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LIFE HISTORIES AND HABITS OF SOME GRASSHOPPERS OF ECONOMIC IMPORTANCE
SHOTWELL, R. L. 1 OF 1

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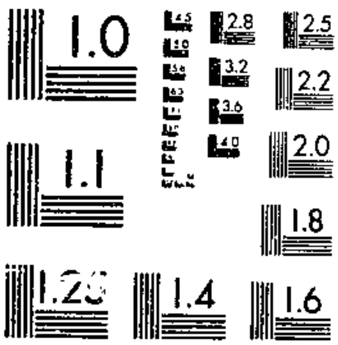

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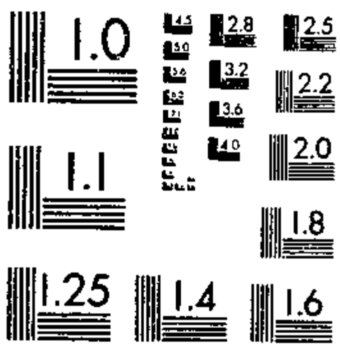

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# Life Histories and Habits of Some Grasshoppers of Economic Importance on the Great Plains[1]

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## CONTENTS



## INTRODUCTION

From 1923 to 1937, inclusive, special studies were made of the life histories and habits of 12 of the species of grasshoppers commonly found in the northern Great Plains area. These studies included field observations and laboratory experiments. A uniform method adopted for the study of each species consisted of rearing specimens in the laboratory to obtain data for descriptions of the various stages of development and to study the rate of development of both eggs and nymphs under various constant temperatures. Records of the seasonal and life histories in the field were also kept from year to year, and observations were made of feeding and migratory habits. Al-

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though the species were studied separately, their nymphal development and seasonal history were found to be similar in many respects.

A complete list of the species considered in this bulletin is as follows:

*Melanoplus bivittatus* (Say).
*M. differentialis* (Thos.).
*M. mexicanus* (Sauss.).
*M. femur-rubrum* (Deg.).
*M. gladstoni* (Scudd.).
*M. dawsoni* (Scudd.).
*M. packardii* (Scudd.).
*Phoetaliotes nebrascensis* (Thos.).
*Dissosteira carolina* (L.).
*Camnula pellucida* (Scudd.).
*Aulocara elliotti* (Thos.).
*Ageneotettix deorum* (Scudd.).

## PREVIOUS WORK ON GRASSHOPPERS

Criddle, Parker, the writer, and others have done similar work in the past, and each has emphasized certain species. At the time of his death, in 1933, Criddle was describing the nymphal stages of all species of grasshoppers common to the Canadian Provinces. He published a key [3] to the identification of the first instars of over 30 species, but a large amount of his work remains in the form of unpublished notes. Parker [4, 5] paid particular attention to the effects of temperature and moisture on *Melanoplus mexicanus* and *Camnula pellucida.* Shotwell [6] specialized on the life history and habits of each of the economic species and published on *M. mexicanus.*

As there have been over 1,500 publications on grasshoppers and a large portion of them contain some life-history work, the writer will not attempt to discuss this vast bibliography. In the present bulletin, which includes the recent work done on this subject as it pertains to the northern Great Plains area, *Melanoplus bivittatus* and *M. differentialis* are discussed more in detail than the other species because they represent grasshoppers of the so-called solitary type and are of outstanding economic importance.

## ECONOMIC IMPORTANCE OF GRASSHOPPERS

In 1931 the two species *Melanoplus bivittatus* and *M. differentialis* were responsible for the destruction of 25 to 75 percent of all crops in an area of 30,000 square miles in South Dakota and northeastern Nebraska.[7] Thousands of acres of corn (pls. 1 and 2), alfalfa (pl. 2, *B*), and small grains were utterly destroyed and trees and shrubs in shelterbelts and along streams were stripped of their foliage and their bark eaten (pl. 3, *A* and pl. 4). In some instances trees and shrubs put out new leaves three times during that summer. Plate 4, *B*, illustrates how the leaves came out the year following the heavy defoliation and decortication of the boxelder illustrated in pl. 4, *A*. This was the last struggle made by the tree, which did not survive another year.

Referring again to plate 2, the blowing of the soil in these destroyed cornfields, which started in the fall of 1931, was the beginning of the Dust Bowl formed in this area in 1934–36. In plate 5 a general view

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[3] CRIDDLE, NORMAN. STUDIES OF THE IMMATURE STAGES OF MANITOBAN ORTHOPTERA. Roy. Soc. Canada, Proc. and Trans., sect. V, 1926: 505–525, illus. 1926.

[4] PARKER, J. R. OBSERVATIONS ON THE CLEAR-WINGED GRASSHOPPER. Minn. Agr. Expt. Sta. Bul. 214, 44 pp., illus. 1924.

[5] ——— SOME EFFECTS OF TEMPERATURE AND MOISTURE UPON MELANOPLUS MEXICANUS MEXICANUS SAUSSURE AND CAMNULA PELLUCIDA SCUDDER (ORTHOPTERA). Mont. Agr. Expt. Sta. Bul. 223, 132 pp., illus. 1930.

[6] SHOTWELL, R. L. A STUDY OF THE LESSER MIGRATORY GRASSHOPPER. U. S. Dept. Agr. Tech. Bul. 190, 35 pp., illus. 1930.

[7] PARKER, J. R., and SHOTWELL, R. L. DEVASTATION OF A LARGE AREA BY THE DIFFERENTIAL AND THE TWO-STRIPED GRASSHOPPERS. Jour. Econ. Ent. 25: 174–187. 1932.

of the Hamill, S. Dak., area in 1931 shows the complete destruction of all crops. The farmers in this district are firmly convinced that the Dust Bowl east of Winner was the result of grasshopper damage in 1931. This area, 23 miles south of Hamill and 5 miles wide by 25 miles long, had more grasshoppers and suffered more severe damage than any area of like size in the State. Great drifts of soil buried orchards, houses, barns, and fences. Before 1931 this was a beautiful farming district, but in 1936 it was a waste of swirling black dirt.

In addition to their destructiveness to crops in 1931, grasshoppers were truly a pest in other ways. They entered houses, chewed holes in curtains and upholstery and also in the family wash hanging outdoors, and stained the clothes with salivary secretions so that rewashing became necessary. They became a nuisance to motorists, as they chewed the upholstery in the cars and flew into drivers' faces, causing accidents, in one of which two persons were killed. Windshields and finish were smeared by crushed bodies of the grasshoppers. The clogging of radiators with their bodies caused overheating and necessitated the use of screens. Last, and probably the most irritating to the women, the "'hoppers" caused runs in their silk hose!

*Melanoplus bivittatus* was the dominant species in the 1932–33 outbreaks in Minnesota, and both *M. bivittatus* and *M. differentialis* have figured prominently in all the later outbreaks in Iowa, Kansas, Nebraska, Missouri, Colorado, Wyoming, Arkansas, and Texas. In 1936 much corn in Iowa, Nebraska, Kansas, Missouri, and Oklahoma was destroyed by these two species.

## Some Food Preferences of Grasshoppers

Grasshoppers are voracious feeders, especially when the weather is hot and dry, and anything moist has a great attraction for them. Under dry conditions and during an outbreak they will feed on moist earth, wood, cotton, wool, linen, or silk fabrics, and the foliage and bark of trees, but they do show some preferences. Of the trees in a certain shelterbelt in South Dakota in 1931, the mulberry seemed to be the first choice, then apple, Chinese elm, honeylocust, caragana, boxelder, spruce, and poplar, in the order given. These were stripped of their foliage. The leaves of the poplar were not eaten but the petioles were chewed through and the leaves dropped. The only trees in the shelterbelt that seemed immune to grasshopper attack were those of the green ash. Evidently the grasshoppers did not care for the foliage or bark of this tree.

Of the small grains they seemed to prefer barley, oats, wheat, and rye, in the order given. Green barley seems to be a favorite food for both *Melanoplus bivittatus* and *M. differentialis*. The small grains are preferred to alfalfa or corn. These last, however, are particularly susceptible to damage in the young shoot stage. During rather dry weather the stalks of wild lettuce (*Lactuca* sp.) and corn were eaten down into the ground. The juicy blossoms of the prickly pear (*Opuntia* sp.) are also well liked.

Even when there are not enough grasshoppers in a field to destroy the foliage, great damage can be done to the ears of corn where practically no damage is noticeable from the road. The insects have a distinct preference for the corn silk and will eat this down to the cob, blasting from 25 to 60 percent of the kernels. Often part of the cob is eaten. The damage to the leaves is of two types, either they are chewed to the midrib or they are cut off from the stalk at the axils (pl. 1).

Other distinct types of damage due to certain food preferences of the grasshoppers are the shattering of oats, the feeding on the kernels of wheat in the head while it is in the dough stage, and the cutting off of heads of wheat and bolls of flax by chewing through the stems. Seed pods of alfalfa are bitten into and the growth stopped, which creates havoc with certified seed production. The most serious damage to alfalfa comes after the first cutting when the grasshoppers begin feeding on new shoots. This either checks the growth or kills the plants (pl. 2, *B*).

Having discussed some of the food preferences of grasshoppers, it seems well to mention their outstanding aversion to the sorghums after that crop has reach a certain stage in growth. In the years previous to 1931, the farmers of South Dakota learned that the grasshoppers did little damage to kafir and sorgo. Therefore, to protect their corn in 1931, they planted barriers of these two sorghums around their cornfields. They did not prove of any value as barriers but did become excellent examples illustrating the grasshopper's aversion to these plants.

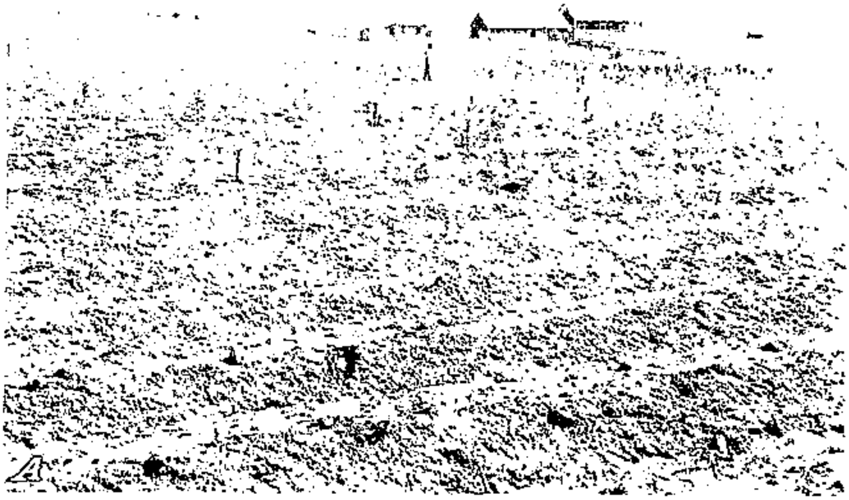
Plate 3, *B* is a photograph of a cornfield which had been completely surrounded by a barrier of kafir and sorgo. The picture shows a corner of that field with sorgo on the left and kafir in the background. The corn was entirely destroyed. There were many fields like this in South Dakota in 1931, and although the sorghums failed as barriers they did afford fodder in a district where all other crops were entirely destroyed.

