *Phyllophaga lanceolata,* and the chrysomellids, *Pachybrachys litigosus* and *P. luridus* in the herbs, the tenebrionid, *Eleodes opaca,* and the blister beetle, *Macrobasis segmentata* (Say) on the ground surface; in the autumnal aspect the fly, *Oscinella minor,* and the gryllid, *Oecanthus niveus,* helped characterize the herb society.

(d) Both herb and ground surface populations showed a major peak of abundance in the estival aspect and a less well defined autumnal high.

(e) Daily fluctuations in total numbers of invertebrates and in relative numbers of prevalent, subprevalent, and conspicuous species were found coincident with daily shifts in physical factors of the atmosphere in the herb stratum.

(f) Certain species found here in the estival and early autumnal aspects appeared largely dependent upon the postclimax habitats for hibernating cover.

(g) The true prairie (subseral) invertebrate communities were found to be structurally related to those of both postclimax habitats, most closely to those of the tall grass.

Analysis of the population patterns of prevalent species has illustrated the following ecological conditions or processes:

(a) Aspectional sequence of ravine and upland sites (postclimax and subseral vegetation): Prevernal precedence of the protected ravine sites (*Delphacodes* sp., *Piesma cinerea, Melanoplus bivittatus*); autumnal lag of the protected sites (*Crematogaster lineolata, Melanoplus bivittatus*).

(b) Pre-hibernation (autumnal) and post-hibernation (prevernal) movement, both horizontal and vertical, of a major crop pest (*Blissus leucopterus*) and other grassland species into tall-grass and shrub hibernation areas (*Balclutha abdominalis, Piesma cinerea, Lygus pratensis*).

(c) Wide distribution through several habitats at any given time, but with evident habitat preference (*Amara* sp., *Piesma cinerea, Balclutha abdominalis, Prenolepis imparis, Crematogaster lineolata, Melanoplus bivittatus*).

(d) Confinement to habitat (*Dorymyrmex pyramicus, Chalcoides fulvicornis, Geotomus robustus, Ataenius cognatus*).

(e) Stratal confinement (*Erythroneura* sp., *Dikraneura abnormis*).

(f) Deep stratal distribution, i.e., disregard for stratal barriers apparently regulatory upon other species (*Prenolepis imparis*).

(g) Operation of biological forces in the stratification of invertebrates: Coaction (*Prenolepis imparis, Anoecia graminis, Chalcoides fulvicornis*).

(h) Daily fluctuations (*Erythroneura* sp.).

(i) Seasonal integrity (*Amara* sp., *Dikraneura abnormis, Chalcoides fulvicornis*).

(j) Forcing of peaks of total population by singe species (*Geotomus robustus, Leiobunum* sp.).

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TABLE 1.—Amount of rainfall* recorded by rain gauge in Station 1 (true prairie subsere).

Two-week period ending	Inches	Total for season	Two-week period ending	Inches	Total for season
1938					
Jan. 18	0.01		Dec. 17	0.00	
Jan. 31	0.26		Dec. 31	0.16*	
Feb. 14	0.00		1939		
Feb. 28	1.44†		Jan. 14	0.15	
Mar. 14	0.55		Jan. 28	0.22	
Mar. 28	1.57	3.88 Hiemal	Feb. 11	0.00	
Apr. 11	1.04†		Feb. 25	2.28*	
Apr. 25	2.44		Mar. 11	1.32	
May 9	3.99		Mar. 25	1.08	6.90 Hiemal
May 23	1.17	8.64 Prevernal-vernal	Apr. 8	1.68	
			Apr. 22	0.91	
			May 6	0.06	
Jun. 6	0.93		May 20	0.25	2.90 Prevernal-vernal
Jun. 20	2.38				
Jul. 4	4.65		Jun. 3	1.92	
Jul. 18	0.33		Jun. 17	1.67	
Aug. 1	0.42	8.71 Estival	Jul. 1	2.57	
Aug. 15	1.14		Jul. 15	1.60	
Aug. 29	0.52		Jul. 29	1.06	8.82 Estival
Sep. 12	4.92		Aug. 12	1.84	
Sep. 24	0.82		Aug. 26	0.50	
Oct. 8	0.00		Sep. 9	0.00	
Oct. 22	0.72	8.12 Autumnal	Sep. 23	0.10	
Nov. 5	1.66		Oct. 7	0.69	
Nov. 19	0.03		Oct. 21	0.28	3.41 Autumnal
Dec. 3	0.00		Nov. 4	0.00	

* Some winter records determined from melted snow probably not exact.

† Melted snow.

TABLE 2.—Air temperature in degrees F. at 0.1 meter above the surface of the ground in Station 1 (true prairie subsere).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1937							
Nov. 16	76.0	21.5	60.6	36.6	46.9	54.5	23.9
Nov. 30	60.5	0.0	36.2	18.8	26.2	60.5	17.3
Dec. 14	53.0	0.0	32.2	15.3	22.7	53.0	16.8
Dec. 21*	48.0	20.5	39.7	23.4	30.3	27.5	16.3
1938							
Jan. 4	62.5	12.5	46.0	23.1	32.8	50.0	22.8
Jan. 18	56.5	0.0	42.8	20.0	28.4	56.5	22.8
Jan. 31*	62.0	—7.5	33.8	16.4	25.1	69.5	17.4
Feb. 14	67.0	9.5	44.3	24.0	33.3	57.5	20.3
Feb. 28†	46.0	8.5	33.3	22.8	27.2	37.5	11.2
Mar. 14	74.0	20.0	48.7	31.2	38.4	54.0	17.6
Mar. 28	81.5	32.5	59.2	39.7	49.2	49.0	19.5
Apr. 11	68.0	21.5	50.0	33.1	39.5	46.5	16.9
Apr. 25	83.0	34.0	70.5	48.8	59.0	49.0	21.7
May 9	82.0	33.5	71.0	51.2	58.3	48.5	19.8
May 23	77.0	41.0	65.5	50.1	58.3	36.0	15.3
Jun. 6	84.5	42.5	76.1	56.0	65.5	42.0	20.2
Jun. 20	84.5	50.0	80.2	59.1	69.2	34.5	21.1
Jul. 4	101.0	53.0	87.0	65.6	74.8	48.0	21.4
Jul. 18†	102.0	59.0	91.0	66.0	78.4	43.0	25.0
Aug. 1	103.0	58.5	97.3	65.0	79.4	44.5	32.2
Aug. 15	112.0	58.5	99.3	71.1	83.7	53.5	27.9
Aug. 29	107.5	56.0	92.0	66.7	78.5	51.5	25.3
Sep. 12	103.0	61.0	91.6	57.6	77.6	42.0	24.0
Sep. 24*	100.0	38.0	80.0	52.0	63.8	62.0	28.0
Oct. 8	98.5	52.0	92.5	58.0	73.4	46.5	34.6
Oct. 22	92.0	37.0	81.0	51.7	64.6	55.0	29.3
Nov. 5	87.0	32.5	73.2	43.7	53.7	54.5	29.4
Nov. 19	64.0	19.0	51.6	30.2	40.2	45.0	21.4
Dec. 3	68.0	2.0	43.8	18.0	30.3	66.0	25.8
Dec. 17	57.0	6.0	43.4	21.3	30.6	51.0	22.1
Dec. 31	—	—	—	—	—	—	—
1939							
Jan. 14	67.5	15.0	48.4	24.0	33.3	52.5	24.5
Jan. 28	58.0	2.5	37.0	17.2	25.7	45.5	19.8
Feb. 11‡	54.0	—5.0	42.8	17.7	25.9	59.0	25.1
Feb. 25	47.0	—6.0	29.3	11.0	19.5	53.0	18.3
Mar. 11	52.0	11.0	37.0	22.6	28.7	41.0	14.3
Mar. 25	83.0	12.5	57.3	29.0	41.6	70.5	28.4
Apr. 8	76.0	23.5	52.0	32.7	41.3	52.5	19.2
Apr. 22	73.5	17.0	58.1	36.3	44.7	56.5	21.6
May 6	88.0	42.0	81.0	51.6	65.5	46.0	29.4
May 20	95.0	40.0	79.6	50.7	64.2	55.0	29.0
Jun. 3	100.0	48.0	87.8	59.8	72.7	52.0	28.0
Jun. 17†	101.0	52.5	79.5	61.0	70.0	48.5	18.5
Jul. 1	100.0	56.5	91.0	63.0	75.1	43.5	28.1
Jul. 15	113.0	61.5	96.4	69.0	82.2	41.5	27.4
Jul. 29	110.5	61.0	97.3	67.1	80.9	49.5	30.1
Aug. 12	104.0	52.0	91.4	62.7	75.9	52.0	28.7
Aug. 26	98.0	49.0	88.7	60.2	72.8	49.0	28.5
Sep. 9	108.0	58.0	98.0	66.9	81.0	50.0	31.1
Sep. 23	104.0	47.5	95.1	60.7	77.3	56.5	34.4
Oct. 7	100.5	30.5	80.8	44.0	60.1	70.0	37.0
Oct. 21	84.0	26.5	70.1	40.8	54.1	57.5	29.3
Nov. 4	84.0	16.5	62.4	33.7	46.9	67.5	28.7

* Short period. † Record for 1 week. ‡ Record for 12 days.

TABLE 3.—Air temperature in degrees F. at 0.1 meter above the surface of the ground in Station 2 (postclimax tall grass).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	63.0	—10.5	49.9	10.6	25.7	73.5	39.2
Jan. 31*	66.0	—22.0	36.3	12.0	24.1	88.0	24.3
Feb. 14	69.5	5.5	48.3	20.2	32.5	64.0	28.1
Feb. 28	52.0	—5.0	30.7	13.2	21.5	57.0	16.8
Mar. 14	81.0	13.0	52.3	27.8	40.5	68.0	25.2
Mar. 28†	87.0	26.0	65.8	34.8	48.2	61.0	31.0
Apr. 11	71.5	13.5	53.0	28.7	38.5	58.0	24.3
Apr. 25	85.0	25.5	74.3	45.4	58.0	59.5	28.9
May 9	86.0	29.5	68.9	44.8	57.8	56.5	24.1
May 23	80.5	36.5	69.6	46.2	57.3	44.0	23.4
Jun. 6	88.0	35.5	79.4	51.8	64.9	52.5	27.6
Jun. 20	89.0	45.5	89.7	56.5	68.3	43.5	34.1
Jul. 4	101.5	51.5	86.8	64.6	74.1	50.0	22.2
Jul. 18‡	101.0	52.0	91.5	61.5	76.1	49.0	30.0
Aug. 1	103.5	51.5	96.0	59.9	76.4	52.0	36.1
Aug. 15	107.5	46.5	99.6	68.2	82.5	61.0	31.4
Aug. 29	107.0	47.0	91.0	62.8	76.0	60.0	28.1
Sep. 12	101.0	57.0	91.5	64.4	76.3	44.0	27.0
Sep. 24*	99.5	30.0	80.3	45.9	60.6	69.5	34.3
Oct. 8	98.0	43.5	89.9	51.3	68.2	54.5	38.6
Oct. 22	92.0	28.0	80.8	45.4	60.6	64.0	35.4
Nov. 5	85.5	23.0	71.7	37.9	50.2	65.5	33.7
Nov. 19	69.0	12.5	55.3	22.2	37.9	65.5	31.5
Dec. 3	74.5	—2.0	47.9	16.0	28.5	76.5	31.8
Dec. 17	61.0	2.0	47.5	18.9	32.2	59.0	28.5
Dec. 31	55.0	—2.0	39.4	11.5	24.4	57.0	27.9
1939							
Jan. 14	74.0	11.5	55.1	22.9	34.7	62.5	32.1
Jan. 28	67.0	4.5	39.3	12.5	25.7	71.5	25.3
Feb. 11	60.0	14.0	59.1	34.3	23.1	66.0	24.8
Feb. 25	49.0	—10.0	32.0	6.4	19.0	59.0	25.6
Mar. 11	49.5	8.5	37.0	20.6	27.6	41.0	16.4
Mar. 25	87.0	11.5	60.0	27.7	41.8	75.5	32.4
Apr. 8	67.0	17.0	51.5	29.6	39.4	50.0	21.9
Apr. 22	74.0	9.0	58.8	33.4	44.4	65.0	26.0
May 6‡	89.0	37.0	82.3	45.8	63.1	52.0	34.9
May 20	96.0	31.5	79.1	44.8	62.3	64.5	34.3
Jun. 3	102.5	42.5	88.7	56.4	71.9	60.0	32.4
Jun. 17	103.0	50.0	85.3	56.9	70.1	53.0	30.7
Jul. 1	99.0	49.0	91.1	58.5	74.1	50.0	32.5
Jul. 15	106.5	55.0	96.5	64.5	79.9	51.1	32.0
Jul. 29	108.5	53.0	96.6	62.4	79.0	55.5	34.2
Aug. 12	108.5	45.5	95.0	51.4	75.1	63.0	36.4
Aug. 26‡	104.5	41.5	90.1	55.9	71.8	63.0	34.2
Sep. 9‡	107.5	49.0	98.8	62.2	81.0	58.5	36.6
Sep. 23	105.0	38.5	98.2	57.0	76.7	66.5	41.1
Oct. 7	107.0	22.0	80.3	44.0	60.0	85.0	36.3
Oct. 21	85.0	17.0	70.8	33.6	50.8	68.0	37.2
Nov., 4‡	89.5	14.0	64.9	28.9	44.8	75.5	35.2

* Short period. † Record for 1 week. ‡ Record for 12 days.