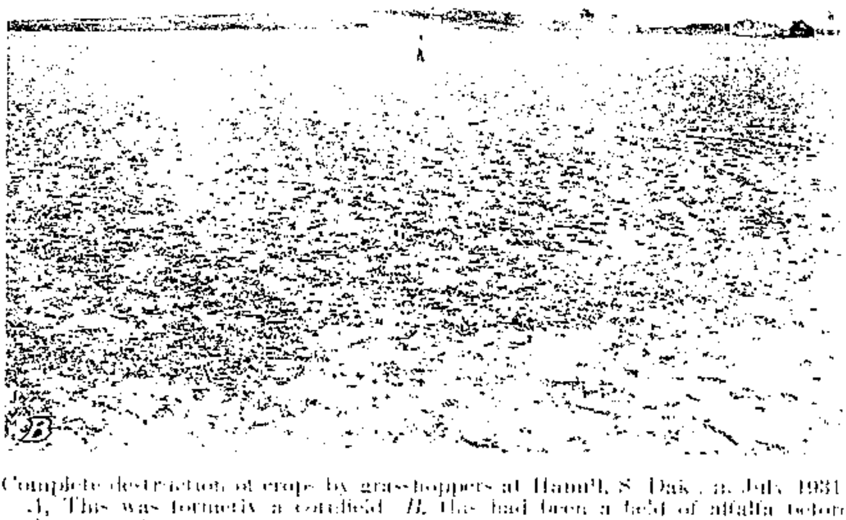
## SEASONAL HISTORY

The seasonal history of grasshoppers from an economic standpoint is divided into the egg, hatching, nymphal, and adult periods. From the standpoint of life history, hatching is not a stage but a process; from a seasonal or economic standpoint, however, it is a prolonged period due to variation in hatching time, not only between different species but within a given species. It is an important period because the newly hatched nymphs more easily succumb to adverse weather conditions than do older forms. If a general hatching takes place early in the season when the crops are small, complete destruction can occur in a short time and control measures be of little avail. When the hatching period is prolonged, the number of applications and quantities of poisoned bait necessary for effective control are greatly increased. For these important reasons it is necessary to consider hatching as a period in the seasonal history.

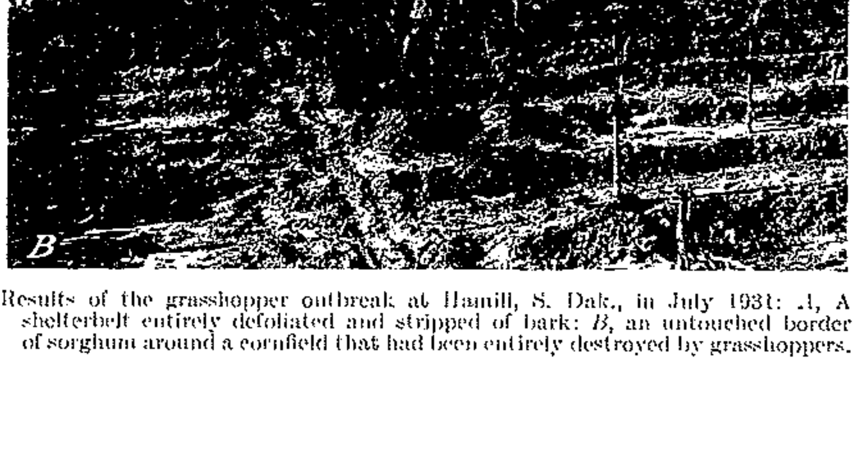
There is no definite time when events in the life history of grasshoppers occur. These events are influenced largely by weather and vary considerably from year to year. To show this variation in seasonal history, there are presented in table 1 the dates of the observed first occurrence in the northern Great Plains area of some of the important events in the life history of common economic grasshoppers during 14 years. They may not be actual first occurrences but are sufficiently close for practical purposes. The common economic grasshoppers referred to in table 1 and the following discussion are mainly

Grasshoppers feeding on a single stalk of corn at Hamill, S. Dak., in July 1931. This is the beginning of complete destruction of the stalk.



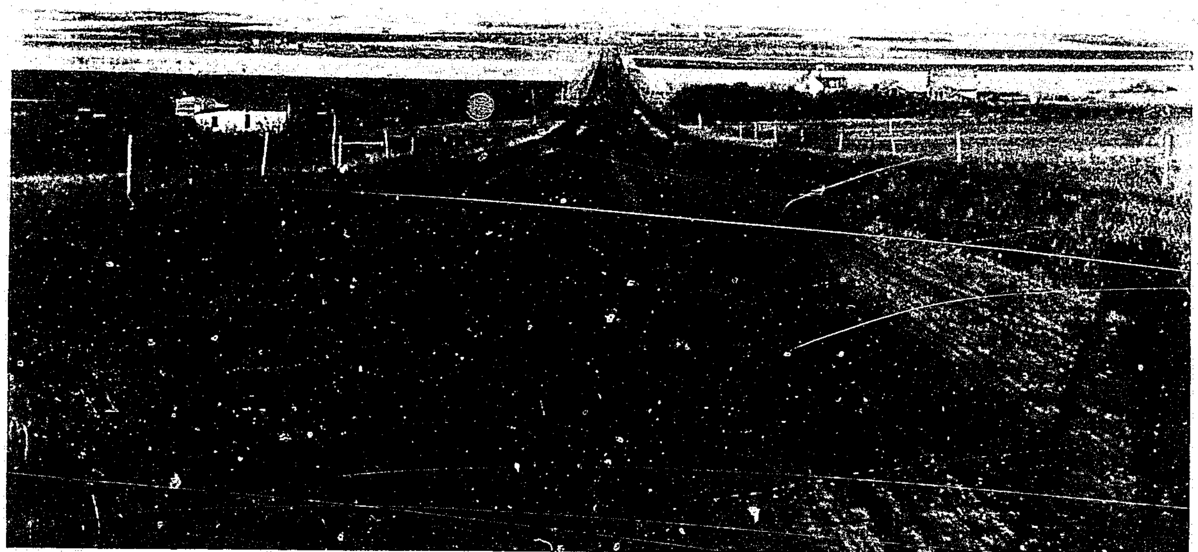


Complete destruction of crops by grasshoppers at Hamill, S. Dak., in July 1931. *A*, This was formerly a cornfield. *B*, This had been a field of alfalfa before the attack by the grasshoppers.



Results of the grasshopper outbreak at Hamill, S. Dak., in July 1931: *A*, A shelterbelt entirely defoliated and stripped of bark; *B*, an untouched border of sorghum around a cornfield that had been entirely destroyed by grasshoppers.


Grasshopper injury to a boxelder tree at Hamill, S. Dak., in July 1931: *A*, The tree entirely defoliated and stripped of bark in 1931; *B*, the same tree as it leafed out in 1932, its last effort at life.



A general view of the Hamill, S. Dak., area in July 1931. The black fields were cornfields entirely destroyed by grasshoppers; the lighter were fields of small grain that was destroyed.

*Melanoplus mexicanus* and *M. bivittatus*, whose seasonal life histories are practically the same, and both appear 2 or 3 weeks earlier than *M. differentialis*.

TABLE 1.—*First occurrence of events in the life histories of some common economic grasshoppers as observed for the years 1923–36, inclusive*

| Year | State | Date of first occurrence | | | |
|---|---|---|---|---|---|
| | | Hatching | Adult | Copulation | Oviposition |
| 1923 | Montana | May 4 | June 14 | July 7 | July 12 |
| 1924 | do | May 20 | June 24 | July 10 | July 17 |
| 1925 | do | May 15 | June 25 | July 26 | July 29 |
| 1926 | do | Apr. 20 | June 3 | -------- | -------- |
| 1927 | do | May 30 | July 10 | -------- | -------- |
| 1928 | do | May 15 | July 1 | -------- | -------- |
| 1929 | North Dakota | June 6 | July 12 | Aug. 1 | Aug. 10 |
| 1930 | do | June 1 | do | July 25 | -------- |
| 1931 | do | Apr. 24 | June 12 | June 16 | July 9 |
| 1932 | do | May 4 | do | -------- | July 10 |
| 1933 | Montana | May 17 | June 21 | July 10 | July 17 |
| 1934 | do | Apr. 25 | May 30 | -------- | -------- |
| 1935 | do | May 15 | June 20 | -------- | -------- |
| 1936 | do | Apr. 20 | June 1 | -------- | July 1<br>Sept. 18[1] |

[1] Second generation of *Melanoplus mexicanus* in Iowa.

From this table it appears that for the 14-year record hatching began anywhere from April 20 to June 6, a difference of 47 days. Adults made their first appearance from May 30 to July 12, a difference of 43 days. Oviposition began from July 9 to August 10, a difference of 32 days. It can readily be seen what varied effects such differences in seasonal history would have on the abundance of the nsects and their control.

Two years, 1935 and 1936, were years of drought and extremely high temperatures during the summer months. In 1935 hatching began the third week in May along Yellowstone Valley, Mont., and about June 7 in northern North Dakota. Adults appeared during the last week or 10 days of June. After July 1, 1935, Arkansas, Illinois, Oklahoma, and Texas were added to the territory under observation from the Bozeman laboratory. These States added a wider range of conditions and a wider variation in seasonal histories, hatching of a second generation in 1935 taking place about the last of August in Iowa. These individuals became adult and were able to lay eggs in October and November.

The first hatching over the whole area in 1936 was from April 20 to May 15. The first adults appeared June 1. Oviposition in 1936 was early enough in July to permit a partial second generation of *Melanoplus mexicanus* in Iowa, Nebraska, and Kansas. This second generation hatched the last week of August.

In northwestern Iowa in 1936, *Melanoplus bivittatus* had completed its life cycle, laid its eggs, and gone by August 10. By September 18 *M. differentialis* had done the same thing along the Missouri River bottoms in Iowa, Nebraska, and Kansas. At the same time this species, delayed by extreme heat and lack of green food, had just begun oviposition in the upland country of Kansas and in Oklahoma.

Differences in seasonal histories between species are discussed in detail in a later section on the effects of temperature on development.

### The Hatching Period

During the latter half of the summer of 1932, females of the species *Melanoplus bivittatus*, *M. mexicanus*, and *Camnula pellucida* were caged at Crookston, Minn., and the eggs of each species that were deposited prior to or between certain dates were kept separate. In September these eggs were placed in the soil next to the thermal units of soil thermographs at Mandan, N. Dak., and Bozeman, Mont., and kept there until the last week of April 1933, when they were brought into the laboratory at Bozeman and kept at the temperature of the outdoor insectary.

In table 2 the percentages of the total number of eggs that hatched are given for all the dates on which hatching took place. The original numbers of eggs used were 4,371 of *Melanoplus bivittatus*, 1,562 of *M. mexicanus*, and 1,401 of *Camnula pellucida*.

The periods of oviposition for *Melanoplus bivittatus* were August 1 to 9 and 15 to 23. There seemed to be no difference in the time of hatching in the spring as a result of this rather short difference in the time of oviposition. There was a difference, however, in the time of hatching between the Mandan and Bozeman eggs, 60 percent of the Mandan eggs having hatched by May 20, whereas it was not until May 29 that 60 percent of the Bozeman eggs had hatched. The soil temperature did not rise above the minimum hatching temperature of 60° F. at either place before April 3. Between April 3 and 24 the soil temperature went above this point on two days at Bozeman and on nine days at Mandan. After April 24 the eggs were all subjected to the same temperature in the laboratory at Bozeman. The difference in the soil temperatures between Mandan and Bozeman during the period April 3–24 was such as to advance the development of the Mandan eggs 9 days. The soil temperature for Bozeman was never above 70°, but for Mandan it was as high as 81°, going above 70° on five days during this period.

The eggs of *Camnula pellucida* deposited prior to August 5 began to hatch on June 5, or 9 days before those that were laid the first week of September. The Mandan eggs were 5 days earlier than the Bozeman eggs in the first hatching.

Eggs of *Melanoplus mexicanus* and *M. bivittatus* deposited between August 1 and 9 and overwintered at Mandan began to hatch May 15 and half or more than half of those of each species had hatched by May 21. Eggs of *Camnula pellucida* deposited prior to August 5, overwintered at Mandan under the same conditions and treated the same throughout, began to hatch June 5, and more than 50 percent were hatched by June 9. There was about 3 weeks' difference between the hatching periods of the two former and the latter species.

With constant temperature (table 13) it took the eggs of *Camnula pellucida* twice as long to hatch at 68° and 77° F. as it did those of *Melanoplus bivittatus*. These would approximate the mean soil temperatures of the hatching period. Eggs of *M. mexicanus* deposited during the first week of September hatched 3 days earlier than eggs of *C. pellucida* deposited during the same period (lots 6 and 9, table 2).

TABLE 2.—*Time of oviposition and hatching of Melanoplus bivittatus, M. mexicanus, and Camnula pellucida, showing the percentage hatched by each date*

| Lot No. | Species and oviposition date [1] | Proportion [2] hatched on date indicated | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | May 1933 | | | | | | | | | | | | | | | | |
| | | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
| | | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* |
| 1 | *Melanoplus bivittatus*, Aug. 1–9 ... M | 0.4 | 2.0 | 17.7 | 5.0 | 19.9 | 5.2 | 0.1 | --- | 0.1 | 0.5 | 0.5 | 0.1 | --- | 0.1 | 1.9 | 0.4 | --- |
| 2 | *M. bivittatus*, Aug. 15–23 ... M | .2 | 2.3 | 1.4 | 1.5 | 3.4 | 52.8 | 2.2 | --- | 1.3 | 6.2 | 11.8 | 4.3 | 0.1 | 1.1 | 3.0 | 1.5 | 0.9 |
| 3 | *M. bivittatus*, Aug. 1–9 ... B | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 4 | *M. bivittatus*, Aug. 15–23 ... B | --- | --- | --- | --- | --- | 1.8 | .2 | --- | .8 | 1.4 | 15.7 | 16.2 | --- | 11.1 | 15.6 | 14.0 | 0.8 |
| 5 | *M. mexicanus*, Aug. 1–9 ... M | 10.0 | 25.3 | 8.9 | 1.7 | 1.0 | 16.1 | 2.1 | --- | --- | 2.7 | 15.8 | 5.4 | .1 | 1.6 | .8 | .7 | .2 |
| 6 | *M. mexicanus*, Sept. 2–9 ... M | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 7 | *M. mexicanus*, prior to Aug. 23 ... B | --- | --- | --- | --- | --- | 28.8 | 4.0 | 0.5 | 17.5 | 3.5 | 4.6 | .8 | --- | .3 | 30.6 | --- | --- |
| 8 | *Camnula pellucida*, prior to Aug. 5 ... M | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 9 | *C. pellucida* Sept. 2–9 ... M | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 10 | *C. pellucida*, prior to Aug. 5 ... B | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |

| Lot No. | Species and oviposition date | Proportion hatched on date indicated | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | June 1933 | | | | | | | | | | | | | | |
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| | | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* |
| 1 | *Melanoplus bivittatus* Aug. 1–9 ... M | --- | --- | 0.1 | --- | --- | --- | --- | --- | --- | --- | 0.1 | 12.1 | 12.1 | 13.1 | 5.7 |
| 2 | *M. bivittatus*, Aug. 15–23 ... M | 0.6 | 0.9 | .6 | 0.5 | 0.3 | 0.6 | 0.1 | 0.3 | 0.6 | 0.2 | .4 | .5 | --- | --- | --- |
| 3 | *M. bivittatus*, Aug. 1–9 ... B | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | 92.9 | --- | --- | --- | --- |
| 4 | *M. bivittatus*, Aug. 15–23 ... B | 2.5 | 4.5 | 1.4 | .9 | .3 | 1.1 | .4 | .4 | .4 | .5 | .4 | .2 | --- | --- | --- |
| 5 | *M. mexicanus*, Aug. 1–9 ... M | .1 | --- | .1 | --- | --- | 1.0 | 1.3 | .1 | .2 | .8 | --- | .4 | .8 | .3 | --- |
| 6 | *M. mexicanus*, Sept. 2–9 ... M | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | 8.3 | 24.4 | --- | .4 | 3.7 |
| 7 | *M. mexicanus*, prior to Aug. 23 ... B | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 8 | *Camnulla pellucida*, Prior to Aug. 5 ... M | --- | --- | --- | --- | 7.5 | 17.8 | 15.0 | 3.5 | 21.7 | 16.0 | 11.7 | .3 | .9 | 1.9 | 1.3 |
| 9 | *C. pellucida*, Sept. 2–9 ... M | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | 10.9 | --- |
| 10 | *C. pellucida*, prior to Aug. Aug. 5 ... B | --- | --- | --- | --- | --- | --- | --- | --- | --- | 24.3 | 47.7 | 10.9 | 2.0 | 4.2 | 3.5 |

| Lot No. | Species and oviposition date | Proportion hatched on date indicated | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | June 1933 | | | | | | | | | | | | | | |
| | | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| | | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* |
| 1 | *Melanoplus bivittatus* Aug. 1–9 ... M | 1.5 | 0.4 | 0.2 | 0.3 | 0.2 | 0.1 | 0.1 | --- | --- | --- | --- | 0.2 | --- | --- | --- |
| 2 | *M. bivittatus*, Aug. 15–23 ... M | .3 | --- | --- | --- | --- | --- | --- | --- | 0.1 | --- | --- | --- | --- | --- | --- |
| 3 | *M. bivittatus*, Aug. 1–9 ... B | --- | --- | --- | 3.6 | --- | --- | --- | --- | --- | 3.6 | --- | --- | --- | --- | --- |
| 4 | *M. bivittatus*, Aug. 15–23 ... B | .8 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 5 | *M. mexicanus*, Aug. 1–9 ... M | .3 | --- | .1 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 6 | *M. mexicanus*, Sept. 2–9 ... M | 5.8 | 26.5 | 20.3 | 2.1 | --- | 0.2 | 2.1 | --- | --- | --- | 0.4 | --- | --- | --- | --- |
| 7 | *M. mexicanus*, prior to Aug. 23 ... B | .3 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 8 | *Camnula pellucida*, prior to Aug. 5 ... M | 1.7 | .6 | .1 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 9 | *C. pellucida*, Sept. 2–9 ... M | 31.8 | --- | --- | --- | --- | 2.2 | 2.2 | 13.0 | 6.5 | 6.5 | 2.2 | 13.0 | --- | 8.7 | --- |
| 10 | *C. pellucida*, prior to Aug. 5 ... B | 3.8 | .3 | --- | 1.7 | .5 | --- | .8 | .2 | --- | .2 | --- | .2 | --- | --- | --- |

[1] M=Overwintered at Mandan, N. Dak. B=Overwintered at Bozeman, Mont.
[2] All figures are percentages of total hatch.

Other things of interest and importance were brought out in this experiment. The most vital from an economic standpoint was the length of the hatching period of eggs of the same species deposited at the same time and overwintered under the same conditions. The longest was for *Melanoplus bivittatus* (lot 1, table 2), which extended from May 15 to June 27, a period of 6 weeks. In this case there were two major hatches, May 17–20, inclusive, when approximately 48 percent hatched, and June 12–15, inclusive, when 43 percent hatched. Outside these two periods the hatching was very light and sporadic. Considering all three species and similar overwintering conditions but not oviposition periods, heavy hatching was going on for a month.

The fact that the hatching period was so prolonged under the uniform conditions just described leaves little question but that this period must be even more prolonged under natural conditions involving different degrees of shading, soil temperature, and soil moisture. If observations on other species that appear later in the season had been included, the length of the hatching period would have been still more prolonged.

Moisture plays an important part in the hatching of grasshopper eggs. Incubation of eggs in the laboratory has shown that they will not hatch if the soil in which they are placed is allowed to get too dry. In the field it has been observed repeatedly that a shower brought on a fresh hatching.

Another way in which moisture may influence hatching was observed in 1929 at a point near Mandan, where eggs of *Melanoplus differentialis* were massed in soddy ground around a rock pile in the center of a wheatfield. On June 24 there were a number of newly hatched nymphs, but most of the eggs were still unhatched. The ground was extremely hard and dry, and the temperature was 79° F. at egg depth and 93° at the surface. Some of the vermiform nymphs were loose within the hard, packed soil but unable to make their way to the surface less than an inch above them. When freed from the soil these vermiform nymphs immediately became active and cast their first skins. Many of the eggs hatched within 2 or 3 minutes when brought to the surface. For 3 consecutive days it was observed that the eggs would hatch when freed from the hard, packed earth, and on each of these days the soil temperature was high enough for hatching. In addition to unhatched eggs, numbers of individuals which could not make their way to the surface were found dead in the vermiform stage partly or wholly out of the egg case. The normal June precipitation for Mandan is 3.33 inches, but the total rainfall for June 1929 was only 0.99 inch, whereas the totals for Beach and Dickinson, N. Dak., where normal hatching had already occurred, were 7.99 and 2.89 inches, respectively. Owing to the lack of moisture at Mandan the soil had become too dry and hard to allow the nymphs to burst their egg cases, even though they were alive and ready to hatch and the temperature was right for hatching.

Eggs may be killed by desiccation. Parker [8] in actual laboratory experiments dried eggs to a point where the loss of moisture equaled 65 percent of the total weight before all the eggs failed to hatch when brought again under moist conditions. With a loss of 51 percent moisture, 34 percent of the eggs hatched; and with a loss of 30 percent, 80 percent hatched. *Melanoplus differentialis* and other species

[8] See footnote 5, p. 2.

that lay their eggs close to the surface in the crowns of short grasses suffer the most from drought. Eggs of this species have been found dried to a powder under excessive heat and drought. It was a rather common occurrence to find eggs in this condition in Sully County, S. Dak., during the progress of the egg survey in September 1932. The whole preceding month had been above normal in temperature and below normal in rainfall. Mortality of eggs of *Melanoplus mexicanus* due to drought was also observed in November 1934 at Beach, N. Dak. The soil was extremely dry and the eggs were dehydrated to a powder in pods clinging to the roots of wheat stubble. In a few places there were as many dried-up eggs as good eggs. Without doubt extreme drought plays an important role in the reduction of grasshopper abundance by dehydration of the eggs.

## Length of Life Stages

Males and females of *Melanoplus bivittatus* reared in the laboratory at room temperatures were paired as soon as they became adult. Records were kept of the number of days from hatching to becoming adult and from then to first copulation, from first copulation to first oviposition, and from the beginning of the adult stage to death. The number of pods and eggs deposited by each female were also recorded. The data obtained with five such pairs are given in table 3.

Table 3.—*Life cycle of five pairs of Melanoplus bivittatus at room temperatures from hatching to death*

| Pair | Sex | Length of period | | | | Pods | Eggs |
|---|---|---|---|---|---|---|---|
| | | Hatching to adult | Adult to copulation | Copulation to oviposition | Adult to death | | |
| | | *Days* | *Days* | *Days* | *Days* | *Number* | *Number* |
| A | Male | 50 | 8 | | 50 | | |
| | Female | 46 | 7 | 30 | 64 | 2 | 161 |
| B | Male | 44 | 6 | | 23 | | |
| | Female | 44 | 6 | 18 | 69 | 4 | 205 |
| C | Male | 43 | 5 | | 20 | | |
| | Female | 42 | 8 | 7 | 18 | 2 | 80 |
| D | Male | 42 | 5 | | (1) | | |
| | Female | 42 | 5 | 16 | 25 | 1 | 75 |
| E | Male | 40 | 7 | | (1) | | |
| | Female | 40 | 7 | 21 | 35 | 2 | 117 |
| Average | | 43.3 | 6.4 | 18.4 | 38 | 2 | 127 |

[1] Unknown.