TABLE 4.—Air temperature in degrees F. at 0.1 meter above the surface of the ground in Station 3 (postclimax deciduous shrub).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	55.0	—10.0	42.6	14.1	25.3	65.0	28.4
Jan. 31*	59.0	—19.5	34.5	15.9	24.4	78.5	19.4
Feb. 14	67.0	4.0	46.0	22.0	32.5	63.0	24.0
Feb. 28	47.0	—2.0	27.8	14.6	20.8	49.0	13.2
Mar. 14	73.0	15.0	48.4	27.6	30.6	58.0	20.8
Mar. 28	82.0	21.5	65.4	32.3	45.8	60.5	33.0
Apr. 11	73.0	14.5	52.0	30.2	39.9	58.5	21.8
Apr. 25	86.0	24.5	75.2	45.7	58.1	61.5	29.3
May 9	90.0	32.0	74.9	48.7	59.7	58.0	26.2
May 23	84.0	36.0	71.0	48.5	58.7	48.0	22.5
Jun. 6	90.0	36.0	80.8	52.9	65.1	54.0	27.9
Jun. 20	90.0	49.0	84.1	58.5	68.1	41.0	25.6
Jul. 4	101.0	50.0	89.6	66.4	75.0	51.0	23.1
Jul. 18	100.0	53.0	92.7	64.6	76.8	47.0	28.0
Aug. 1	96.0	51.0	89.7	59.6	72.1	45.0	30.1
Aug. 15	103.5	49.5	94.9	66.7	79.2	54.0	28.1
Aug. 29	101.5	49.5	87.8	62.6	73.5	52.0	25.1
Sep. 12	93.5	57.0	86.5	64.4	73.0	36.5	22.0
Sep. 24*	83.0	32.0	73.5	45.8	50.4	51.0	27.7
Oct. 8	86.0	43.5	80.9	49.1	62.6	42.5	31.9
Oct. 22	81.0	30.5	73.5	44.7	56.5	50.5	28.8
Nov. 5	77.0	26.0	64.6	36.2	48.0	51.0	28.4
Nov. 19	63.5	15.5	52.4	26.4	37.3	48.0	26.0
Dec. 3	64.0	—1.5	44.4	13.4	26.8	65.5	29.3
Dec. 17	58.0	2.0	44.5	18.6	29.1	56.0	25.9
Dec. 31†	45.0	2.5	40.5	25.2	25.6	42.5	25.3
1939							
Jan. 14	70.0	12.5	51.4	22.5	33.5	57.5	28.8
Jan. 28†	57.0	—6.0	36.7	12.0	23.5	63.0	24.7
Feb. 11	57.5	—13.0	37.1	13.3	21.1	70.5	25.2
Feb. 25	59.5	1.5	42.4	18.5	29.9	58.0	23.9
Mar. 11	64.0	10.0	50.9	29.8	38.5	54.0	21.0
Mar. 25	93.0	18.5	68.7	34.6	49.4	74.5	34.2
Apr. 8	75.0	21.0	54.7	30.9	41.9	54.0	30.9
Apr. 22	76.5	12.0	60.0	35.4	57.1	64.5	24.7
May 6	95.0	33.5	86.5	46.9	64.8	61.5	39.5
May 20	103.0	33.5	85.0	46.3	63.2	69.5	38.7
Jun. 3	96.0	43.5	89.8	58.3	70.3	52.5	31.5
Jun. 17	94.0	53.0	84.1	59.8	70.0	41.0	24.9
Jul. 1	96.0	53.5	87.9	62.2	72.9	42.5	25.8
Jul. 15‡	104.0	56.5	95.3	66.3	78.3	47.5	29.0
Jul. 29	106.5	55.0	95.2	64.4	77.2	51.5	30.2
Aug. 12	102.0	47.0	90.3	59.7	73.2	55.0	30.6
Aug. 26	95.5	45.0	87.0	57.5	70.4	50.5	30.1
Sep. 9†	103.0	62.5	95.4	65.6	78.2	40.5	29.8
Sep. 23	106.5	37.0	95.9	57.0	74.1	69.5	38.9
Oct. 7	99.0	25.5	72.0	44.1	59.1	73.5	35.0
Oct. 21	88.0	21.0	69.1	38.2	52.3	64.0	30.8
Nov. 4	84.0	9.5	62.4	27.9	43.7	74.5	34.6

* Short period. † Record for 1 week. ‡ Record for 12 days.

TABLE 5.—Relative humidity at 0.1 meter above the surface of the ground in Station 1 (true prairie subsere).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1937							
Nov. 16	94.0	16.0	97.0	48.2	60.6	78.0	35.5
Nov. 30	91.0	23.0	82.3	47.8	66.1	68.0	34.5
Dec. 14*	88.0	26.0	74.6	43.6	60.0	62.0	34.3
Dec. 21†	88.5	42.0	85.3	51.6	73.3	46.5	33.7
1938							
Jan. 4	94.0	17.0	82.5	40.5	64.9	77.0	40.8
Jan. 18	98.0	27.5	84.5	44.8	67.7	70.5	36.8
Jan. 31	92.0	26.5	81.9	55.3	69.9	65.5	26.6
Feb. 14	100.0	21.5	87.2	49.6	71.6	78.5	35.3
Feb. 28‡	99.5	70.0	95.5	79.9	91.6	29.5	12.7
Mar. 4	100.0	30.0	96.6	57.2	83.1	70.0	39.3
Mar. 28	100.0	16.5	81.7	35.8	62.5	83.5	45.9
Apr. 11	85.5	18.0	72.8	30.5	57.7	67.5	42.2
Apr. 25	84.0	22.0	78.8	32.4	58.1	62.0	46.6
May 9	100.0	20.5	86.5	42.1	72.2	79.5	44.8
May 23	100.0	33.0	95.6	57.8	79.6	67.0	44.1
Jun. 6	96.0	35.0	92.4	50.9	74.4	61.0	41.4
Jun. 20‡	92.5	48.0	91.9	22.3	75.3	44.5	39.6
Jul. 4	100.0	37.5	87.8	52.7	73.1	62.5	37.1
Jul. 18‡	93.0	31.0	87.1	42.7	64.1	62.0	44.3
Aug. 1§	94.5	17.5	89.7	30.8	63.1	77.0	58.8
Aug. 15	92.0	19.5	81.7	31.3	57.5	72.5	50.5
Aug. 29	94.5	15.5	84.1	36.1	62.2	79.0	47.9
Sep. 12	93.0	29.5	89.2	43.8	70.0	63.5	46.1
Sep. 24†	93.5	26.5	90.7	40.0	66.9	67.0	50.7
Oct. 8	97.5	19.5	88.4	30.7	59.5	78.0	57.5
Oct. 22	94.5	18.0	84.4	33.3	59.1	76.5	51.0
Nov. 5	85.0	15.5	75.4	30.4	57.3	69.5	45.0
Nov. 19	100.0	23.0	86.6	39.2	54.1	77.0	47.3
Dec. 3	100.0	24.0	90.7	37.4	65.1	76.5	53.2
Dec. 17	100.0	22.5	88.5	41.8	67.4	77.5	46.7
Dec. 31	—	—	—	—	—	—	—
1939							
Jan. 14	96.5	19.5	87.1	41.1	68.4	77.0	47.9
Jan. 28	97.5	30.5	89.1	47.7	71.0	67.0	41.3
Feb. 11*	98.0	22.5	85.8	38.8	66.1	75.5	47.0
Feb. 25	97.5	38.0	87.8	61.4	76.1	59.5	26.4
Mar. 11	98.5	32.0	90.5	58.5	79.2	66.5	32.1
Mar. 25	95.5	15.0	86.9	31.5	63.6	80.5	55.4
Apr. 8	100.0	16.5	87.7	41.4	68.5	83.5	46.3
Apr. 22	98.5	25.5	90.9	40.2	79.9	73.0	50.8
May 6	88.0	18.0	77.2	29.1	52.1	70.0	48.1
May 20	89.0	18.0	76.0	29.4	51.3	71.0	46.6
Jun. 3	88.0	18.0	83.5	31.3	59.4	70.0	52.3
Jun. 17	88.0	14.5	84.1	36.8	61.1	73.5	48.0
Jul. 1§	88.5	22.0	86.3	34.3	62.9	66.5	52.0
Jul. 15	87.5	12.0	77.8	32.5	55.8	75.5	45.2
Jul. 29	88.0	17.0	83.3	28.1	57.2	71.0	54.9
Aug. 12	88.0	13.0	82.7	29.6	55.5	75.0	53.1
Aug. 26§	92.5	16.5	86.8	30.6	58.8	76.0	56.1
Sep. 9§	100.0	10.5	76.6	33.3	55.0	89.5	43.3
Sep. 23	83.5	14.0	63.3	19.2	39.1	69.5	44.1
Oct. 7	94.5	15.5	75.7	26.5	53.0	79.0	49.2
Oct. 21	87.5	15.0	73.8	24.1	51.9	72.5	49.7
Nov. 4	88.0	13.5	85.4	29.4	52.7	74.5	45.9

* Record for 11 days. † Short period. ‡ Record for 1 week. § Record for 12 days.

TABLE 6.—Relative humidity at 0.1 meter above the surface of the ground in Station 2 (postclimax tall grass).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1939							
Aug. 26*	98.0	22.5	91.9	38.2	77.9	75.5	42.2
Sep. 9†	95.0	19.0	81.3	34.5	64.7	76.0	46.8
Sep. 23	95.0	19.0	74.1	25.4	64.9	76.0	49.5
Oct. 7	100.0	10.5	75.4	25.5	51.2	87.0	46.4
Oct. 24	96.0	20.5	87.1	33.3	59.3	75.5	49.1
Nov. 4‡	96.0	18.0	83.2	34.3	59.2	78.0	48.9

* Record for 11 days. † Record for 1 week. ‡ Record for 12 days.

TABLE 7.—Relative humidity at 0.1 meter above the surface of the ground in Station 3 (postclimax deciduous shrub).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Aug. 1	86.0	33.0	85.1	48.5	72.9	53.0	29.5
Aug. 15*	88.0	29.0	86.4	42.3	69.0	59.0	44.2
Aug. 29	90.0	20.0	85.1	49.0	69.4	70.0	36.1
Sep. 12	88.0	38.5	84.4	60.1	76.8	49.5	24.3
Sep. 24†	87.5	31.0	85.2	47.6	72.0	56.5	37.6
Oct. 8	90.0	29.0	87.5	50.1	70.2	61.0	37.4
Oct. 22	90.0	17.5	85.5	44.4	69.0	72.5	41.0
Nov. 5	90.0	16.0	83.5	39.7	67.7	74.0	44.0
Nov. 19	100.0	22.5	90.4	41.3	71.3	77.5	49.1
Dec. 3	96.0	27.0	90.7	37.4	67.9	69.0	53.0
Dec. 17‡	95.0	25.0	89.9	37.9	67.8	70.0	51.9
Dec. 31	95.5	31.0	83.5	43.9	67.6	64.5	39.6
1939							
Jan. 14	92.0	13.5	87.7	41.9	68.7	78.5	45.5
Jan. 28‡	88.5	25.0	86.8	54.2	73.7	63.5	32.6
Feb. 11	95.5	20.0	84.9	41.5	67.5	75.5	43.4
Feb. 25	96.5	31.0	85.7	53.4	72.2	65.5	32.3
Mar. 11	93.0	26.5	86.8	55.4	74.5	66.5	31.4
Mar. 25	95.0	6.5	88.0	29.4	61.9	88.5	58.6
Apr. 8	91.0	16.0	84.8	41.2	66.1	75.0	43.6
Apr. 22	96.0	14.5	85.9	38.4	64.2	81.5	47.4
May 6	—	—	—	—	—	—	—
May 20†	95.0	19.0	92.3	30.1	64.4	76.0	62.1
Jun. 3	94.5	27.0	91.6	58.2	79.6	67.5	33.5
Jun. 17	91.0	43.0	90.1	61.1	80.0	48.0	38.9
Jul. 1*	93.0	46.0	91.6	64.3	82.5	47.0	27.3
Jul. 15†	91.0	24.0	89.5	54.8	76.4	67.0	34.7
Jul. 29†	93.0	26.0	90.1	44.2	73.5	67.0	45.9
Aug. 12§	92.0	26.5	90.4	42.1	71.6	65.5	48.3
Aug. 26	91.5	17.5	84.9	38.8	66.6	74.0	38.8
Sep. 9	93.0	25.0	89.1	37.9	66.4	68.0	51.2
Sep. 23	92.5	10.0	80.2	17.5	48.1	82.5	62.7
Oct. 7	94.0	12.0	81.3	25.8	57.1	82.0	55.5
Oct. 21	91.5	11.0	84.0	29.1	58.8	80.5	54.9
Nov. 4	95.0	12.5	86.0	32.1	61.0	82.5	53.9

* Record for 10 days. † Record for 12 days. ‡ Record for 1 week. § Record for 9 days.

TABLE 8.—Mean wind velocity (MPH) from Nov. 2, 1937 to Nov. 4, 1939 at Lincoln, Nebr.* and at 0.5 meter in Station 1 (true prairie subsere), in Station 2 (postclimax tall grass), and in Station 3 (postclimax deciduous shrub), on basis of two-week periods.

Two-week period ending	Lincoln, Nebraska	Station 1	Station 2	Station 3
1937				
Nov. 16	11.62	11.40	–	–
Nov. 30	9.81	9.13	–	–
Dec. 14	11.05	11.43	–	–
Dec. 21†	8.54	6.19	–	–
1938				
Jan. 4	9.07	9.80	–	–
Jan. 18	10.69	10.96	–	1.27
Jan. 31†	11.57	–	–	2.08
Feb. 14	10.06	–	–	1.29
Feb. 28	8.85	8.31	–	1.71
Mar. 14	9.67	10.58	–	1.56
Mar. 28	11.90	13.18	–	2.31
Apr. 11	13.96	13.92	–	3.15
Apr. 25	10.98	10.12	–	1.83
May 9	12.09	12.38	–	1.44
May 23	8.98	8.56	–	0.60
Jun. 6	8.38	–	–	0.32
Jun. 20	9.29	7.15	–	–
Jul. 4	9.87	7.50	–	0.29
Jul. 18	9.01	6.15	1.05	0.23
Aug. 1	7.32	5.30	0.77	0.23
Aug. 15	11.25	8.49	–	0.36
Aug. 29	9.39	7.13	–	0.36
Sep. 12	8.32	6.83	–	0.11
Sep. 24†	7.11	5.41	–	0.41
Oct. 8	8.13	6.29	1.24	0.15
Oct. 22	10.85	8.91	1.90	0.38
Nov. 5	9.79	8.43	1.95	0.69
Nov. 19	10.80	9.27	1.70	0.36
Dec. 3	8.58	–	–	–
Dec. 17	9.56	–	–	–
Dec. 31	10.48	9.26	1.61	1.15
1939				
Jan. 14	8.68	8.20	1.31	0.77
Jan. 28	10.26	8.78	1.82	1.16
Feb. 11	11.57	–	1.85	1.72
Feb. 25	11.07	11.02	–	1.95
Mar. 11	10.07	10.33	–	1.71
Mar. 25	10.49	12.82	2.92	1.48
Apr. 8	10.61	–	3.31	2.12
Apr. 22	12.25	–	3.91	2.45
May 6	11.17	9.10	–	1.39
May 20	9.22	8.58	2.91	0.88
Jun. 3	9.10	8.63	2.41	0.20
Jun. 17	10.21	9.06	3.09	0.30
Jul. 1	8.52	7.64	1.84	0.15
Jul. 15	8.91	7.74	1.42	0.05
Jul. 29	8.39	7.71	1.08	0.17
Aug. 12	9.02	8.54	–	0.10
Aug. 26	7.65	7.07	–	0.18
Sep. 9	10.59	9.72	–	0.42
Sep. 23	10.45	8.34	2.68	1.06
Oct. 7	11.09	8.46	2.73	0.64
Oct. 21	9.61	7.12	2.27	0.77
Nov. 4	8.91	6.03	1.62	1.19

* Data courtesy of U. S. Weather Bureau, Lincoln, Nebraska. † Short period.

TABLE 9.—Water content of soil, expressed as per cent in excess of the hygroscopic coefficient at a depth of 0 to 0.1 meter, of true prairie subsere (Station 1), of postclimax tall grass (Station 2, ravine), and of postclimax deciduous shrub (Station 3, ravine).

Date	Station 1	Station 2	Station 3
1938			
Jan. 13	17.1	41.5	—
Feb. 5	20.8	55.4	45.4
Mar. 21	29.5	45.9	41.1
Apr. 4	23.5	—	38.6
Apr. 18	34.5	35.3	57.2
May 16	31.0	37.4	46.1
Jun. 21	32.2	32.8	42.1
Jul. 2	29.5	49.2	42.2
Jul. 19	6.5	21.4	20.6
Jul. 26	6.9	17.4	20.0
Aug. 12	5.9	15.2	14.4
Oct. 29	8.4	22.0	16.0
Nov. 5	23.0	35.4	45.6
Nov. 26	13.8	26.5	26.3
1939			
Jan. 7	12.3	19.5	46.6
Mar. 12	29.1	52.4	60.4
Means	20.25	33.82	37.48

TABLE 10.—Soil temperature in degrees F. at 0.1 meter below soil surface in Station 1 (true prairie subsere).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1937							
Nov. 16	57.0	41.0	54.2	48.4	50.7	16.0	5.8
Nov. 30*	44.0	36.0	40.5	37.5	38.3	8.0	3.0
Dec. 14	43.5	31.0	36.5	34.2	35.7	12.5	2.3
Dec. 21†	36.0	33.0	35.4	34.1	34.7	3.0	1.3
1938							
Jan. 4*	36.0	33.0	35.6	33.9	34.8	3.0	1.7
Jan. 18	36.0	30.5	35.1	32.3	31.6	5.5	2.8
Jan. 31‡	38.5	33.0	36.2	34.0	35.4	5.5	2.2
Feb. 14	42.0	22.5	32.6	31.0	32.2	19.5	1.6
Feb. 28	34.5	32.5	34.0	33.6	34.0	2.0	0.2
Mar. 14	50.5	34.0	41.0	37.6	39.2	16.5	3.4
Mar. 28	58.0	40.0	50.4	43.5	46.7	18.0	6.8
Apr. 11	56.0	36.0	48.5	40.9	43.4	20.0	6.6
Apr. 25	64.0	40.0	56.9	48.5	55.6	24.0	8.3
May 9	67.0	38.0	58.6	48.8	53.0	29.0	9.8
May 23	71.0	50.5	64.7	58.0	62.1	20.5	6.6
Jun. 6	76.0	58.0	72.4	65.4	68.7	18.0	7.0
Jun. 20	81.0	65.0	76.5	71.0	74.0	16.0	5.4
Jul. 4	82.0	67.0	77.3	71.8	74.9	15.0	4.5
Jul. 18*	83.0	73.0	80.7	75.5	77.5	10.0	5.2
Aug. 1‡	85.5	76.0	82.8	77.3	79.8	9.5	5.5
Aug. 15	90.0	78.0	87.7	81.5	80.3	12.0	6.2
Aug. 29	89.0	74.5	84.6	80.0	81.5	14.5	5.9
Sep. 12‡	86.5	76.5	81.8	77.7	80.4	10.0	4.6
Sep. 24†‡	79.5	60.5	71.3	65.0	67.0	19.0	6.3
Oct. 8	72.5	64.5	71.0	66.2	68.5	8.0	4.7
Oct. 22	71.0	53.0	64.5	59.6	61.7	18.0	4.8
Nov. 5	60.5	47.0	56.6	51.7	53.5	13.5	4.9

* Record for 11 days. † Short period. ‡ Record for 1 week.

TABLE 11.—Soil temperature in degrees F. at 0.1 meter below soil surface in Station 2 (postclimax tall grass).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	35.0	30.0	33.1	31.1	32.2	5.0	1.9
Jan. 31	35.0	29.0	32.7	31.3	32.0	6.0	1.3
Feb. 14	34.5	28.0	31.6	30.0	30.6	6.5	1.6
Feb. 28	35.0	32.0	33.9	32.9	33.4	3.0	1.0
Mar. 14	41.5	32.0	36.5	34.2	35.7	9.5	2.3
Mar. 28	51.5	41.5	47.2	44.2	45.7	10.0	3.1
Apr. 11	49.0	39.5	45.0	42.6	43.9	9.5	1.7
Apr. 25	55.0	43.0	52.4	48.7	51.0	12.0	3.6
May 9	60.0	47.0	55.6	52.4	54.0	13.0	3.2
May 23	57.0	48.0	54.5	51.9	53.4	9.0	2.5
Jun. 6	61.0	51.0	58.5	55.2	56.9	10.0	3.3
Jun. 20	63.0	55.5	60.6	57.8	59.3	7.5	2.9
Jul. 4	75.0	70.0	72.4	69.9	71.3	5.0	2.4
Jul. 18	74.0	67.5	72.5	69.9	72.1	6.5	2.7
Aug. 1*	71.5	61.0	70.6	67.8	70.2	4.5	2.7
Aug. 15*	73.0	66.0	71.1	78.0	72.0	7.0	2.8
Aug. 29	71.0	65.0	69.4	66.7	71.1	6.0	2.7
Sep. 12	70.5	64.0	68.4	66.2	71.4	6.5	2.1
Sep. 24†	68.0	55.0	63.3	60.1	67.0	13.0	3.2
Oct. 8	62.0	56.5	61.3	58.1	65.9	5.5	3.1
Oct. 22‡	60.0	51.0	58.0	55.5	63.8	9.0	2.1
Nov. 5	56.0	46.5	63.0	45.7	59.1	9.5	7.2
Nov. 19	50.5	42.5	47.2	45.6	47.0	8.0	2.4
Dec. 3	48.0	38.5	43.6	41.7	42.8	9.5	1.9
Dec. 17	46.0	40.0	43.9	42.0	43.2	6.0	1.6
Dec. 31	42.0	38.5	41.1	39.5	40.5	3.5	1.6
1939							
Jan. 14	45.0	38.0	42.1	40.4	41.3	7.0	1.7
Jan. 28†	42.5	38.0	41.1	39.9	40.7	4.5	1.3
Feb. 11	37.0	33.0	35.4	33.9	34.9	4.0	1.3
Feb. 25*	36.0	33.0	35.0	33.8	34.6	3.0	1.2
Mar. 11	34.5	32.5	34.3	32.6	33.9	2.0	1.7
Mar. 25‡	44.0	30.5	36.3	33.9	35.3	13.5	2.4
Apr. 8	45.5	36.5	42.0	39.5	40.9	9.0	2.5
Apr. 22	46.0	37.0	43.4	40.9	42.2	9.0	2.4
May 6	52.0	45.0	49.7	46.2	48.1	7.0	3.4

* Record for 1 week. † Record for 12 days. ‡ Record for 11 days.

TABLE 12.—Soil temperature in degrees F. at 0.1 meter below soil surface in Station 3 (postclimax deciduous shrub).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	30.0	24.0	29.2	28.0	24.9	6.0	1.2
Jan. 31	32.0	26.0	29.0	27.0	30.7	6.0	2.0
Feb. 14	31.0	24.0	28.7	25.9	29.2	7.0	2.9
Feb. 28	31.5	30.0	31.3	30.3	30.2	1.5	2.0
Mar. 14	40.0	30.5	35.6	32.3	31.9	9.5	3.5
Mar. 28	50.5	37.0	44.6	41.1	42.7	13.5	3.5
Apr. 11	48.5	35.0	41.9	38.7	40.2	13.5	3.2
Apr. 25	58.0	41.0	54.1	50.2	51.9	17.0	3.9
May 9	64.5	48.5	59.2	51.5	57.5	16.0	7.7
May 23	62.0	51.5	57.9	55.2	56.9	11.5	2.7

TABLE 12.—(*Continued*)

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Range Max.	Mean Range
Jun. 6	65.5	54.0	62.2	58.9	60.7	11.5	3.4
Jun. 20	68.5	60.0	65.6	63.0	64.3	8.5	2.6
Jul. 4	73.5	63.5	69.8	67.7	68.7	10.0	2.0
Jul. 18	74.0	65.5	71.8	69.0	70.5	8.5	2.8
Aug. 1	70.5	64.5	69.5	66.7	67.9	6.0	2.8
Aug. 15	73.5	65.5	71.5	69.5	70.5	8.0	2.1
Aug. 29	73.0	66.0	70.6	68.2	69.5	7.0	2.3
Sep. 12	73.5	66.5	70.8	69.1	70.3	7.0	1.8
Sep. 24*	71.0	55.0	53.6	60.9	62.5	16.0	2.7
Oct. 8	64.0	59.0	62.7	60.3	61.5	5.0	2.5
Oct. 22	63.5	52.0	59.9	57.7	58.9	11.5	2.2
Nov. 5	57.0	47.0	52.0	49.9	51.1	10.0	2.1
Nov. 19	48.0	39.5	43.1	41.5	42.4	8.5	1.6
Dec. 3	42.5	32.0	37.6	34.4	34.9	10.5	5.7
Dec. 17	36.5	32.0	34.7	32.7	34.1	4.5	2.0
Dec. 31	32.0	28.5	32.0	29.8	30.9	3.5	2.3
1939							
Jan. 14	32.0	29.5	31.7	30.5	30.8	2.5	1.3
Jan. 28	32.0	30.0	31.8	30.3	30.5	2.0	1.5
Feb. 11	31.5	27.5	30.7	29.4	30.2	4.0	1.3

* Record for 12 days.