From hatching to the adult stage the average time was 43.3 days, from adult to first oviposition was about 25 days, and from adult to death 38 days. The greatest span of life observed was 113 days. The length of the periods depends largely on temperature.

By actual count, the greatest number of eggs laid by any female of *Melanoplus bivittatus* in one pod was 104. The greatest number of pods obtained from 1 female was 4. In one observation 40 females of *M. differentialis* deposited between 12,000 and 13,000 eggs, or an average of over 300 eggs per female.

In the field both these species began ovipositing at 72° F. air temperature and 66° soil temperature. When their abdomens were thrust into the ground they remained there, little disturbed by such conditions of cloudy and windy weather as would stop other activities.

The oviposition period is an important one in the matter of the subsequent grasshopper population. A prolonged and favorable period for oviposition increases the numbers of eggs deposited and the chances for a bad outbreak the following year.

## Population Changes Due to a Prolonged Hatching Period and to Movements of Grasshoppers

During June 1933 an attempt was made at Dickinson, N. Dak., to measure the normal population changes on a series of plots not poisoned or tampered with in any manner. The plots were from 5 to 10 acres in size and represented several kinds of crops. The method devised was for the observer to enter the plot and then remain quiet until the grasshoppers had settled. With a net held vertically and trailing close to the ground he then took five quick steps, bringing the net up smartly and with a quick twist of the wrist folding it over the rim to prevent the escape of the insects collected. A count was made of the number of specimens thus caught.

Five such collections were made as the collector moved diagonally across each plot every day for 6 days under the same conditions of time and temperature. Although this method was crude, it was better than a guess insofar as accuracy in estimating the population was concerned. In table 4 the first day's count was used as a basis for calculating the percentages of difference that occurred on each of the 5 succeeding days. These percentages are assumed to be population differences. The dates of the first day's collections are also given.

Table 4.—*Percentage difference in population of grasshoppers on each of 6 consecutive days during June 1933 on each of 10 plots, based on the relation of each day's sweep count to the first day's count, Dickinson, N. Dak.*

| Date of first observation | Kind of crop | First-day count | Percentage of difference for the 5 succeeding days | | | | |
|---|---|---|---|---|---|---|---|
| | | | Second | Third | Fourth | Fifth | Sixth |
| | | | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* |
| June 9 | Wheat | 168 | (1) | +23 | +4 | −45 | −13 |
| June 10 | Oats | 64 | +14 | +0 | +10 | +11 | +145 |
| June 12 | Grass | 114 | +27 | +18 | +18 | −3 | +12 |
| June 12 | Oats | 54 | +50 | +44 | +65 | +22 | +22 |
| June 13 | do | 65 | +3 | +6 | +109 | +28 | +3 |
| June 14 | Alfalfa | 70 | +11 | +111 | +120 | +108 | +31 |
| June 15 | Garden | 113 | −8 | −22 | −9 | −16 | −17 |
| June 17 | Wheat | 147 | +6 | −33 | −9 | −49 | −48 |
| June 19 | Alfalfa | 78 | +38 | −1 | +29 | −18 | −37 |
| June 21 | Wheat | 61 | +5 | +31 | +38 | +43 | +136 |
| Average | | 93 | +16.4 | +18.3 | +38.1 | +8.1 | +23.4 |

[1] Collection not made this day.

There was a general increase in the population of 6 out of the 10 plots, and the changes ranged from minus 48 to plus 145 percent; that is, the populations on the plots in 6 days ranged from 52 percent to 245 percent of the original numbers. These plots were all located within a 10-mile radius and there was little or no difference in their topography. On one plot the population had doubled during the period, and 2 days later it was only 3 percent more than the original number.

Within a large field, 40 acres or more, the grasshoppers are constantly shifting so that a heavy population occurring in a certain part of the field one day may have shifted to another part the next. The population of the entire field may have changed but little whereas that of a smaller portion may have doubled or trebled, or decreased to a similar extent. Shifting, continued hatching, and migration from or into a field combine to make the nymphal populations extremely variable.

## Seasonal Shifts in Population in One Locality

During 1935 and 1936 three surveys of the nymphs, adults, and eggs were made on an area of 10 sections of irrigated and nonirrigated farm land at Huntley, Mont. These sections are divided into 40-acre farms, which in turn are subdivided into smaller fields of from 2 to 20 acres. The whole area is crisscrossed by fences, roads, railroads, irrigation and drainage ditches, and canals. A variety of crops are raised in the area, and the fence rows, roadsides, and ditchbanks form ideal oviposition sites. From 1933 to and including 1936 there was a heavy population of grasshoppers on this area, mostly of *Melanoplus bivittatus, M. mexicanus, M. femur-rubrum, Camnula pellucida,* and certain range-land species.

During the last half of June 1935 a temporary assistant, G. K. Larsen, made a detailed nymphal survey and map of every section. Every field, ditch, roadside, fence row, etc., was mapped and a careful estimate of the number of nymphs per square yard recorded for each. Then in the last half of July an adult survey was conducted in the same manner over the same ground. This was followed by an egg survey in the fall. The next year, 1936, similar surveys were again made on these 10 sections. In table 5 the average numbers of nymphal and adult grasshoppers per square yard are recorded for each type of environment as well as the average number of egg pods per square foot. The table includes the results of the 2 years' work.

Table 5.—*Surveys of seasonal shifts in grasshopper populations near Huntley, Mont., during 1935 and 1936*

| Plant association or environment | 1935 | | | 1936 | | |
|---|---|---|---|---|---|---|
| | June | July | Fall | June | July | Fall |
| | Nymphs per square yard | Adults per square yard | Pods per square foot | Nymphs per square yard | Adults per square yard | Pods per square foot |
| | *Number* | *Number* | *Number* | *Number* | *Number* | *Number* |
| Alfalfa | 34 | 15 | 8 | 28 | 18 | 0.13 |
| Beans | (1) | 7 | 0 | (1) | 11 | 0 |
| Beets | (1) | 5 | 0 | 2 | 6 | 0 |
| Corn | (1) | 2 | 0 | 1 | 7 | 0 |
| Small grain | 6 | 6 | 3 | 10 | 11 | .07 |
| Clover | 6 | 8 | 2 | 15 | 10 | .25 |
| Pasture | 3 | 3 | 1.6 | 12 | 12 | .13 |
| Upland grass | 1 | 4 | ... | 14 | 10 | 0 |
| Military grass | (1) | (1) | 0 | 11 | 6 | 0 |
| Coulee | 3 | 7 | 1.3 | 25 | 11 | 0 |
| Mustard | 2 | 10 | 2 | 30 | 15 | 0 |
| Weeds | 14 | 25 | 4 | 22 | 15 | .12 |
| Canal bank | 67 | 13 | 23 | 50 | 24 | 4.60 |
| Drain ditchbank | 14 | 10 | 21 | 29 | 19 | .76 |
| Ditchbank | 21 | 12 | 11 | 27 | 17 | 1.37 |
| Fencerow | 17 | 13 | 10 | 23 | 17 | .67 |
| Railroad | 24 | 12 | 8 | 25 | 18 | .05 |
| Roadside | 17 | 11 | 12 | 20 | 17 | 1.64 |
| Wasteland | 18 | 9 | ... | 22 | 16 | 0 |

[1] Less than 1 per square yard.

The infestations began along the edges of the cultivated fields, and field observations showed that banks of the larger irrigation and drainage ditches facing south had the heaviest populations. Alfalfa was also a source of infestation. On the open prairie, coulee bottoms produced the greater numbers. In intensively cultivated fields containing crops such as beans, sugar beets, and corn, there was no infestation except that which came from the uncultivated edges. During the periods of hatching and oviposition the grasshoppers became more congregated.

Very few eggs were found in the fall survey of 1936, as during the summer considerable effective control work had been done, and some of the grasshoppers had migrated out of the area.

While the nymphal and adult surveys were being made the amount of damage done to each crop and the numbers of grasshoppers per square yard in the fields at the time of the observation were recorded (table 6). It is difficult to determine the number of grasshoppers per square yard required to cause a certain amount of damage since the estimated number of grasshoppers present when the damage is observed may or may not be the number present when the damage was done. Approximations were made, however, from numerous observations taken during the surveys of adult grasshoppers after most of the damage that was to be expected had been done. Both the range in population and the percentage of damage done, together with the averages, as observed for each crop, are shown in table 6. The figures given in tables 5 and 6 are only approximations but are considered accurate enough to give a reliable picture of the shifts in population.

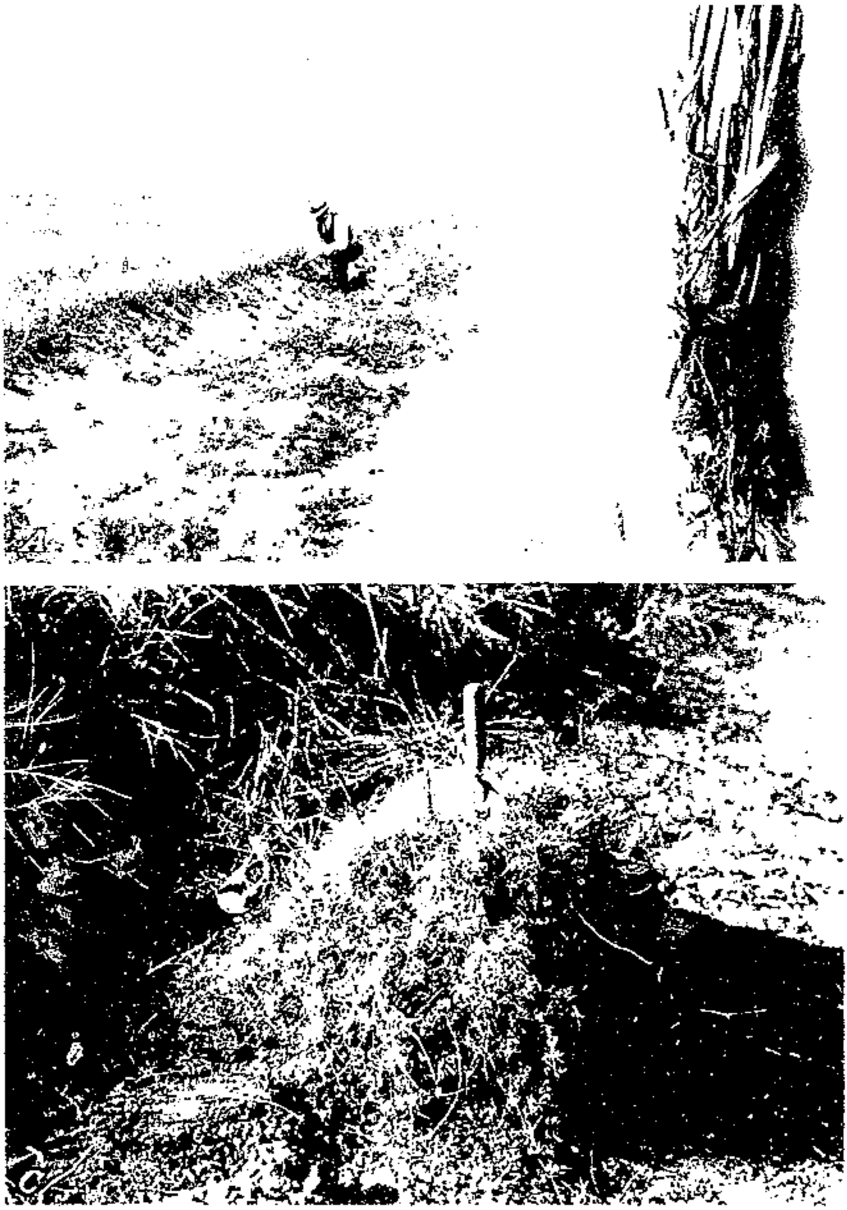
TABLE 6.—*Estimated numbers of grasshoppers per square yard required to do a certain amount of damage to different crops*

| Crop | Grasshoppers per square yard | | Damage done | |
|---|---|---|---|---|
| | Range | Average | Range | Average |
| | *Number* | *Number* | *Percent* | *Percent* |
| Alfalfa | 13–50 | 26 | 15–100 | 52 |
| Beans | 5–15 | 10 | 18–75 | 47 |
| Beets | 4–15 | 10 | 15–50 | 37 |
| Oats | 5–20 | 12 | 20–100 | 57 |
| Barley | 8–15 | 12 | 50–65 | 57 |
| Wheat | 10–20 | 15 | 20–100 | 48 |
| Clover | | 20 | | 25 |
| Sweetclover | 30–40 | 35 | 50–100 | 75 |
| Mustard | | 30 | | 100 |

In alfalfa, grasshopper populations as high as 10 per square yard prevent a new crop from developing from 10 to 14 days after the first cutting. The damage to alfalfa shown in table 6, however, represents only the percentage of plants actually killed. The recorded damage to oats is based largely on the destruction of the heads. In the wheat and barley it pertains to both heads and foliage. The damage to sweetclover includes defoliation and decortication.

A B

Egg pods and eggs of grasshoppers of the genus *Melanoplus:* *A*, Egg pods of *M. bivittatus*, natural size; *B*, eggs of *M. differentialis* in a clump of sod, showing the pods broken open.



The kinds of locations in which grasshopper eggs are commonly found: *A*, Roadside ditchbank facing south, an ideal egg-laying spot for *Melanoplus bivittatus*. *B*, a pod of eggs of *M. bivittatus* deposited in a crown of western wheatgrass along a headland; *C*, a clump of buffalo grass sod broken off from a ditchbank, which was plugged full of egg pods of *M. differentialis*.

# THE EGGS

## Description of the Eggs

The eggs of the different economic species vary in color, size, and arrangement in the pod, but the individual eggs all have a somewhat similar reniform or bananalike shape. The number of eggs per pod varies with the species and also with the individual. The pods of the same species often differ in size and shape. Eggs of *Melanoplus bivittatus* (pl. 6, *A*) and *M. differentialis* (pl. 6, *B*) are olive in color, whereas those of *Dissosteira carolina* are reddish, those of *M. mexicanus*, *M. femur-rubrum*, and *M. packardii* cream colored or whitish, and those of *Camnula pellucida* tan colored.

The average sizes of the eggs and the numbers of eggs per pod are given in table 7 for some of the important species. These data are based on 100 specimens of field-laid eggs of each species brought into the laboratory for study. It must be remembered that the individual eggs increase in size during the period between oviposition and hatching, and that they will shrivel under dry conditions and become plump under moist conditions.

TABLE 7.—*Sizes of eggs and numbers of eggs per pod of seven economic grasshoppers*

| Species | Dimensions of egg | | Eggs per pod |
|---|---|---|---|
| | Average length | Average width | |
| | *Millimeters* | *Millimeters* | *Number* |
| *Melanoplus bivittatus* | 5.12 | 1.53 | 43–104 |
| *M. differentialis* | 5.14 | 1.53 | 45–90 |
| *M. femur-rubrum* | 4.60 | 1.50 | 24–29 |
| *M. mexicanus* | 4.46 | 1.29 | 8–28 |
| *M. packardii* | 4.70 | 1.30 | 17–29 |
| *Camnula pellucida* | 4.72 | 1.50 | 10–36 |
| *Phoetaliotes nebrascensis* | 4.30 | 1.00 | 15–20 |

## Location of the Eggs in the Soil

*Melanoplus bivittatus* and *M. differentialis* select similar places for egg deposition. The eggs of these two species are seldom laid in open soil, unprotected by the roots of plants; instead they are concentrated along roadsides and field margins in certain favored locations such as the extreme edge of soddy roadside banks facing south, east, or west (preferably south in the more northern States), the ridges of sod in headlands, fence rows, and ditchbanks (pl. 7, *A*), and among the roots of various plants such as sweetclover, sunflowers, ragweed, lambsquarters, and corn stubble. The raised plant crowns of somewhat isolated clumps of sod, such as that of the short buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.), are especially attractive to *M. differentialis*. Plate 7, *C* shows a clump of buffalo-grass sod that had broken from the edge of a roadside ditchbank and lay in the bottom of the ditch. It was literally plugged full of egg pods of *M. differentialis*. The similar habit of *M. bivittatus* is illustrated in plate 7, *B*, which shows a small clump of western wheatgrass (*Agropyron smithii* Rydb.) taken from a headland where eggs of this species were numerous.

*Camnula pellucida* lays a loose egg pod in the crowns of the short bunchgrass which is often found in headland, pastures, ditchbanks, etc. Small overgrazed pastures are favorite places for oviposition by this species. In the Centennial Valley, Mont., a high mountain valley, this species selects the crowns of alkali-grass (*Puccinellia* spp.) for egg deposition.

The egg pods of *Melanoplus mexicanus* are more scattered and are often found throughout grainfields clinging to the roots of the stubble. This distribution may be fairly uniform over the entire field, with some concentration around the edges of the fields and in the vicinity of strawstacks. The egg pods are often concentrated in the wind-blown sandy loam hummocks or ridges along the headlands. *M. mexicanus* will also oviposit in the soil under Russian-thistles, in the crowns of alfalfa, or in the open soil between alfalfa plants. In stump pasture land, eggs of this species have been found in the bare packed soil between the projecting roots of the stumps and concentrated on the south side of them.

*Melanoplus packardii* prefers the open ledges of soil washed down from a cut bank or a blown sand ridge of a fence row. The pods of *Melanoplus femur-rubrum* are usually found scattered in locations similar to those adopted by *M. bivittatus*, *M. differentialis*, and *M. mexicanus*. *Dissosteira carolina* places its eggs deeper in the silt deposited by the run-off from the fields or in blown sand ridges or banks. They are seldom found among the roots of grass or other plants. Certain prairie forms such as *Aulocara elliotti* and *Ageneotettix deorum* lay a small, tough pod containing five or six pearly-white eggs. These pods are deposited in the upper one-fourth inch crust of open, packed ground or bare spots in grainfields, native sod pastures, or hayfields. The egg pods of *Aulocara* are larger than those of *Ageneotettix*.

## THE NYMPHS

### External Structural Changes During Nymphal Development

#### NUMBER OF INSTARS

Of the important species studied in the northern Great Plains area, *Melanoplus differentialis* was the only one observed to undergo 6 instars regularly in its nymphal development. The rest usually exhibited 5 although often 6 instars. Table 8 shows the percentage of males and females of the species reared through to maturity in the laboratory that had 5 or 6 instars in their nymphal development. *M. differentialis* is not included because not one case of deviation from the 6 instars was discovered among the 500 or more individuals reared. In 1925 a number of specimens of *M. differentialis* were reared at room temperatures, and several of these were recorded as having 7 instars. This phenomenon has never been duplicated, however, among several hundred specimens since reared to maturity, and 7 instars are of rare occurrence.

TABLE 8.—*Proportion of males and females of various species of grasshoppers that had five and six instars in laboratory rearings*

| Species | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | Specimens | Five instars | Six instars | Specimens | Five instars | Six instars |
| | *Number* | *Percent* | *Percent* | *Number* | *Percent* | *Percent* |
| *Melanoplus bivittatus* | 244 | 93.0 | 7.0 | 241 | 59.3 | 40.7 |
| *M. mexicanus* | 18 | 77.8 | 22.2 | 15 | 60.0 | 40.0 |
| *M. femur-rubrum* (from Montana) | 78 | 97.4 | 2.6 | 95 | 96.8 | 3.2 |
| *M. femur-rubrum* (from Tennessee) | 27 | .0 | 100.0 | 20 | 10.0 | 90.0 |
| *M. packardii* | 77 | 92.2 | 7.8 | 57 | 71.9 | 28.1 |
| *M. gladstoni* | 1 | 100.0 | .0 | 9 | 77.8 | 22.2 |
| *Dissosteira carolina* | 119 | 96.6 | 3.4 | 115 | 78.3 | 21.7 |
| *Camnula pellucida* | 28 | 100.0 | .0 | 35 | 97.1 | 2.9 |

Two principal facts are brought out in this summary, (1) that the females are more likely to go through six instars than are the males and (2) that most of the specimens of *Melanoplus femur-rubrum*

FIGURE 1.—The extra instar in *Melanoplus bivittatus*. Beginning from the left the instars shown are the second, the third, the extra instar, and the fourth.

reared from eggs collected in Tennessee went through six instars whereas those from eggs collected in Montana usually went through five.

### THE EXTRA INSTAR

The extra instar has been discussed by the writer in an earlier publication.[9] After a careful study of numbers of specimens of *Melanoplus bivittatus* and others, no differences have been discovered between individuals in the first three instars which might indicate that certain of them were going through six instars. After the third molt the tegmina and wing pads of the five-instar individuals turn dorsad. Of those that will go through six instars, the pads remain pointing ventrad until in the fifth instar. This is shown in figures 1, 2, and 3.

The individual in the extra instar is somewhat larger than the regular third-instar specimen but smaller than the regular fourth-instar specimen, the fifth instar of these showing the development of the regular fourth stage of five-instar grasshoppers. Size in the fifth

[9] See footnote 6, p. 2.