TABLE 13.—Number of cubic centimeters evaporated from porous cup atmometers (reduced to standard) in the aerial strata studied in Station 1 (true prairie subsere), in Station 2 (postclimax tall grass), and in Station 3 (postclimax deciduous shrub).

Two-week period ending	Station 1 0.35 meter	Station 2 0.35 meter	Station 3 0.35 meter	Station 3 2.0 meters
1938				
Jul. 4	136.68*	86.52*	64.60*	130.78
Jul. 18	159.27	97.43	78.17	151.86
Aug. 1	200.70	114.48	84.31	155.77
Aug. 15	372.35	186.77	149.59	260.14
Aug. 29	234.19	120.12	122.02	209.15
Sep. 12	136.40*	—	78.17	149.52

* Based on record for 1 week.

TABLE 14.—Light intensity in foot candles at surface of the ground in true prairie subsere (Station 1), postclimax tall grass (Station 2), and postclimax deciduous shrub (Station 3). (Average of 10 readings at intervals of 1.0 meter along a random transect, 11:30 A.M. to 12:30 P.M. on July 1, 1938.)

Station 1	Station 2	Station 3
3890.0	1190.7	750.5

TABLE 15.—Analysis of soil samples (8 replicate) from each station.

	Station	Organic matter %	Volatile matter %	Nitrogen %	Hygroscopic coefficient %	pH
Prairie subsere	(1)	4.8	6.3	0.207	7.6	6.4
Tall grass	(2)	5.6	7.2	0.226	9.6	6.6
Shrub	(3)	8.6	10.0	0.350	12.2	6.8

TABLE 16.—Summary of seasonal and annual means of aerial factors and of soil temperature and moisture, and range of soil temperature as determined during the period of study in true prairie subsere (Station 1), postclimax tall grass (Station 2), and postclimax deciduous shrub (Station 3).

	Prevernal-vernal			Estival			Autumnal			Hiemal			Annual		
	Station			Station			Station			Station			Station		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Aerial temperature (°F.)															
Mean	53.8	52.6	55.4	74.8	72.8	72.5	71.9	69.9	68.6	33.5	32.3	32.6	54.2	53.5	53.6
Mean range	21.6	27.1	29.2	25.2	31.1	27.6	29.8	34.7	29.9	21.1	28.3	25.8	23.9	33.3	27.7
Relative humidity (%)															
Mean	63.8	—	64.9	64.6	—	77.5	57.4	63.6	66.2	67.8	—	69.3	64.1	—	69.3
Mean range	46.2	—	51.0	47.3	—	33.3	49.9	46.8	44.3	39.2	—	44.6	44.3	47.1	43.0
Wind velocity															
Mean	10.44	3.38	1.73	7.38	1.66	0.215	7.69	2.16	0.411	9.71	1.85	1.40	8.82	2.06	0.94
Evaporation rate															
Mean (herb)	—	—	—	166.55	99.46	75.69	247.64	153.44	116.59	—	—	—	206.60	121.60	96.16
(shrub)	—	—	—	—	—	146.13	—	—	206.37	—	—	—	—	—	179.20
Soil temperature (°F.)															
Mean	53.5	47.6	51.6	75.0	65.9	66.4	73.2	68.5	65.2	38.9	39.0	33.9	55.3	52.8	49.7
Mean range	7.8	2.7	4.4	5.5	2.8	2.7	5.4	2.7	2.2	3.0	2.1	2.3	4.7	2.4	2.7
Abs. max.	71.0	60.0	64.5	85.5	75.0	74.0	90.0	73.0	83.5	60.5	56.0	57.0	90.0	75.0	74.0
Abs. min.	36.0	39.5	35.0	65.0	51.0	54.0	53.0	51.0	52.0	22.5	28.0	24.0	22.5	28.0	24.0
Max. range	35.0	20.5	29.5	20.0	24.0	20.0	37.0	22.0	21.5	38.0	28.0	33.0	68.5	47.0	50.0
Soil moisture															
Mean	29.7	36.3	47.3	18.8	30.2	31.8	5.9	15.2	14.4	19.2	37.3	40.2	20.25	33.82	37.48

TABLE 17.—Daily and nightly means of temperature and relative humidity in Station 1 (true prairie subsere) at times of collection (see Table 32) during period of day-night studies.

	Temperature °F.				Relative Humidity %			
	Day		Night		Day		Night	
Date 1938	A.M.	P.M.	P.M.	A.M.	A.M.	P.M.	P.M.	A.M.
Jun. 12	—	79.3	—	—	—	—	—	—
17	76.2	79.8	—	—	73.4	55.0	—	—
18	—	—	73.7	—	—	—	77.0	—
19	—	—	—	68.2	—	—	—	90.5
21	—	82.2	—	—	—	67.0	—	—
23	78.0	91.0	80.1	—	79.5	63.0	82.5	—
25	68.2	—	—	—	87.9	—	—	—
28	68.6	—	—	—	61.5	—	—	—
29	—	—	80.0	—	—	—	79.5	—
30	—	91.0	—	75.5	—	49.8	—	85.5
Jul. 1	89.7	99.0	—	—	68.1	46.7	—	—
2	—	90.3	—	—	—	52.0	—	—
5	—	90.3×	—	—	—	42.4	—	—
7	—	81.3×	70.8×	—	—	49.8	72.7	—
8	71.2	—	—	—	61.6×	—	—	—
9	76.8	87.7×	—	—	66.5	46.0×	—	—
18	—	—	71.0	—	—	—	75.3	—
19	—	—	—	65.3	—	—	—	85.5
21	—	—	71.7	—	—	—	79.8	—
22	76.5	91.0	—	—	59.0	28.9	—	—
26	—	86.7	—	—	—	52.2	—	—
28	—	86.0	74.1	—	—	58.1	83.3	—
29	81.4	—	—	—	51.5	—	—	—
Aug. 1	—	98.2	—	—	—	23.9	—	—
2	86.2	—	—	—	48.2	—	—	—
3	—	—	71.7	—	—	—	67.0	—
4	—	—	81.0	—	—	—	65.2	—
5	93.2	109.0	—	—	45.7	26.9	—	—
6	—	—	—	76.5	—	—	—	71.0
10	—	—	60.8	—	—	—	81.5	—
11	—	—	—	52.5	—	—	—	89.7
12	—	87.0	—	—	—	21.7	—	—
15	—	77.0	—	—	—	59.2	—	—
22	—	94.2	—	—	—	24.0	—	—
25	—	81.7	—	—	—	46.7	—	—
29	75.0	—	—	—	60.3	—	—	—
Sep. 3	—	—	58.0	—	—	—	85.8	—
5	—	76.3	—	—	—	74.2	—	—
7	80.3	—	—	—	52.6	—	—	—
12	63.0	—	—	—	81.7	—	—	—
18	—	64.0×	—	—	—	40.0×	—	—
Oct. 1	66.6	—	—	—	73.0	—	—	—
7	—	—	70.5	—	—	—	43.8	—
8	67.2	—	—	—	69.2	—	—	—
15	59.0	—	—	—	71.0	—	—	—
21	—	—	60.8	—	—	—	45.0	—
22	43.5	—	—	—	64.3	—	—	—
29	45.8	—	—					
Av. of				—	70.3	—	—	—
means	71.8	86.8	71.1	67.6	65.5	46.3	72.2	84.4

× Interpolated.

TABLE 18.—Daily and nightly means of temperature* in Station 2 (postclimax tall grass) at times of collection (see Table 32) during period of day-night studies.

	Temperature °F.			
	Day		Night	
Date	A.M.	P.M.	P.M.	A.M.
1938				
Jun. 12	—	78.7	—	—
17	81.3	81.3	—	—
18	—	—	74.0	—
21	—	79.4	—	—
23	83.0	89.5	75.7	—
25	69.0	—	—	—
28	67.7	—	—	—
29	—	—	76.5	—
30	—	—	—	70.2
Jul. 1	91.0	82.0	—	—
5	—	92.3	—	—
7	—	81.0	64.2	—
8	88.5	—	—	—
15	—	88.3	—	—
18	—	—	74.0	—
19	—	—	—	57.8
21	—	—	68.2	—
22	—	91.2	—	—
28	—	83.3	68.5	—
29	89.4	—	—	—
Aug. 3	—	—	66.3	—
4	—	—	78.8	—
5	100.2	102.3	—	—
6	—	—	—	75.0
10	—	—	64.3	—
11	—	—	—	51.7
12	—	94.0	—	—
15	—	93.5	—	—
Sep. 3	—	—	61.5	—
5	—	‡	—	—
9	93.6	—	—	—
18	—	63.0	—	—
Oct. 1	62.5†	—	—	—
7	—	—	59.7	—
8	85.3	—	—	—
15	81.0	—	—	—
21	—	—	52.5	—
22	‡	—	—	—
29	61.2	—	—	—
Av. of means	81.0	85.0	68.0	63.7

* Relative humidity records were not secured in this station in 1938. † Interpolated. ‡ No record.

TABLE 19.—Daily and nightly means of temperature and relative humidity in Station 3 (postclimax deciduous shrub) at times of collection (see Table 32) during period of day-night studies.

	Temperature °F.				Relative Humidity %			
	Day		Night		Day		Night	
Date	A.M.	P.M.	P.M.	A.M.	A.M.	P.M.	P.M.	A.M.
1938								
Jun. 12	—	81.7	—	—	—	×	—	—
17	76.5	81.7	—	—	×	×	—	—
18	—	—	68.0	—	—	—	×	—
21	—	84.3	—	—	—	×	—	—
23	82.3	—	—	—	×	—	—	—
25	83.8	—	—	—	×	—	—	—
28	73.2	—	—	—	×	—	—	—
Jul. 1	89.5	90.5	—	—	×	×	—	—
7	—	85.8	—	—	—	×	—	—
15	—	88.7	—	—	—	61.5	—	—
21	—	—	52.9	—	—	—	84.3	—
22	—	83.8	—	—	—	33.4	—	—
28	—	78.2	—	—	—	75.1	—	—
Aug. 2	80.7	—	—	—	67.1	—	—	—
3	—	—	65.5	—	—	—	82.2	—
5	—	98.8	—	—	—	44.5	—	—
6	—	—	—	72.2	—	—	—	79.6
11	—	—	—	54.4	—	—	—	85.0
25	—	84.3	—	—	—	54.5	—	—
Oct. 7	—	—	56.5	—	—	—	80.2	—
18	—	58.7	—	—	—	48.9	—	—
22	43.0	—	—	—	65.0	—	—	—
29	45.3	—	—	—	72.0	—	—	—
Av. of means	71.9	83.3	60.7	63.3	68.0	53.0	82.2	82.3

× No record.

TABLE 20.—Mean day and night wind velocities (MPH), at Lincoln, Nebraska,* June 12 (sunrise) to October 29 (sunrise), 1938, on basis of two-week periods.

Day (Sunrise to sunset)		Night (Sunset to sunrise)	
Two-week period	Mean MPH	Two-week period	
Jun. 12-19†	10.12	Jun.12-20†	10.17
Jun. 20-Jul. 3	10.06	Jun. 20-Jul. 4	9.30
Jul. 4-17	9.86	Jul. 4-18	7.65
Jul. 18-31	8.12	Jul. 18-Aug. 1	6.00
Aug. 1-14	12.49	Aug. 1-15	9.59
Aug. 15-28	10.12	Aug. 15-29	12.14
Aug. 29-Sep. 11	8.84	Aug. 29-Sep. 12	7.10
Sep. 12-23	8.17	Sep. 12-24	5.74
Sep. 24-Oct. 7	8.71	Sep. 24-Oct. 8	5.19
Oct. 8-21	11.98	Oct. 8-22	10.25
Oct. 22-28†	11.12	Oct. 22-29	7.49
Av. of means	9.96		8.25

* Wind velocity data courtesy U. S. Weather Bureau, Lincoln, Nebraska. † Record for 1 week.