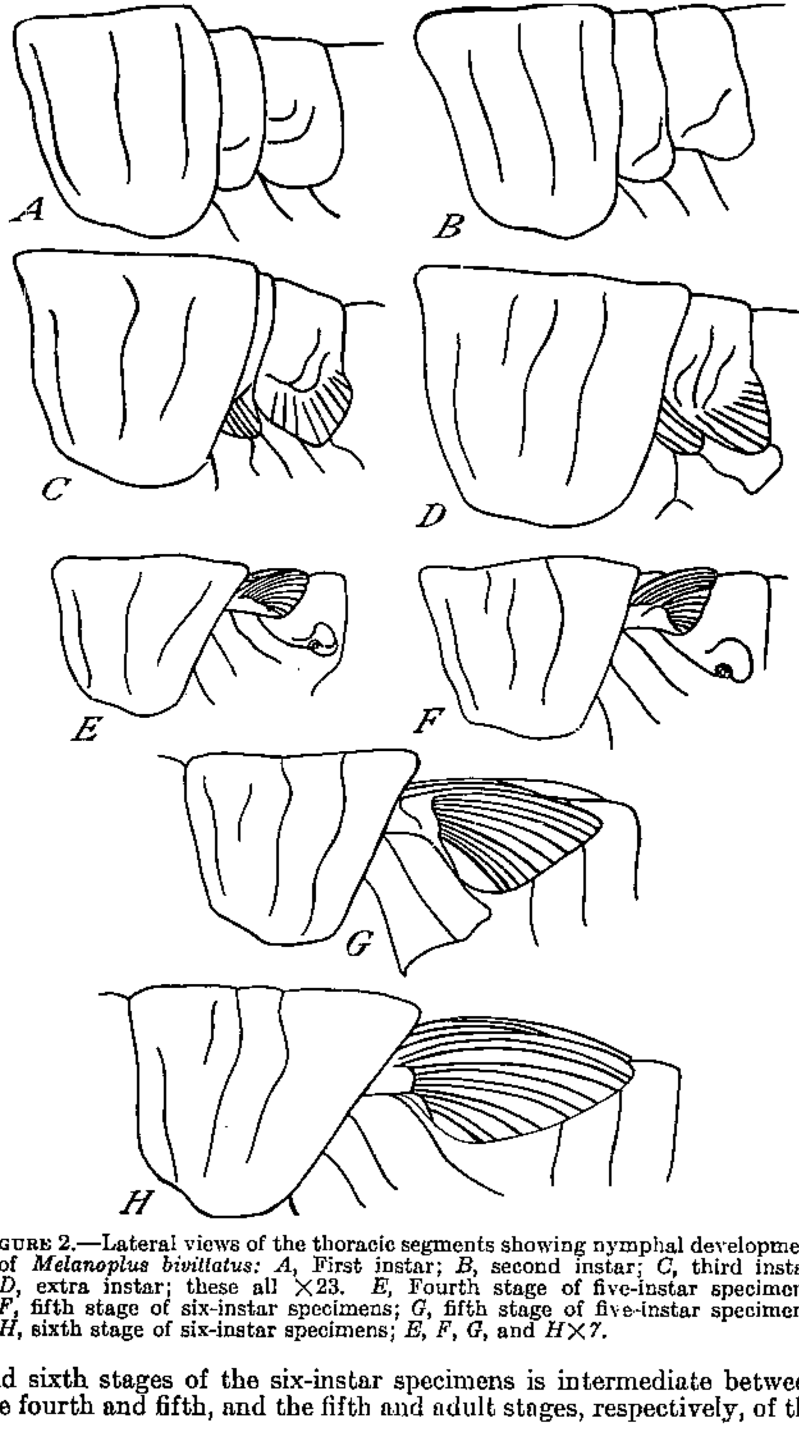



FIGURE 2.—Lateral views of the thoracic segments showing nymphal development of *Melanoplus bivittatus*: *A*, First instar; *B*, second instar; *C*, third instar; *D*, extra instar; these all ×23. *E*, Fourth stage of five-instar specimens; *F*, fifth stage of six-instar specimens; *G*, fifth stage of five-instar specimens; *H*, sixth stage of six-instar specimens; *E*, *F*, *G*, and *H* ×7.

and sixth stages of the six-instar specimens is intermediate between the fourth and fifth, and the fifth and adult stages, respectively, of the

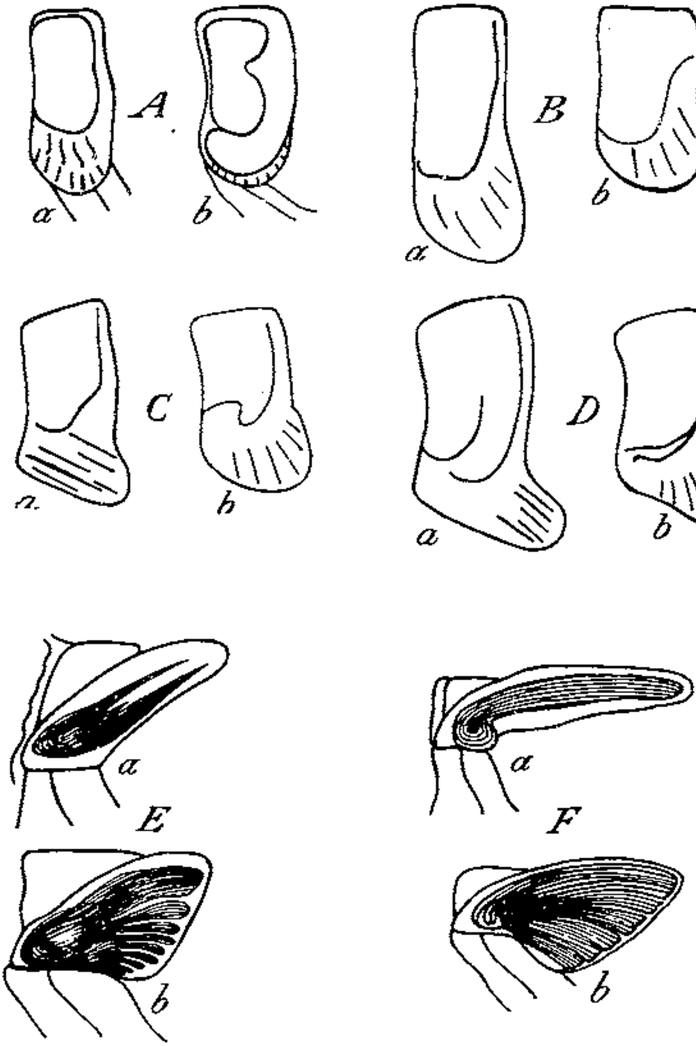



FIGURE 3.—Tegmina and wing pads separated out to show nymphal development of *Melanoplus bivittatus*: *A*, First instar; *B*, second instar; *C*, third instar; *D*, extra instar; *E*, fourth instar; *F*, fifth instar. *a* and *b* indicate in each pair the tegmina and wing pad, respectively.

five-instar grasshoppers of the same species. This is shown in figure 2, where the first four drawings, those of the first, second, third, and extra instar, are enlarged 23 times, and the four drawings of the last two stages, both of five- and six-instar grasshoppers, are enlarged 7 times. The stage of development of the fifth and sixth stages of the six-instar specimens is the same as for the fourth and fifth of the five-instar individuals but the insects are larger in both cases. Adults of the six-instar series are usually larger and in case of *Melanoplus bivittatus*

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have two more segments in the antennae than do those showing the usual development.

### CHANGES IN SIZE DURING NYMPHAL DEVELOPMENT

Table 9 indicates the nymphal development of the different species, based on the length of the hind femur and on the number of segments in the antennae. The length of the hind femur was selected as an index of size because of the ease in making this measurement and its higher correlation with the other easily measurable characters. To prove this, variations in the lengths of prothorax, hind femur, and tegmina were correlated for a large number of adults of *Melanoplus mexicanus*, male and female. These correlations are listed in table 10.

TABLE 9.—*Average number of antennal segments and length of hind femur for each instar, including six instar-forms, for nine of the common economic grasshoppers*

| Stage of development | *Melanoplus bivittatus* | | | | *M. differentialis* | | *M. mexicanus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Five-instar specimens | | Six-instar specimens | | | | Five-instar specimens | | Six-instar specimens | |
| | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur |
| | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* |
| First instar | 13 | 3.06 | 13 | 3.06 | 12 | 2.50 | 12 | 2.39 | 12 | 2.39 |
| Second instar | 17 | 4.28 | 17 | 4.28 | 16 | 3.83 | 15 | 3.30 | 15 | 3.30 |
| Third instar | 19 | 5.58 | 19 | 5.58 | 18 | 5.37 | 18 | 4.71 | 18 | 4.71 |
| Fourth instar | 20 | 8.43 | 22 | 6.80 | 20 | 7.37 | 20 | 6.58 | 19 | 5.92 |
| Fifth instar | 22 | 11.90 | 23 | 10.08 | 23 | 8.67 | 22 | 8.05 | 22 | 7.62 |
| Sixth instar | | | 24 | 13.68 | 25 | 9.72 | ...... | ...... | 23 | 9.31 |
| Adult male | 24 | 16.82 | 26 | 18.1 | 26 | 15.42 | ...... | 12.49 | ...... | ...... |
| Adult female | 24 | 16.82 | 26 | 18.1 | 26 | 18.01 | ...... | 13.62 | ...... | ...... |

| Stage of development | *M. femur-rubrum* | | *M. packardii* | | *M. gladstoni* | | *Phoetaliotes nebrascensis* | | *Camnula pellucida* | | *Dissosteira carolina* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur | Antennal segments | Length of hind femur |
| | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* | *Number* | *Mm.* |
| First instar | 12 | 2.40 | 12 | 3.38 | 12 | 2.50 | 11 | 2.57 | 11 | 2.54 | 11 | 2.72 |
| Second instar | 16 | 3.37 | 16 | 4.54 | 15 | 3.31 | 15 | 3.73 | 12 | 3.63 | 14 | 4.04 |
| Third instar | 18 | 4.58 | 19 | 5.96 | 18 | 4.85 | 18 | 5.35 | 17 | 4.42 | 18 | 5.76 |
| Fourth instar | 20 | 6.49 | 20 | 8.37 | 20 | 6.77 | 20 | 7.55 | 18 | 6.44 | 20 | 7.72 |
| Fifth instar | 22 | 8.93 | 21 | 10.16 | 21 | 8.69 | 23 | 9.66 | 20 | 8.20 | 23 | 10.67 |
| Sixth instar | | | | | | | | | | | | |
| Adult male | 24 | 10.41 | 24 | 13.70 | 23 | 9.5 | 23 | 10.43 | 23 | 10.5 | 24 | 14.0 |
| Adult female | 24 | 11.65 | 24 | 16.50 | 23 | 11.7 | 23 | 13.30 | 23 | 12.7 | 24 | 17.0 |

The length of the tegmina was the most variable character and, of course, could not be used as a measure of size. The correlation between the lengths of the hind femur and the prothorax was high, but the correlation between the length of the hind femur and the length of the tegmina was higher than that between the length of the prothorax and that of the tegmina. Therefore it should be the best measurement of the differences in size between specimens of a single species of grasshopper. The measurements given in table 9 bear out the value of using the length of the hind femur as a measurement for showing development in size. Whenever available, measurements of individuals undergoing six instars were included.

TABLE 10.—*Correlation coefficients between lengths of hind femur, prothorax, and tegmina of Melanoplus mexicanus*

MALES

| Place | Specimens | Correlation between— | | |
|---|---|---|---|---|
| | | Prothorax and hind femur | Prothorax and tegmina | Hind femur and tegmina |
| | *Number* | | | |
| Brockton, Mont. | 122 | 0.7458±0.0271 | 0.6189±0.0377 | 0.6314±0.0367 |
| Havre, Mont. | 83 | .6837± .0394 | .4985± .0566 | .6169± .0459 |

FEMALES

| Place | Specimens | Prothorax and hind femur | Prothorax and tegmina | Hind femur and tegmina |
|---|---|---|---|---|
| Brockton | 80 | 0.8067±0.0251 | 0.6790±0.0387 | 0.6557±0.0416 |
| Havre | 78 | .7318± .0359 | .4156± .0640 | .5692± .0523 |

## CHANGES IN THE THORACIC SEGMENTS

When grasshoppers first hatch, the head, thorax, and hind femora are large in proportion to the short, pinched abdomen. This relationship recurs to a decreasing extent with every instar immediately after molting. When several specimens are reared together in a tube, it can easily be told which of these has just molted if the length of the abdomen is noted. Toward the end of each instar the abdomen becomes much elongated.

The median carina of the prothorax is more knifelike in the first instar than later, but as the nymph approaches maturity the prothorax becomes more rounded. The length of the insect increases from four to seven times between hatching and maturity.

From the very first the tegmina and wing pads are free at the apices of the mesothoracic and metathoracic segments and form flaps of the integument (figs. 1 and 2). In the first two instars it is rather difficult to distinguish any changes in the general appearance of these parts. The venation is very slight and the only noticeable change is in the bulging at the apex of the metathoracic segment in the second instar. There is a decided change in the third instar in which the venation becomes clearly visible and the wing pads assume a characteristic triangular shape. After the third molt the tegmina and wing pads of most specimens turn dorsad for the first time. These individuals will go through five instars. In others, even of the same species, the pads remain pointing ventrad, more obliquely caudad, and are more elongated and rounded at the apices (figs. 1 and 2, *D*). This is the fourth instar of the specimens that undergo six instars.

In the next to the last instar the pads are turned dorsad for the first time, but do not extend to the end of the first abdominal segment. In the last instar they become more elongated and extend beyond the second abdominal segment. During these last two instars, the wing pads overlie the tegmina. In the final stage of the last molting process the adult distends its tegmina and wings so that the latter hang down to dry, and as they dry they fold up under the tegmina. The relative positions are thus reversed.

### CHANGES IN THE POSTERIOR ABDOMINAL SEGMENTS

Some very noticeable changes take place, from hatching to maturity, in the parts making up the tip of the abdomen. These are shown in figures 4, 5, and 6. In both males and females the cerci are very

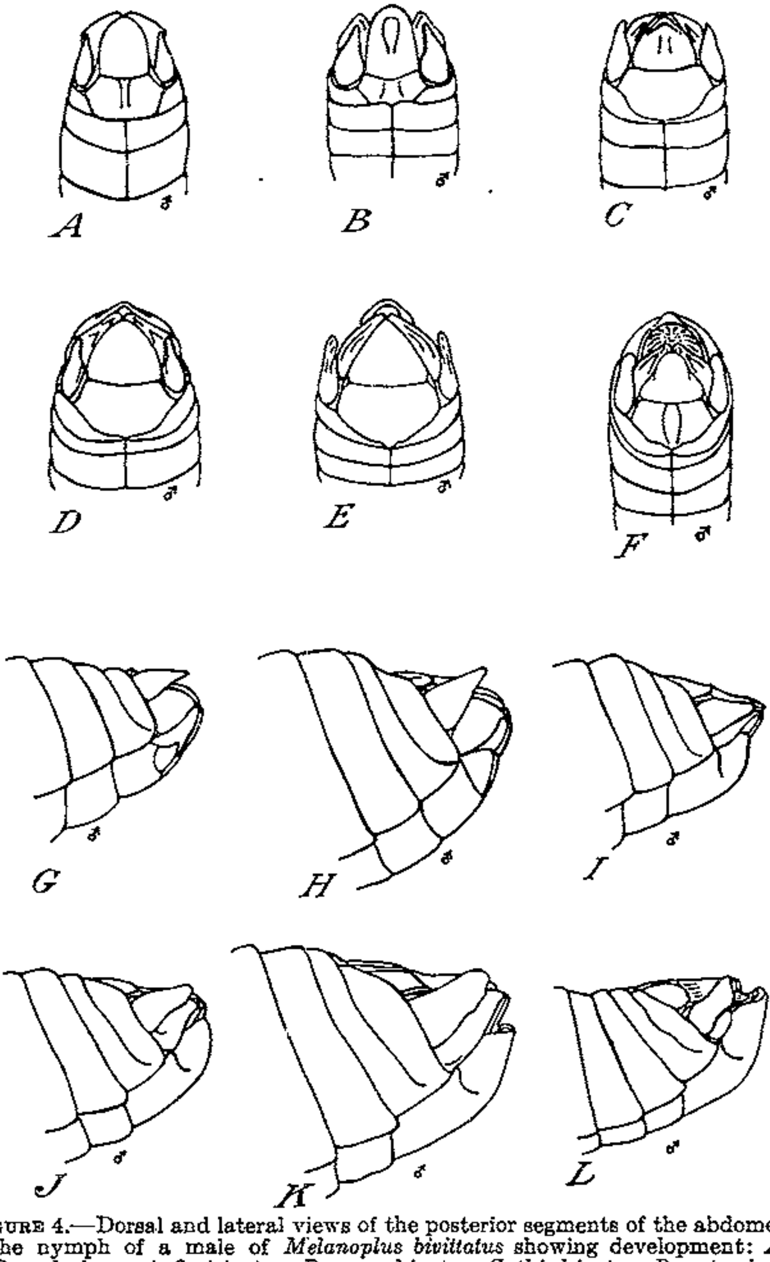



FIGURE 4.—Dorsal and lateral views of the posterior segments of the abdomen of the nymph of a male of *Melanoplus bivittatus* showing development: *A–F*, Dorsal views; *A*, first instar; *B*, second instar; *C*, third instar; *D*, extra instar; *E*, fourth instar; *F*, fifth instar. *G–L*, Lateral views; *G*, first instar; *H*, second instar; *I*, third instar; *J*, extra instar; *K*, fourth instar; *L*, fifth instar.

prominent spinelike structures in the first instar. During the development of the female these become less and less prominent until in the

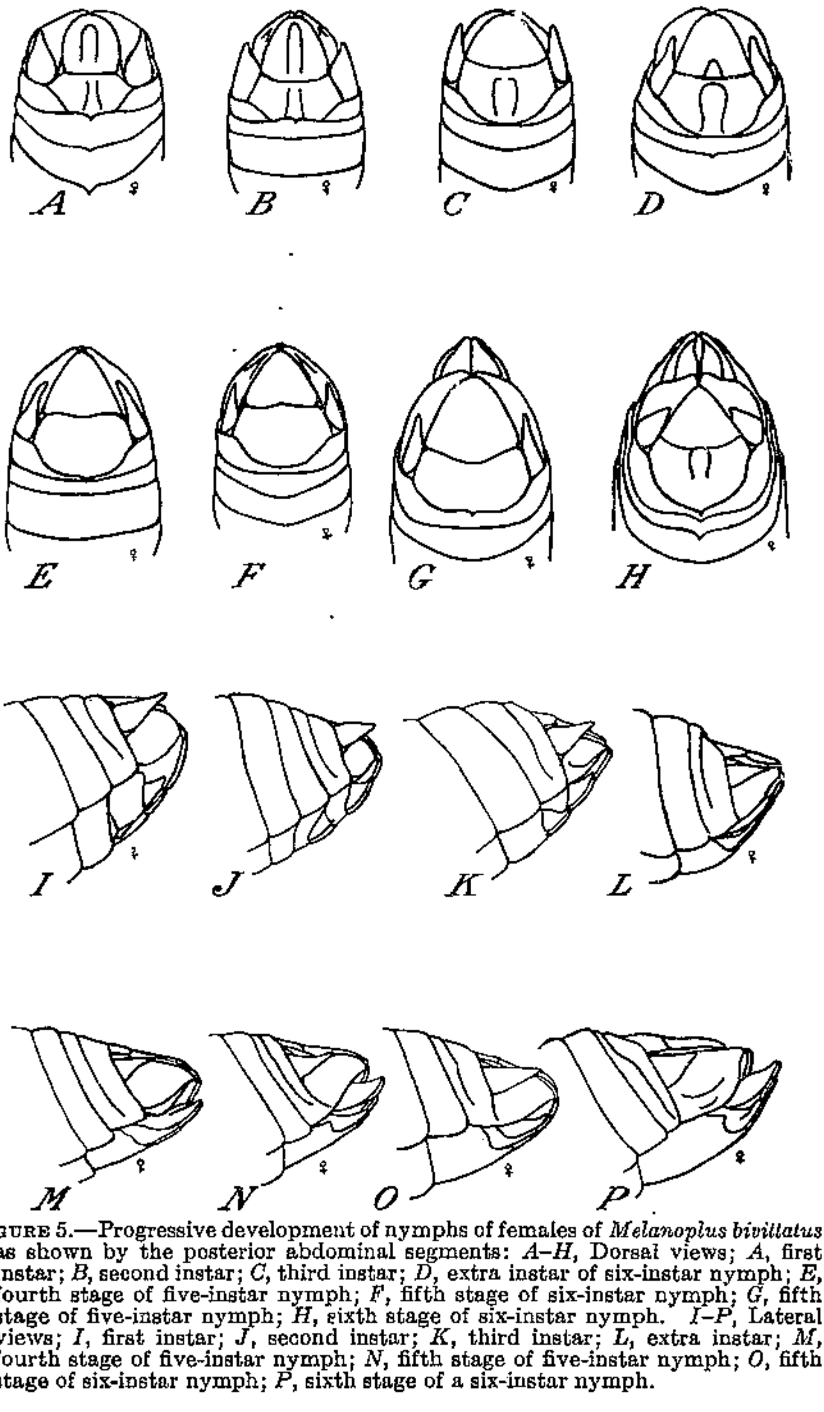



FIGURE 5.—Progressive development of nymphs of females of *Melanoplus bivittatus* as shown by the posterior abdominal segments: *A–H*, Dorsal views; *A*, first instar; *B*, second instar; *C*, third instar; *D*, extra instar of six-instar nymph; *E*, fourth stage of five-instar nymph; *F*, fifth stage of six-instar nymph; *G*, fifth stage of five-instar nymph; *H*, sixth stage of six-instar nymph. *I–P*, Lateral views; *I*, first instar; *J*, second instar; *K*, third instar; *L*, extra instar; *M*, fourth stage of five-instar nymph; *N*, fifth stage of five-instar nymph; *O*, fifth stage of six-instar nymph; *P*, sixth stage of a six-instar nymph.

adult stage they are inconspicuous (fig. 5; fig. 6, *A. C*). The prominence of the cerci is not so much reduced in the male as in the female (fig. 4; fig. 6, *B. D*). Instead, the male cerci change from spinelike to more or less flattened structures used in clasping the female during coition. The male cerci possess specific characters upon which are based much of the taxonomy of the genus *Melanoplus*.

Of the paraprocts and the epiproct not much is to be said regarding definite changes during development. From being very prominent in the first instar they become somewhat dwarfed by the increase in size of the subgenital plate (fig. 4) or the valves of the ovipostor (fig. 5) as the nymphs develop to adults (fig. 6).

There is a marked development in the subgenital plate (fig. 4). During the first instar it is much submerged beneath the epiproct and paraprocts and is deeply notched. This notch gives it the appearance of being two triangular appendages issuing posteriorly from the last ventral abdominal segment. These appendages are easily confused with the dorsal valves of the ovipositor of the female and impede the determination of sex in the first instar. However, the females can be distinguished by the fact that the ventral valves of the ovipositor issue as budlike structures from the end of the eighth abdominal segment and at the base of the dorsal valves (fig. 5). The subgenital plate becomes relatively larger and more prominent throughout development, losing much or all of its notched character. It gradually extends until it exceeds the apex of the epiproct and paraprocts and assumes the specific characters which are used for taxonomic classifications (figs. 4 and 6).