TABLE 21.—Average wind velocities (MPH) at Lincoln, Nebraska* during the hours specified of those days and nights on which sweep collections were made. (See Table 32.)

	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-3 A.M.
Av. MPH	9.56	10.18	7.96	9.53

* Wind velocity data courtesy U. S. Weather Bureau, Lincoln, Nebraska.

TABLE 22.—Average numbers of invertebrates per unit collection taken by sweep net method of sampling invertebrate populations (187 unit collections, day sweeps) in the herb stratum of true prairie subsere (Station 1 and substations), postclimax tall grass (Station 2 and substation, ravine), and postclimax deciduous shrub (Station 3 and substations, ravine), on basis of two-week periods.

Population breakdown	Number of specimens collected	Station	Station totals	Average numbers per unit collection for two-week period ending																							Seasonal averages per unit collection				
				1937 Nov. 16	1938 Mar. 28	Apr. 11	25	May 9	23	Jun. 6	20	Jul. 4	18	Aug. 1	15	29	Sep. 12	24*	Oct. 8	22	Nov. 5	19	Dec. 3	1939 Jan. 14	Feb. 11	Mar. 25	Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
Araneida (spiders)	2,455	1	1,037	0	0	0	2—	3—	2—	9	18	1	15	23	27	29	15	38	16	8	1—	0	0	0	1	1—	0	1+	18	25	1—
		2	510	0	1—	1—	1—	5—	4—	9	9	7	14	32	25	43	17	24	23	7	4	3—	2—	0	0	1—	1—	2+	15	20	2—
		3	908	5—	5	2	6	14	35	20	21	16	44	45	45	69	x	32	26	24	19	16	5—	2	0	3—	5—	14	25	37	7
Orthoptera (grasshoppers, walking sticks, etc.)	3,716	1	2,044	0	0	0	1	15	75	60	52	51	31	83	63	25	13	8	1	2	1—	0	0	0	0	2—	2+	5	44	29	1—
		2	1,186	0	1	1	1	20	41	30	27	41	28	33	55	54	3	6	0	1—	1—	0	0	0	0	0	0	23	41	21	1—
		3	486	3	1	1—	1	11	8	20	54	18	21	9	12	14	x	5—	2	1	1—	1—	0	0	0	0	1—	16	21	6	1—
Homoptera (leafhoppers, aphids, etc.)	12,748	1	5,343	4—	1—	0	2—	14	15	154	275	143	112	118	56	33	75	137	124	88	7	7	2	1	1	12	3—	8	149	67	4—
		2	1,825	2—	1—	0	0	15	76	63	37	52	58	93	67	28	42	11	46	38	4+	4—	2—	1	0	1	1+	23	59	44	2+
		3	5,580	4+	1	2	10	9	56	65	114	140	151	281	242	391	x	81	350	549	230	55	5	5	7	36	3+	32	146	311	49
Hemiptera (true bugs)	2,990	1	605	3+	3—	0	1	3	6	5—	18	21	29	12	7	3	2—	10	6	4—	1—	0	0	0	0	1—	3	3—	19	5	1—
		2	1,121	34	11	3—	3—	62	35	34	13	8	11	10	8	2	6	5	20	116	23	5	3—	0	0	5	26	25	13	37	7
		3	1,264	58	26	2—	2—	20	49	46	24	15	14	18	5	9	x	8	73	149	60	14	1	0	0	1	44	18	20	51	12
Diptera (flies)	9,986	1	1,795	1—	21	2	4	20	19	40	76	38	40	37	5	14	61	53	31	27	2—	1—	1	0	0	3	7	11	43	26	1+
		2	2,128	2—	2—	13	6	35	95	89	36	53	74	88	46	7	80	66	60	42	8	2	2—	3—	0	2—	2—	37	64	51	3—
		3	6,063	8	19	8	18	67	107	98	118	98	160	155	145	75	x	24	557	1282	115	22	2	2+	0	4—	11	50	118	442	23
Coleoptera (beetles)	4,674	1	2,913	1—	6	0	4—	4	0	26	237	105	57	91	21	18	8	10	18	27	1—	0	1—	0	0	1—	2+	2—	102	17	1—
		2	812	2+	2	2—	3	20	11	36	50	26	24	24	8	52	7	2	17	10	2—	1—	2—	1	0	1—	2+	9	30	13	1—
		3	949	2	3—	2+	11	20	12	55	93	29	89	25	8	22	x	8	32	24	4	5	0	0	0	1—	2+	11	46	17	1+
Winged Hymenoptera (bees, wasps)	2,979	1	883	0	0	0	1—	4—	2—	47	31	26	33	26	7	4	12	8	4	5—	1—	0	0	0	0	1—	0	1+	30	7	1—
		2	857	2—	7	1—	0	9	10	32	9	18	30	44	47	14	12	10	33	31	1	1—	1—	0	0	1—	3+	5	25	29	1—
		3	1,239	6	0	1	4—	19	18	23	26	24	54	43	24	40	x	6	70	220	30	3	0	0	0	0	4—	10	31	76	5
Formicidae (ants)	3,372	1	1,166	0	0	0	0	5	4—	25	30	22	28	27	23	44	6	10	5	2	0	0	0	0	0	0	0	2+	26	22	0
		2	703	1—	0	0	0	15	27	46	33	24	9	5	9	155	7	5	1	2—	0	1—	0	0	0	0	1—	11	22	19	1—
		3	1,503	0	1—	0	9	53	61	50	72	51	50	25	11	8	x	11	75	121	48	14	0	0	0	0	1—	30	51	46	9
Other invertebrates†	272	1	65	0	0	0	0	0	0	0	5—	2	1—	1—	1—	1+	1	2+	1	0	0	0	0	0	0	0	0	0	2—	1+	0
		2	80	1—	3	1—	1—	1—	1—	0	3—	3+	1	1—	4+	0	3	0	6	1+	0	0	0	0	0	1—	1+	1—	2+	3—	1—
		3	127	1—	12	1—	1—	3—	0	0	3+	4	4	4	1	4	x	2—	9	3	2—	2—	0	0	0	5—	4+	1	3+	3	2—
Larvae‡	1,226	1	527	0	0	0	1	3—	2—	17	11	10	4	11	8	4	9	46	11	9	0	0	0	0	0	0	0	1+	10	12	0
		2	250	1—	1—	1—	1	5	5—	16	19	5	2	7	6	5	2—	2	11	6	1+	2	0	1—	0	1—	1—	3—	8	5	1+
		3	449	0	1	1+	3—	21	56	19	22	20	7	2	4—	3	x	2	8	9	1	1	1—	0	1	0	1—	20	16	5—	1—
Total population (as studied)	44,418	1	16,378	11	31	3	14	65	56	342	756	434	354	428	218	175	200	323	217	170	11	8	4	1	2	10	17	34	452	210	6
		2	9,472	42	26	19	14	182	337	384	258	237	251	335	276	360	177	131	217	255	44	18	9	5	0	9	37	138	275	241	16
		3	18,568	77	68	19	62	293	434	405	489	415	596	595	495	635	x	177	1202	2382	507	134	14	10	8	25	74	202	477	933	107

* Short period. † Mollusca (snails), Ixodoidea (ticks), Phalangida (harvestmen), Odonata (dragon-flies and damsel-flies), Ephemerida (May-flies), Neuroptera (lacewing flies), and Lepidoptera (butterflies and moths). ‡ Larvae of Neuroptera, Lepidoptera, and Coleoptera. x No collection.

TABLE 23.—Average numbers of invertebrates per unit collection taken by sweep net method of sampling invertebrate populations (24 unit collections, day sweeps) in the shrub stratum (1-2 meters) of postclimax deciduous shrub of ravine in true prairie subsere (Station 3 and substations), on basis of two-week periods.

Population Breakdown	Number of specimens collected*	Average numbers for two-week period ending												Seasonal averages per unit collection			
		1938 Apr. 25	May 9	23	Jun. 6	20	Jul. 4	18	Aug. 1	15	29	Sep. 24	1939 Mar. 25	Prevernal-vernal	Estival	Autumnal	(Late) Hiemal†
Araneida (spiders)	119	23	28	25	28	30	28	8	33	45	30	0	5	25	26	25	5
Orthoptera (grasshoppers, walking sticks, etc.)	71	0	0	0	3—	5	29	40	25	35	25	0	0	0	21	20	0
Homoptera (leafhoppers, aphids, etc.)	519	10	30	15	55	63	156	133	355	215	215	0	0	18	147	143	0
Hemiptera (true bugs)	31	15	10	8	3—	5	2	18	10	0	5	0	0	11	6	2—	0
Diptera (flies)	716	228	365	178	98	143	123	145	193	50	75	0	0	257	137	42	0
Coleoptera (beetles)	360	220	188	75	98	103	31	38	15	15	45	0	10	161	55	20	10
Winged Hymenoptera (bees and wasps)	555	120	175	38	75	165	145	198	110	85	40	0	0	111	142	42	0
Formicidae (ants)	241	73	133	65	108	53	22	33	33	10	40	0	0	90	44	17	0
Other Orders‡	28	3—	5	3—	0	7	8	0	3—	5	0	0	50	3+	5—	2—	50
Larvae§	142	85	130	28	20	25	13	13	0	5	15	0	0	81	15	7	0
Total Population (as studied)	2782	775	1063	433	485	600	557	623	775	465	490	0	65	757	596	318	65

* Unit collections were comprised of only 10 sweeps in this stratum; actual population values so derived are multiplied by 5 for comparison with unit collections in the herb stratum. † Based on 1 collection. ‡ Lepidoptera (butterflies and moths), Neuroptera (lacewing flies), and Ephemerida (May-flies). § Larvae of Lepidoptera and Coleoptera.

TABLE 24.—Average numbers of invertebrates per unit collection taken by enclosed quadrat method of sampling invertebrate populations (102 unit collections) in the litter stratum of true prairie subsere (Station 1 and substations), postclimax tall grass (Station 2 and substation, ravine) and postclimax deciduous shrub (Station 3 and substations, ravine).

Population breakdown	No. of specimens collected	Station	Station totals	Seasonal averages: Late Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal	Yearly averages
		1	7	1—	1—	0	0	0	1—
Mollusca	263	2	4	0	0	0	1	0	1—
(snails)		3	252	4+	8	18	8	0	7
		1	59	1—	3—	4+	0	1—	2—
Annelida	941	2	212	4+	13	19	0	1	7
(earthworms)		3	670	10	62	4	0	15	19
		1	64	3—	1	1—	1—	3+	2—
Araneida	560	2	162	3—	4	2+	2—	10	5
(spiders)		3	334	2—	3—	2+	11	20	9
		1	46	6	1—	1—	1—	2—	1+
Hemiptera	880	2	351	2+	8	1—	6	25	12
(true bugs)		3	483	9	4—	1—	10	32	13
		1	181	3+	8	7	3—	4—	5
Coleoptera	1229	2	567	10	8	5	4—	40	19
(beetles)		3	481	8	8	6	17	21	13
		1	77	3—	5	3—	0	1—	2
Formicidae	467	2	165	1—	17	7	1	1—	6
(ants)		3	225	11	11	7	1+	4—	6
		1	58	2—	2—	1—	3—	1+	2+
Other	348	2	102	15	2+	1	1	2—	3+
Arthropods*		3	188	1—	2+	1+	5+	9	5
		1	38	1—	3	1—	1—	1—	1
Larvae†	294	2	84	1—	5—	1	4—	3	3—
		3	172	2+	4+	1+	4+	9	5—
Total		1	530	17	22	16	6	11	14
population	4982	2	1647	35	57	34	19	81	55
(as studied)		3	2805	89	101	46	56	111	78

* Myriapoda (centipedes and millipedes), Chelonethida (pseudoscorpions), Orthoptera (grasshoppers and crickets), Isoptera (termites), Homoptera (leafhoppers), Diptera (flies), winged Hymenoptera (bees and wasps), and undetermined pupae.

† Larvae of Neuroptera (lacewing flies), Lepidoptera (butterflies and moths), and Coleoptera.

TABLE 25.—Average numbers of invertebrates per unit collection taken by enclosed quadrat and soil washer method of sampling invertebrate populations (63 unit collections) in the soil stratum (10 cms.) of true prairie subsere (Station 1 and substations), postclimax tall grass (Station 2 and substation, ravine), and postclimax deciduous shrub (Station 3 and substations, ravine), on basis of seasons.

Population breakdown	No. of specimens collected	Station	Station totals	Seasonal averages: Prevernal-vernal	Estival	Autumnal	Hiemal	Yearly averages
		1	2	0	1—	0	0	1—
Mollusca	67	2	0	0	0	0	0	0
(snails)		3	65	5—	4—	1	3+	3+
		1	21	3—	1	0	0	1—
Annelida	47	2	21	2—	2	2—	1—	1+
(earthworms)		3	5	1—	1—	0	0	1—
Araneida	21	2	2	1—	0	0	1—	1—
(spiders)		3	14	0	0	1—	1—	1—
		1	0	0	0	0	0	0
Hemiptera	73	2	2	0	0	1—	1—	1—
(true bugs)		3	71	1—	1—	12	8	4—
		1	71	2+	3—	4	3+	3
Coleoptera	277	2	88	6	2+	1	6	5—
(beetles)		3	118	1	2+	12	9	6—
		1	3	0	0	1—	1—	1—
Formicidae	24	2	4	0	0	1—	1—	1—
(ants)		3	17	1—	3—	1—	1—	1—
		1	14	0	1—	0	1—	1—
Other	37	2	4	1—	1—	0	1—	1—
Arthropods*		3	19	1—	1—	1	1	1—
		1	95	2—	3+	13	3—	4
Larvae†	143	2	13	1—	1	0	1—	1—
		3	35	2+	5—	1	1—	2—
Total		1	211	7	8	17	7	9
population	689	2	134	9	6	4	8	7
(as studied)		3	344	10	14	29	19	17

* Myriapoda (centipedes and millipedes), Isopoda (sow-bugs), Orthoptera (grasshoppers and crickets), Diptera (flies), winged Hymenoptera (bees and wasps), and undetermined pupae.

† Larvae of Neuroptera (lacewing flies), Lepidoptera (butterflies and moths), and Coleoptera.

TABLE 26.—Total numbers per two-week periods and seasonal av erages of invertebrates taken by alcohol pitfall at the ground surface (76 unit collections) in true prairie subsere (Station 1), postclimax tall grass (Station 2, ravine), and postclimax deciduous shrub (Station 3, ravine), April 8 to November 4, 1939. (Leafhoppers, true flies, bees, wasps, lacewing flies, butterflies, and moths omitted from pitfall studies.)

Population breakdown	No. of specimens collected	Station	Station totals	Total numbers for two-week period ending															Seasonal average per unit collection			
				1939 Apr. 22	May 6	May 20	Jun. 3	Jun. 17	Jul. 1	Jul. 15	Jul. 29	Aug. 12	Aug. 26	Sep. 9	Sep. 23	Oct. 7	Oct. 21	Nov. 4	Vernal	Estival	Autumnal	Hiemal
Mollusca (snails)	64	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		2	9	×	×	×	0	0	1	5	0	0	1	1*	0	1	0	0	×	0	2+	0
		3	55	×	×	×	4	1	25	12	5	3	4	0	1	0	0	0	×	30	40	1
Isopoda (sow-bugs)	7	1	6	0	1	1	2	0	0	1	0	0	0	0	0	0	1	0	1—	1—	1—	0
		2	1	×	×	×	0	0	0	0	0	0	1	0	0	0	0	0	×	0	1—	0
		3	0	×	×	×	0	0	0	0	0	0	0	0	0	0	0	0	×	0	0	0
Myriapoda (centipedes and millipedes)	73	1	9	0	1	1	0	1	0	0	0	2	1	0	0	0	3	0	1—	1—	1	0
		2	39	×	×	×	2	4	0	1	1	0	1	3*	6	8	9	4	×	2—	5—	4
		3	25	×	×	×	1	0	0	0	0	2	0	3	1	0	7	11	×	1—	2+	11
Chelonethida (pseudo-scorpions)	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		2	1	×	×	×	0	0	0	1	0	0	0	0	0	0	0	0	×	1—	0	0
		3	3	×	×	×	0	0	1	0	0	0	1	0	1	0	0	0	×	1—	1—	0
Phalangida (harvestmen)	401	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		2	14	×	×	×	0	0	0	0	0	0	0	13*	1	0	0	0	×	0	2+	0
		3	387	×	×	×	0	17	12	99	21	2	7	198	27	3	0	1	×	30	40	1
Araneida (spiders)	846	1	403	15	34	14	8	18	19	31	27	14	69	24*	39	43	27	21	21	21	36	21
		2	250	×	×	×	25	22	22	26	31	9	7	11*	28	23	26	20	×	25	17	20
		3	193	×	×	×	34	14	7	25	14	12	13	22	13	12	14	13	×	19	14	13

TABLE 26.—(*Continued*)

Population breakdown	No. of specimens collected	Station	Station totals	1939 Apr. 22	May 6	May 20	Jun. 3	Jun. 17	Jul. 1	Jul. 15	Jul. 29	Aug. 12	Aug. 26	Sep. 9	Sep. 23	Oct. 7	Oct. 21	Nov. 4	Vernal	Estival	Autumnal	Hiemal
				Total numbers for two-week period ending															Seasonal average per unit collection			
Orthoptera		1	312	1	14	14	21	41	39	32	15	30	20	27*	24	17	6	11	10	30	21	11
(grasshoppers,	821	2	222	×	×	×	24	18	22	14	16	10	11	23*	31	30	14	9	×	19	20	9
etc.)		3	287	×	×	×	11	19	42	88	29	7	3	25	24	22	13	4	×	38	16	4
		1	31	1	2	4	2	3	1	1	1	0	2	2*	6	3	2	1	2+	2—	3—	1
Hemiptera	1,552	2	57	×	×	×	2	0	0	0	1	1	2	0	3	17	25	6	×	1—	8	6
(true bugs)		3	1,464	×	×	×	28	14	9	3	5	39	200	963	166	21	12	4	×	12	234	4
		1	1,085	40	76	59	132	298	132	116	45	45	17	23*	47	37	15	3	58	145	31	3
Coleoptera	2,906	2	718	×	×	×	103	145	77	62	43	20	23	39*	60	93	30	23	×	86	44	23
(beetles)		3	1,103	×	×	×	51	72	67	82	87	191	135	128	125	87	59	19	×	72	121	19
Hymenoptera		1	1,989	3	25	27	56	76	220	450	283	212	99	158*	154	144	47	35	18	217	136	35
(ants and	3,266	2	888	×	×	×	50	62	95	66	53	36	37	71*	68	229	73	48	×	65	88	48
velvet ants		3	389	×	×	×	11	20	32	15	7	8	5	12	52	100	89	38	×	17	44	38
		1	896	4	8	4	7	4	21	143	53	136	188	265*	49	13	1	0	5	46	130	0
Larvae	1,221	2	208	×	×	×	12	4	20	19	12	30	27	48*	15	12	6	3	×	13	23	3
		3	117	×	×	×	12	12	37	13	3	8	12	6	7	4	3	0	×	15	7	0
Total		1	4,731	64	161	124	228	441	432	774	424	439	396	499	319	257	102	71	116	460	335	71
population	11,161	2	2,407	×	×	×	218	255	237	194	157	106	110	209	212	413	183	113	×	212	206	113
(as studied)		3	4,023	×	×	×	152	169	232	337	171	272	380	1357	417	249	197	90	×	212	479	90

* Collection for second week lost; two-week total derived by interpolating for the second week the average of the preceding and following week. × No collection.

TABLE 27.—Annotated list of prevalents.

Class	Order	Family	Prevalent	Attained prevalence in Station	Stratum	Season
Annelida	Oligochaeta (Class)	Enchytraeidae	Fridericia spp.	True prairie subsere, shrub	Litter	Prevernal-vernal, estival
				Tall grass	Litter	Estival
Arachnida	Phalangida	Phalangidae	Leiobunum sp.	Shrub	Ground surface	Estival
Insecta	Orthoptera	Acrididae	Melanoplus bivittatus (Say)	Tall grass	Herb	Prevernal-vernal
	Hemiptera	Miridae	Lygus pratensis (Linnaeus)	Tall grass	Herb	Autumnal
		Lygaeidae	Blissus leucopterus (Say)	Tall grass	Litter	Prevernal-vernal, hiemal
		Cydnidae	Geotomus robustus (Uhler)	Shrub	Soil & ground surface	Autumnal
		Tingidae	Piesma cinerea Say	True prairie subsere, tall grass	Litter	Hiemal
	Homoptera	Cicadellidae	Balclutha abdominalis (V.D.)	True prairie subsere	Herb	Prevernal-vernal, estival and autumnal
				Tall grass	Herb	Estival
				Shrub	Herb	Prevernal-vernal
			Dikraneura abnormis (Walsh)	Shrub	Herb	Autumnal
			Erythroneura sp.	Shrub	Shrub	Estival-autumnal
		Fulgoridae	Delphacodes sp.	True prairie subsere	Herb	Hiemal
		Aphidae	Anoecia graminis Gillette & Palmer	Shrub	Herb	Early hiemal
	Coleoptera	Carabidae	Amara sp.	True prairie subsere	Soil	Annual
					Litter	Autumnal
					Ground surface	Prevernal-vernal
				Tall grass	Soil	Annual
		Scarabaeidae	Ataenius cognatus Lec.	Shrub	Soil	Early hiemal
		Chrysomelidae	Chalcoides fulvicornis (Fabr.)	Shrub	Shrub	Prevernal-vernal
	Hymenoptera	Formicidae	Crematogaster lineolata Say	True prairie subsere	Ground surface	Autumnal, early hiemal
				Tall grass	Ground surface	Estival
			Prenolepis imparis Say	Tall grass and shrub	Ground surface	Early hiemal
			Dorymyrmex pyramicus Roger	True prairie subsere	Ground surface	Estival

TABLE 28.—Annotated list of subprevalents.

Class	Order	Family	Subprevalent	Attained subprevalence in Station	Stratum	Season
Mollusca	Pulmonata	Pupillidae	Gastrocopta armifera (Say)	Shrub	Litter	Estival
Insecta	Orthoptera	Gryllidae	Oecanthus niveus (DeG.)	True prairie subsere	Herb	Autumnal
	Hemiptera	Pentatomidae	Thyanta custator (Fabr.)	Tall grass	Herb	Late autumnal
				Shrub	Herb	Late autumnal
		Anthocoridae	Orius insidiosus Say	Shrub	Litter	Hiemal
	Homoptera	Cicadellidae	Macrosteles divisus (Uhl.)	Tall grass	Herb	Estival
		Cicadellidae	Empoasca sp.	Shrub	Herb	Late autumnal
		Psyllidae	Aphalara veaziei Patch	True prairie subsere	Herb	Early estival
	Coleoptera	Chrysomelidae	Pachybrachys litigiosus Suffr.	True prairie subsere	Herb	Early estival
		Tenebrionidae	Eleodes opaca Say	True prairie subsere	Ground surface	Estival
		Coccinellidae	Hippodamia convergens Guer.	Tall grass	Litter	Hiemal
		Carabidae	Agonoderus pallipes Fabr.	Tall grass	Ground surface	Autumnal
		Staphylinidae	Oxypoda sp.	Shrub	Litter	Hiemal
	Diptera	Chloropidae	Madiza sp.	Shrub	Herb	Vernal
		Chloropidae	Oscinella coxendix (Fitch)	Shrub	Herb	Late autumnal
		Chloropidae	Oscinella minor Adams	True prairie subsere	Herb	Autumnal
		Empididae	Rhamphomyia sp.	Shrub	Herb	Estival
		Empididae	Tachydromia maculipennis Walker	Shrub	Shrub	Preverna1-vernal
	Hymenoptera	Formicidae	Aphaenogaster fulva aquia Buckley	True prairie subsere	Herb	Autumnal
			Tapinoma sessile Say	True prairie subsere	Herb	Autumnal
			Pheidole bicarinata Mays	True prairie subsere	Herb	Autumnal
			Leptothorax curvispinosus ambiguus Emery	Shrub	Litter	Hiemal
			Ponera coarctata pennsylvanicus Buckley	True prairie subsere	Litter	Prevernal-vernal, early estival

TABLE 29.—Spatial and chronological distribution of prevalents of true prairie subsere throughout the periods, stations, and strata in which these animals were collected.

Prevalent	Stratum	Station	Average number per unit collection for two-week period ending: 1937 Nov. 16	1938 Jan. 17	Feb. 14	Mar. 28	Apr. 11	Apr. 25	May 9	May 23	Jun. 6	Jun. 20	Jul. 4	Jul. 18	Aug. 1	Aug. 15	Aug. 29	Sep. 12	Sep. 24*	Oct. 8	Oct. 22	Nov. 5	Nov. 19	Dec. 3	Dec. 17	1939 Jan. 14	Jan. 28	Feb. 11	Mar. 25	Seasonal averages per unit collection: Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
Balclutha abdominalis	Herb	Prairie subsere	0	x	x	0	0	0	12	13	72	235	133	43	25	4	2+	27	67	113	46	1—	0	0	x	0	x	0	0	0	6	93	23	1—
		Tall grass	0	x	x	0	0	0	8	71	48	29	10	10	11	14	8	2	0	4	3	1—	0	0	x	0	x	0	0	0	20	17	6	1—
		Shrub	0	x	x	1	0	3—	43	34	30	33	77	14	1—	0	0	0	0	0	0	0	1	0	x	0	x	0	0	1—	20	43	0	1—
Delphacodes sp.	Herb	Prairie subsere	0	x	x	0	0	0	0	0	3	2+	10	47	48	3—	6	8	13	0	10	5	5	2—	x	1	x	1	4	0	0	25	7	3+
		Tall grass	0	x	x	0	0	0	1	1—	0	2—	9	29	55	27	8	8	0	12	3+	1+	1	1—	x	1—	x	0	1—	0	1—	18	12	1—
Crematogaster lineolata	Herb	Prairie subsere	0	x	x	0	0	0	1	0	5—	6	2+	2—	5	1+	1—	1+	1	0	0	0	0	0	x	0	x	0	0	0	1—	4—	1—	0
		Tall grass	0	x	x	0	0	0	11	15	20	9	6	1	1—	1	0	1	2	0	0	0	0	0	x	0	x	0	0	0	6	6	1—	0
		Shrub	0	x	x	1—	0	3	20	18	11	8	15	11	4—	5—	7	x	1	1	1—	0	0	0	x	0	x	0	0	1—	8	11	3—	0
	Shrub	Shrub	x	x	x	x	x	23	25	30	30	0	2	0	0	5	35	0	0	x	x	x	x	x	x	x	x	x	x	x	26	5	13	x
	Litter	Prairie subsere	x	0	x	2	0	1—	1	7	1	1	1	2	2	0	0	x	x	x	0	0	0	0	0	0	0	0	2—	1	2	1+	0	1—
		Tall grass	x	0	0	0	0	2	9	1—	25	x	0	1	1	x	x	x	x	x	1—	0	0	0	0	0	0	0	0	0	1	5—	1—	0
		Shrub	x	0	0	0	0	0	0	0	6	x	2—	0	0	0	x	x	x	x	0	0	0	0	0	0	0	0	0	0	0	2—	0	0

Prevalent	Stratum	Station		Total numbers for two-week periods ending: 1939 Apr. 22	May 6	May 20	Jun. 3	Jun. 17	Jul. 1	Jul. 15	Jul. 29	Aug. 12	Aug. 26	Sep. 9	Sep. 23	Oct. 7	Oct. 21	Nov. 4		Seasonal averages per unit collection period (two weeks): Vernal	Estival	Autumnal	Early Hiemal
Crematogaster lineolata	Ground surface	Prairie subsere	— — — — — — —	7	6	4	27	32	59	71	207	100	57	97	102	51	31	17	— — — — — — —	6	79	73	17
		Tall grass	— — — — — — —	x	x	x	24	31	42	28	36	14	13	18	14	33	12	5	— — — — — — —	x	32	17	5
		Shrub	— — — — — — —	x	x	x	4	9	11	9	4	6	2	5	12	4	9	2	— — — — — — —	x	7	6	2
Dorymyrmex pyramicus	Ground surface	Prairie subsere	— — — — — — —	0	0	0	0	6	64	293	6	6	2	0	0	0	0	0	— — — — — — —	0	74	1+	0
Amara sp.	Ground surface	Prairie subsere	— — — — — — —	0	18	14	27	70	12	2	0	1—	0	0	0	0	0	0	— — — — — — —	16	22	1—	0
		Tall grass	— — — — — — —	x	x	x	4	6	1	0	0	0	0	0	0	0	0	0	— — — — — — —	x	2+	0	0
		Shrub	— — — — — — —	x	x	x	1—	2—	1—	0	0	0	0	0	0	0	0	0	— — — — — — —	x	1—	0	0

* Short period. x No collection.

Table 30.—Spatial and chronological distribution of prevalents of postclimax tall grass throughout the periods, stations, and strata in which these animals were collected.

Prevalent	Stratum	Station	1937 Nov. 16	1938 Jan. 17	Feb. 14	Mar. 28	Apr. 11	Apr. 25	May 9	May 23	Jun. 6	Jun. 20	Jul. 4	Jul. 18	1	Aug. 15	Aug. 29	Sep. 12	Sep. 24*	Oct. 8	Oct. 22	Nov. 5	Nov. 19	Dec. 3	Dec. 17	1939 Jan. 14	Jan. 28	Feb. 11	Mar. 25	Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
Melanoplus bivittatus	Herb	Prairie subsere	0	x	x	0	0	0	5—	6	17	11	8	8	5	1+	1—	0	0	0	0	0	0	0	x	0	x	0	0	0	3—	9	1—	0
		Tall grass	0	x	x	0	0	0	8	67	46	23	16	15	6	11	3	1—	1	0	1—	0	0	0	x	0	x	0	0	0	19	18	4—	0
		Shrub	0	x	x	0	0	0	14	30	19	10	4+	5	2—	3—	2	x	1	1	0	0	0	0	x	0	x	0	0	0	11	7	1+	0
	Shrub	Shrub	x	x	x	x	x	0	0	0	0	0	2	5	0	10	0	x	0	x	x	x	x	x	x	x	x	x	0	x	0	2—	3+	x
Lygus pratensis	Herb	Prairie subsere	1—	x	x	0	0	0	0	0	0	6	3—	1—	0	0	0	0	1—	0	0	0	0	0	x	0	x	0	1—	1—	0	2+	1—	1—
		Tall grass	14	x	x	5	0	0	0	0	0	0	1—	1—	1	0	0	0	1	7	80	6	1—	0	x	0	x	0	6	11	0	1—	23	2—
		Shrub	27	x	x	20	1	1	3	†	†	0	0	0	0	0	0	x	0	11	19	27	12	1—	x	0	x	0	2—	24	1+	0	6	7
	Litter	Tall grass	x	0	0	0	0	0	0	0	0	x	0	0	0	x	x	x	x	x	0	6	0	0	0	0	0	0	0	0	0	0	2	0
		Shrub	x	3	1	0	1—	0	0	0	0	x	0	0	0	0	x	x	x	x	0	1—	0	5—	4—	5	0	2—	1—	1	1—	0	1—	2+
Blissus leucopterus	Herb	Prairie subsere	0	x	x	0	0	0	0	0	0	0	0	0	0	0	0	1—	1	1	1—	0	0	0	x	0	x	0	0	0	0	0	1—	0
		Tall grass	0	x	x	0	0	0	5	0	4—	0	0	0	0	0	0	0	0	1	9	1—	0	0	x	0	x	0	1—	0	1+	1—	3—	1—
		Shrub	0	x	x	1	0	0	2—	0	0	0	0	0	0	0	1	x	1	0	0	0	0	0	x	0	x	0	0	1—	1—	0	1—	0
	Litter	Prairie subsere	x	0	x	1	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0	0	0	0	0	0	0	0	0	1—	0	0	0	0
		Tall grass	x	0	0	0	16	9	1	0	0	x	0	0	0	x	x	x	x	x	1—	1	3	51	1	0	18	14	1—	0	11	1—	1—	14
		Shrub	x	1	2	3	1	1—	0	0	0	x	0	0	0	0	x	x	x	x	3	3	3	0	17	1	1	2—	1	2+	1—	0	2—	4
Piesma cinerea	Herb	Prairie subsere	0	x	x	0	0	0	1—	0	1—	0	0	0	1—	0	1—	0	1—	0	0	0	0	0	x	0	x	0	0	0	1—	1—	1—	0
		Tall grass	0	x	x	0	0	0	34	4—	0	0	0	0	0	0	0	1—	0	0	1	0	0	0	x	0	x	0	0	0	9	1—	1—	0
		Shrub	0	x	x	0	0	1—	7	3	4—	1—	0	0	0	1—	1—	x	2	11	3	3—	1—	0	x	0	x	0	0	0	3—	1—	2+	1—
	Shrub	Shrub	x	x	x	x	x	0	3—	5	3—	0	1	0	0	0	5	x	0	x	x	x	x	x	x	x	x	x	0	x	3—	1—	2—	x
	Litter	Prairie subsere	x	1	x	0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0	1—	2—	6	0	1	0	2	0	1—	0	0	1—	1+
		Tall grass	x	0	0	1	1	0	1	0	0	x	0	0	0	x	x	x	x	x	4	1	6	18	10	0	24	5—	6	1—	1—	1—	3	10
		Shrub	x	3	0	1—	1	1	1	1—	0	x	0	0	0	0	x	x	x	x	3	5—	8	5	12	18	8	34	4—	1	1—	0	3—	13
Fridericia sp.	Litter	Prairie subsere	x	0	x	0	0	2—	1	0	0	11	7	0	0	0	0	x	x	x	0	0	2	0	0	0	0	0	0	0	3—	4+	0	1—
		Tall grass	x	0	0	9	6	11	21	18	1	x	47	0	0	x	x	x	x	x	0	0	5	0	1—	0	0	2	1—	4+	8	19	0	1
		Shrub	x	0	0	25	75	117	20	15	0	x	13	2—	0	0	x	x	x	x	0	0	77	40	2—	0	0	0	0	13	62	4	0	9
Amara sp.	Litter	Prairie subsere	x	0	x	1—	0	0	3	5—	0	0	1	0	1	0	0	x	x	x	5—	0	0	0	0	0	0	0	11	1—	2—	1—	2—	1
		Tall grass	x	0	0	0	0	4—	1	6	0	x	2	1	0	x	x	x	x	x	0	0	0	0	0	0	0	1	0	0	2—	2+	0	1—
	Soil	Prairie subsere	x	x	x	x	1	0	0	3	4	0	0	0	1	x	x	x	x	0	12	6	0	5	1	x	0	1	x	x	1	1—	4	2+
		Tall grass	x	x	x	x	0	16	3—	2	0	x	3	2	0	x	x	x	x	0	1	0	1	10	1	x	9	1	x	x	5—	1+	1—	4+

* Short period. † Many nymphs. x No collection.

TABLE 31.—Spatial and chronological distribution of the prevalents of postclimax deciduous shrub throughout the periods, stations, and strata in which these animals were collected.

Prevalent	Stratum	Station	1937 Nov. 16	1938 Jan. 17	Feb. 14	Mar. 28	Apr. 11	Apr. 25	May 9	May 23	Jun. 6	Jun. 20	Jul. 4	Jul. 18	Aug. 1	Aug. 15	Aug. 29	Sep. 12	Sep. 24*	Oct. 8	Oct. 22	Nov. 5	Nov. 19	Dec. 3	Dec. 17	Jan. 14	Jan. 28	Feb. 11	Mar. 25	Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
			Average number per unit collection for two-week periods ending																											Seasonal averages per unit collection				
Chalcoides fulvicornis	Shrub	Shrub	x	x	x	x	x	183	167	68	58	45	13	8	0	0	35	x	0	x	x	x	x	x	x	x	x	x	0	x	104	18	12	x
	Herb	Shrub	0	x	x	0	0	5—	2—	1—	2—	1—	0	0	0	0	0	x	0	0	0	0	C	0	x	0	x	0	0	0	2—	1—	0	0
Erythroneura sp.	Shrub	Shrub	x	x	x	x	x	10	10	13	25	5	32	103	175	145	160	x	0	x	x	x	x	x	x	x	x	x	0	x	11	65	102	x
Dikraneura abnormis	Herb	Shrub	0	x	x	0	0	0	0	0	0	0	8	28	122	108	209	x	15	123	102	3	3—	0	x	0	x	0	0	0	0	27	98	1—
Anoecia graminis	Herb	Shrub	1—	x	x	0	0	0	1—	2—	7	3—	8	9	0	0	0	x	2	51	297	129	21	4—	x	1—	x	3	0	1—	1—	5—	81	24
Prenolepis imparis	Herb	Tall grass	1—	x	x	0	0	0	1—	9	4—	7	2—	1—	0	0	0	0	0	0	0	0	1—	0	x	0	x	0	0	0	6	6	1—	0
		Shrub	4—	x	x	0	1—	6	30	29	13	19	4—	3	0	1	0	x	7	70	120	48	14	0	x	0	x	0	0	3—	16	8	41	9
	Shrub	Shrub	x	x	x	x	x	23	25	30	0	0	3—	0	0	0	35	x	0	x	x	x	x	x	x	x	x	x	0	x	24	8	0	x
Leiobunum sp.	Herb	Shrub	0	x	x	0	0	0	0	0	0	1—	1—	1	1	0	1	x	1—	0	0	0	0	0	x	0	x	0	0	0	0	1—	1—	0
Ataenius cognatus	Litter	Shrub	x	0	0	2—	0	2—	0	0	0	x	0	0	1—	0	x	x	x	x	0	0	0	0	0	0	0	0	0	1—	1—	1—	0	0
	Soil	Shrub	x	x	x	x	0	0	0	0	0	x	0	0	0	x	6	x	x	2	4	3	6	11	6	x	6	1	x	x	0	0	4—	5

Prevalent	Stratum	Station		1939 Apr. 22	May 6	May 20	Jun. 3	Jun. 17	Jul. 1	Jul. 15	Jul. 29	Aug. 12	Aug. 26	Sep. 9	Sep. 23	Oct. 7	Oct. 21	Nov. 4		Vernal	Estival	Autumnal	Early Hiemal
			Total numbers for two-week periods ending																	Seasonal averages per unit collection period (two weeks)			
Prenolepis imparis	Ground surface	Prairie subsere	— — — — — — — — —	0	0	0	1	11	2	42	21	37	14	0	18	19	9	4	— — — — — — — — — — — —	0	15	16	4
		Tall grass	— — — — — — — — —	x	x	x	0	9	4	11	0	0	1	0	22	22	29	26	— — — — — — — — — — — —	x	5	12	26
		Shrub	— — — — — — — — —	x	x	x	0	5	0	0	0	0	0	1	33	76	72	36	— — — — — — — — — — — —	x	1	30	36
Leiobunum sp.	Ground surface	Tall grass	— — — — — — — — —	0	0	0	0	0	0	0	0	0	0	13	1	0	0	0	— — — — — — — — — — — —	0	0	2	0
		Shrub	— — — — — — — — —	x	x	x	0	17	12	99	21	2	7	198	27	3	0	1	— — — — — — — — — — — —	x	30	40	1
Geotomus robustus	Ground surface	Shrub	— — — — — — — — —	x	x	x	24	12	7	1	2	22	181	940	159	7	2	0	— — — — — — — — — — — —	x	9	219	0
Ataenius cognatus	Ground surface	Shrub	— — — — — — — — —	x	x	x	11	4	0	11	30	163	108	36	5	16	21	1	— — — — — — — — — — — —	x	11	58	1

* Short period. x No collection.

TABLE 32.—Actual unit collection numbers of invertebrates taken by sweep net method of sampling invertebrate populations (169 unit collections; 117 day, 52 night) in the herb stratum of true prairie subsere (Station 1) and postclimax tall grass (Station 2), and in the herb and shrub strata of postclimax deciduous shrub (Station 3), during delimited periods comprising forenoon, afternoon, early night, and late night. Based on 57,277 specimens taken from June 12 to October 29, 1938, the first week of the hiemal aspect, as defined in this study, being included in the autumnal here.

ESTIVAL

Date	Station 1 Herb 8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	Station 2 Herb 8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	Station 3 Herb 8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	Station 3 Shrub* 8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.
1938, Jun. 12	—	563	—	—	—	304	—	—	—	532	—	—	—	800	—	—
17	798	907	—	—	180	291	—	—	502	334	—	—	470	520	—	—
18	—	—	944	—	—	—	215	—	—	—	472	—	—	—	680	—
19	—	—	—	496	—	—	—	—	—	—	—	—	—	—	—	—
21	—	653	—	—	—	231	—	—	—	657	—	—	—	615	—	—
23	614	452	650	—	237	204	196	—	530	—	—	—	285	—	—	—
25	296	—	—	—	135	—	—	—	146	—	—	—	—	—	—	—
28	440	—	—	—	188	—	—	—	355	—	—	—	635	—	—	—
29	—	—	159	—	—	—	109	—	—	—	—	—	—	—	—	—
30	—	231	—	140	—	—	—	114	—	—	—	—	—	—	—	—
30	—	—	—	169	—	—	—	—	—	—	—	—	—	—	—	—
Jul. 1	309	522	—	—	201	463	—	—	499	326	—	—	695	555	—	—
2	—	466	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	—	374	—	—	—	198	—	—	—	—	—	—	—	—	—	—
7	—	384	393	—	—	162	324	—	—	333	—	—	—	525	—	—
8	399	—	—	—	197	—	—	—	—	—	—	—	—	—	—	—
9	259	462	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	445	—	—	—	859	—	—	—	720	—	—
18	—	—	457	—	—	—	543	—	—	—	—	—	—	—	—	—
19	—	—	—	346	—	—	—	429	—	—	—	—	—	—	—	—
21	—	—	381	—	—	—	237	—	—	—	264	—	—	—	290	—
22	359	317	—	—	—	386	—	—	—	613	—	—	—	425	—	—
26	—	583	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28	—	386	705	—	—	340	443	—	—	577	—	—	—	1125	—	—
29	462	—	—	—	293	—	—	—	—	—	—	—	—	—	—	—
Aug. 1	—	245	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	117	—	—	—	—	—	—	—	495	—	—	—	—	—	—	—
3	—	—	409	—	—	—	489	—	—	—	495	—	—	—	470	—
4	—	—	427	—	—	—	413	—	—	—	—	—	—	—	—	—
5	175	323	—	—	246	317	—	—	—	495	—	—	—	465	—	—
6	—	—	—	231	—	—	—	213	—	—	—	530	—	—	—	355
6	—	—	—	261	—	—	—	181	—	—	—	—	—	—	—	—
10	—	—	324	—	—	—	351	—	—	—	—	—	—	—	—	—
10	—	—	238	—	—	—	346	—	—	—	—	—	—	—	—	—
11	—	—	—	380	—	—	—	166	—	—	—	259	—	—	—	510
12	—	193	—	—	—	257	—	—	—	—	—	—	—	—	—	—

* Actual collection numbers multiplied by 5.

Table 32.—(*Continued*)

Autumnal		12	—	214	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	258	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		15	—	485	—	—	—	353	—	—	—	—	—	—	—	—	—	—
		22	—	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		22	—	233	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		22	—	78	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		25	—	72	—	—	—	—	—	—	—	635	—	—	—	490	—	—
		25	—	199	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		25	—	101	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		29	207	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Sep.	3	—	—	241	—	—	—	214	—	—	—	—	—	—	—	—	—
		5	—	250	—	—	—	259	—	—	—	—	—	—	—	—	—	—
		5	—	183	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		7	159	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		9	—	—	—	—	95	—	—	—	—	—	—	—	—	—	—	—
		12	603	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		18	—	187	—	—	—	132	—	—	—	—	—	—	—	0	—	—
		18	—	178	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Oct.	1	217	—	—	—	225	—	—	—	1202	—	—	—	—	—	—	—
		7	—	—	438	—	—	—	510	—	—	—	925	—	—	—	—	—
		8	234	—	—	—	258	—	—	—	2614	—	—	—	—	—	—	—
		15	106	—	—	—	156	—	—	—	2149	—	—	—	—	—	—	—
		15	—	—	—	—	382	—	—	—	—	—	—	—	—	—	—	—
		18	—	—	—	—	—	—	—	—	—	206	—	—	—	—	—	—
		18	—	—	—	—	—	—	—	—	—	148	—	—	—	—	—	—
		21	—	—	25	—	—	—	101	—	—	—	965	—	—	—	—	—
	Early	22	3	—	—	—	6	—	—	—	316	—	—	—	—	—	—	—
	hiemal	29	30	—	—	—	41	—	—	—	697	—	—	—	—	—	—	—
		29	—	—	—	—	85	—	—	—	—	—	—	—	—	—	—	—
Total number of specimens	Estival		3936	6300	3689	1151	1431	3024	2067	543	2032	4231	736	—	2085	5285	970	—
	Autumnal		1851	3254	2102	872	1494	1318	2424	560	7473	1484	2385	789	—	955	470	865
	Jun. 12-Oct. 29		5787	9554	5791	2023	2925	4342	4491	1103	9505	5715	3121	789	2085	6240	1440	865
Total number of collections	Estival		9	13	7	4	7	10	7	2	5	8	2	0	4	8	2	0
	Autumnal		10	16	7	3	9	5	7	3	6	4	3	2	0	3	1	2
	Jun. 12-Oct. 29		19	29	14	7	16	15	14	5	11	12	5	2	4	11	3	2
Average number of specimens per collection	Estival		437	485	527	288	204	302	295	272	406	529	368	—	521	661	485	—
	Autumnal		185	203	300	291	166	264	346	187	1246	371	795	395	—	318	470	433
	Jun. 12-Oct. 29		305	329	414	289	183	289	321	221	864	476	624	395	521	567	480	433

* Actual collection numbers multiplied by 5.

TABLE 33.—Average numbers of prevalents per unit collection taken by sweep net method of sampling invertebrate populations (169 unit collections; 117 day, 52 night) in the herb stratum of true prairie subsere (Station 1) and postclimax tall grass (Station 2), and in the herb and shrub strata of postclimax deciduous shrub (Station 3), during delimited periods comprising forenoon, afternoon, early night, and late night. Averages are seasonal and for the entire period of the day-night studies, June 12 to October 29, 1938, the first week of the hiemal aspect, as defined in this study, being included in the autumnal here.

Prevalent		Station 1 Herb				Station 2 Herb				Station 3 Herb				Station 3 Shrub			
		8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.
Chalcoides	Estival	0	0	0	0	0	0	0	0	0	1—	1—	—	20	17	15	—
fulvicornis	Autumnal	0	0	0	0	0	0	0	0	0	0	0	0	—	12	0	10
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	0	1—	1—	0	20	15	10	10
Erythroneura	Estival	0	0	0	0	0	0	0	0	0	0	0	—	35	74	23	—
sp.	Autumnal	0	0	0	0	0	0	0	0	0	0	0	0	—	101	135	163
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	0	0	0	0	35	81	60	163
Balclutha	Estival	86	101	87	27	8	18	6	4	60	37	48	—	0	0	0	—
abdominalis	Autumnal	42	9	22	2+	4	6	8	4	0	0	0	0	—	0	0	0
	Jun. 12-Oct. 29	63	50	55	17	6	14	7	4	27	24	19	0	0	0	0	0
Delphacodes	Estival	26	26	21	5	20	21	39	15	0	0	0	—	0	0	0	—
sp.	Autumnal	10	5	14	21	9	15	66	24	0	0	0	0	—	0	0	0
	Jun. 12-Oct. 29	19	14	17	12	15	19	52	20	0	0	0	0	0	0	0	0
Melanoplus	Estival	7	9	6	5—	14	16	19	11	5	5	8	—	3—	1+	13	—
bivittatus	Autumnal	1—	1—	3—	3	1+	6	11	15	1—	2	1—	4—	—	3+	0	8
	Jun. 12-Oct. 29	4—	4+	4+	4—	7	11	15	13	3—	4	3+	4—	3—	2—	8	8
Lygus	Estival	1—	3+	1—	4—	1—	1—	1—	4	0	0	0	—	0	0	0	—
pratensis	Autumnal	0	1—	1—	0	30	1—	1—	0	17	0	9	0	—	0	0	0
	Jun. 12-Oct. 29	1—	2—	1—	2+	17	1—	1—	2—	9—	0	6	0	0	0	0	0
Dikraneura	Estival	0	0	0	0	0	0	0	0	6	40	18	—	0	0	0	—
abnormis	Autumnal	0	0	0	0	0	0	0	0	76	83	66	101	—	0	0	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	44	54	47	101	0	0	0	0
Anoecia	Estival	0	0	0	0	0	0	0	0	11	0	3—	—	0	0	0	—
graminis	Autumnal	0	0	0	0	0	0	0	0	161	1	35	0	—	0	0	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	78	1—	22	0	0	0	0	0
Crematogaster	Estival	4—	3+	3+	1+	2	7	1—	1—	13	9	13	—	3—	0	0	—
lineolata	Autumnal	1—	1—	4—	1	1—	1	3	3—	1—	4—	2—	17	—	13	55	28
	Jun. 12-Oct. 29	2—	2	3+	1+	1+	5—	2—	2—	8	7	6	17	3—	4—	18	28
Prenolepis	Estival	0	1—	0	0	1	3+	3+	1	7	6	20	—	3—	3+	0	—
imparis	Autumnal	1—	0	0	0	0	0	1—	4—	78	4—	32	3	—	0	0	3—
	Jun. 12-Oct. 29	1—	1—	0	0	1—	2+	2+	3—	39	5	27	3	3—	2+	0	3—
Leiobunum	Estival	0	0	0	0	0	0	1—	0	1—	1—	2	—	0	0	0	—
sp.	Autumnal	0	0	0	0	0	0	0	1—	0	1—	0	1	—	0	1	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	1—	1—	1—	1—	1—	1	0	0	1—	0
Blissus leoucopterus	Estival	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
	Autumnal	1—	1—	0	0	3+	0	1—	0	0	1—	0	0	—	0	0	0
	Jun. 12-Oct. 29	1—	1—	0	0	2—	0	1—	0	0	1—	0	0	0	0	0	0
Piesma	Estival	1—	1—	0	0	0	0	0	0	0	1—	1—	0	0	1—	0	—
cinerea	Autumnal	1—	1—	0	0	1—	1—	0	0	4—	2—	3	0	—	2+	0	0
	Jun. 12-Oct. 29	1—	1—	0	0	1—	1—	0	0	2	1—	2	0	0	1—	0	0