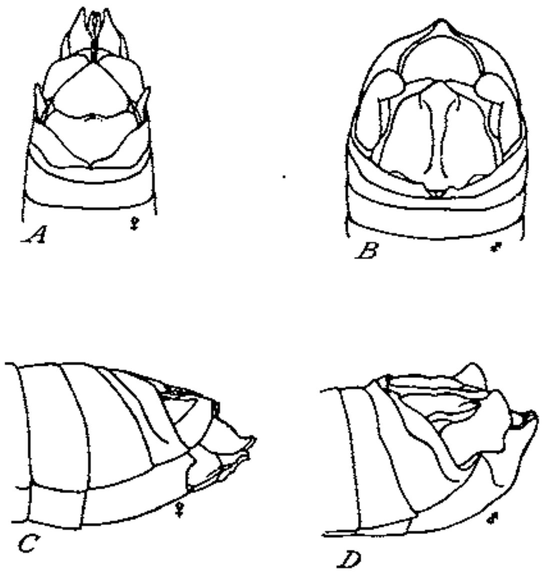



FIGURE 6.—Posterior abdominal segments of adults of *Melanoplus bivittatus*: *A*, dorsal view, female; *B*, dorsal view, male; *C*, lateral view, female; *D*, lateral view, male.

The valves of the ovipositor are submerged beneath the epiproct and paraprocts in the first instar. They, too, gradually elongate and become more prominent in each instar until they finally exceed the apices of these other structures. The ventral valves are curved dorsad and remain shorter than the dorsal valves until the adult stage. In the adult stage they become equal to the dorsal valves in length and curve ventrad, forming, together with the two upward-curving dorsal valves, four horny, sharp-pointed, toothed appendages which are used to work the abdomen into the ground during oviposition (figs. 5 and 6).

## Key to the Instars

A generalized key is given here for the identification of the instars based on what are probably the most apparent external structural changes that take place, namely, changes in the mesothoracic and metathoracic segments bearing the tegmina and wing pads (figs. 2 and 3).

1. Tegmina and wings in the form of pads .......... 2
   Tegmina and wings fully developed .......... 7
2. Tegmina and wing pads pointing ventrad .......... 3
   Tegmina and wing pads pointing dorsad .......... 6
3. Tegmina and wing pads with indistinct venation .......... 4
   Tegmina and wing pads with distinct venation .......... 5
4. Wing pads rounded, with no visible bulge at the apex .......... First instar
   Wing pads rounded, with a visible bulge at the apex .......... Second instar
5. Wing pads more sharply triangular and pointed ventrad more vertically .......... Third instar
   Wing pads more elongated, rounded and pointed ventrad more obliquely .......... Extra instar
6. Wing pads short, not extending beyond the first abdominal segment, and more truncate .......... Fourth instar
   Wing pads elongate, extending beyond the second but hardly beyond the third abdominal segment, more pointed at the apex .......... Fifth instar
7. Tegmina and wings fully developed, the tegmina overlying the folded wings .......... Adult

Further characters that may be used in determining the various instars are given in table 11.

TABLE 11.—*Nymphal development of grasshoppers*

| Instar | Wings | Cerci | Posterior segments of the abdomen | | | | |
|---|---|---|---|---|---|---|---|
| | | | Supra-anal plates | Podical plates | Subgenital plates | Valves of the ovipositor | |
| | | | | | | Dorsal | Ventral |
| 1 | Wing pads with apex bluntly rounded, pointed ventrad, without distinct venation. | Long, slender, spinelike, very prominent. | Bluntly rounded at apex, forming tip of abdomen. | Prominent, forming tip of abdomen; equal to supra-anal plate. | Deeply notched, appearing much like dorsal valve of ovipositor. | Extending half way to apex of supra-anal plate. | Buds issuing from eighth abdominal segment. |
| 2 | Wing pads with apex rounded but bulged, pointed ventrad, without distinct venation. | Not extending to tip of abdomen. | Increasingly triangular and less rounded at apex. | do | Becoming less notched | Some change | Not extending to tenth abdominal segment. |
| 3 | Wing pads with apex sharply triangular, pointed ventrad with distinct venation. | Spinelike in female, more flattened in male. | do | Little change | do | Extending to apex of supra-anal plate. | Extending to tenth abdominal segment. |
| Extra | Wing pads more elongate, pointed more obliquely caudad. | do | Little change | do | Extending to or beyond apex of supra-anal plate. | Some change | Extending beyond tenth abdominal segment. |
| 4 | Wing pads pointed dorsad, truncate, not reaching beyond first abdominal segment. | Rudimentary in female; more flattened, curving inward, in male. | Not forming tip of abdomen, more triangular and characteristic of species. | Change in relative size, smaller. | do | Extending slightly beyond apex of supra-anal and podical plates. | Do. |
| 5 | Wing pads elongate, extending beyond second abdominal segment. | do | do | Some change | Very prominent | Very prominent | Still shorter than dorsal valves, prominent. |
| Adult | Tegmina and wings fully developed. | Very rudimentary spines in female, characteristic of species in male. | Characteristic of species. | Not so prominent in male as in female. | Characteristic of species. | Fully developed | Curved down at tip for first time, equal in length to dorsal valves. |

## RELATION OF TEMPERATURE TO DEVELOPMENT AND ACTIVITY

Temperature is one of the most important factors affecting the life history and development of grasshoppers. The relation of temperature to incubation and hatching of eggs, development of nymphs, and activities of nymphs and adults was therefore studied, both in the laboratory under controlled conditions and in the field. The laboratory work was done at Billings and Bozeman, Mont., whereas field observations were made in Montana, North Dakota, and South Dakota. Since most of the rearing work was done in temperature cabinets under controlled conditions, differences in the location of the two laboratories should make no difference in the results. Any differences encountered in the field studies at various places are already accounted for in the recorded conditions under which the observations were made.

### Correlation Between Temperature and Grasshopper Development

For the study of the relation of temperature to the incubation and hatching of the eggs, and to the development of the nymphs, a large number of grasshopper eggs were incubated and nymphs reared at constant temperatures from 65° to 105° F. The number of days required for the incubation of the egg before hatching and for nymphal development to the adult stage was recorded for each individual. From the number of days required for development the percentage rate of development per day was calculated. A scatter of different individual rates of development was thus obtained within each temperature class. Since the total number of specimens used varied for each temperature class it was necessary to show the scatter in individual rates of development as percentages of the total number of specimens reared at each temperature. With this data it was possible to set up a linear correlation table with the percentage rate of development per day along the $Y$ axis and the temperature in degrees Fahrenheit on the $X$ axis. Table 12 is an example of how this was done with data from the rearing of nymphs of *Melanoplus bivittatus* at controlled temperatures. The same method was applied to the data obtained from the incubation of eggs.

The linear correlation between rate of development and temperature was then obtained from the formula $r=\frac{\Sigma(xy)-c_{xy}}{n\ \sigma_x\ \sigma_y}$. The linear regression of $X$ on $Y$ was calculated from the formula $b_{xy}=\frac{\Sigma(xy)}{\Sigma(y^2)}$. From the coefficient of regression thus obtained it was possible to determine the number of degrees required to change the rate of development 1 percent of total development per day, assuming, of course, a straight-line relation between time of development and temperature. The existence of a near relationship of this sort has been observed within a range of temperature of from 68° to 104° F.

The minimum effective temperature below which, theoretically, no development takes place is obtained from the formula $M_x-\bar{M}_yX$, where $M_x$ is the mean temperature, $M_y$ the true mean of rate of development expressed in units of percentage of total development per day, and $X$ is the number of degrees necessary to bring about a 1 percent change in rate of development. In the above example

$M_x=86°$, $M_y=3.2572$ percent, and $X=10.2375°$ F., the coefficient of correlation being $0.8730 \pm 0.0071$. In other words, the rate of development per day at 86° is 3.2572 percent of the total development. If it takes 10.2375° to bring about a 1 percent change in rate of development, then zero development would occur at $86° - (3.2572 \times 10.2375°)$, or 52.66°, which is the minimum effective temperature below which no nymphal development of *Melanoplus bivittatus* occurs.

TABLE 12.—*Linear correlation between rate of development of nymphs of Melanoplus bivittatus and temperature*

| Percentage rate of development per day | Temperature | | | | | Total |
|---|---|---|---|---|---|---|
| | 68° F. | 77° F. | 86° F. | 95° F. | 104° F. | |
| | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* |
| 5.4 | | | | | 8 | 8 |
| 5.2 | | | | | | |
| 5.0 | | | | | | |
| 4.8 | | | | 4 | 23 | 27 |
| 4.6 | | | | 11 | 15 | 26 |
| 4.4 | | | 16 | 23 | | 39 |
| 4.2 | | | 16 | 8 | 8 | 32 |
| 4.0 | | | 26 | 15 | | 41 |
| 3.8 | | | 10 | 27 | 23 | 60 |
| 3.6 | | | 10 | 4 | 15 | 20 |
| 3.4 | | | 6 | | 8 | 14 |
| 3.2 | | | 16 | 4 | | 20 |
| 3.0 | | | | 4 | | 4 |
| 2.8 | | | | | | |
| 2.6 | | 17 | | | | 17 |
| 2.4 | | 54 | | | | 54 |
| 2.2 | | 12 | | | | 12 |
| 2.0 | 36 | 17 | | | | 53 |
| 1.8 | 36 | | | | | 36 |
| 1.6 | | | | | | |
| 1.4 | 28 | | | | | 28 |
| Frequency | 100 | 100 | 100 | 100 | 100 | 500 |

Too much value should not be placed on the different minimum effective temperatures given in tables 14 and 18, for there was considerable variation in different experiments in which the same species was used. The tables do indicate, however, an approximate temperature at which embryonic or nymphal development begins.

Development is measured in units required to complete development and is expressed in terms of percentage of total development caused by a temperature 1 Fahrenheit degree above the minimum effective temperature, acting through 1 day of time. The formula for determining this number is $(T-M)\,D$, where $T$ is the temperature of incubation or rearing, $M$ the minimum effective temperature, and $D$ the number of days necessary for development at that temperature.

## EFFECT OF TEMPERATURE ON HATCHING OF EGGS

Under normal conditions the most important physical factor affecting the rate of embryonic development in the spring is temperature. There is, however, some variation in their reactions to temperature among eggs from different egg pods of the same species. Grasshopper eggs deposited in the summer and fall do not hatch in the spring at intervals equal to those elapsing between the dates on which they were deposited, although wide differences in time of oviposition may cause differences in the time of hatching. In the fall embryonic development often reaches an advanced state in which the eyes, antennae, legs, and body segments are distinct. Often this advanced state is reached early in the fall and is followed by a long period of temperatures sufficient to cause hatching. Generally, however, no hatching occurs until the following spring, although eggs of *Melanoplus mexicanus* collected in Montana in the fall have been known to hatch within 3 days after collection when maintained at a constant temperature of 85° F. Farther south almost a complete second generation of *M. mexicanus* has hatched in the field, reached maturity, and laid eggs late in the summer and in the fall.

The main interest, from a practical economic standpoint, lies in the influence of temperature on embryonic development in the spring. To obtain information on this subject, eggs were gathered in the field during the fall and kept under outdoor conditions until ready for use. In one experiment pods were broken open and equal numbers of eggs from a single pod were incubated at different constant temperatures. The eggs used were therefore deposited at the same time and had the same degree of embryonic development. In another experiment, time-temperature curves were based on lots of 100 eggs each, taken at random and incubated at constant temperatures. In this case the percentages hatching under each temperature were also obtained for the different species. The results are shown in tables 13, 14, and 15, and the figures represent the rate of development that normally would occur in the spring.

TABLE 13.—*Average number of days required for the incubation of overwintered, field-collected grasshopper eggs when subjected to the constant temperatures shown*

RECORDED AT BILLINGS, MONT.

| Species | Sample | Average incubation period at— | | | |
|---|---|---|---|---|---|
| | | 75° F. | 85° F. | 95° F. | 105° F. |
| | | *Days* | *Days* | *Days* | *Days* |
| *Melanoplus bivittatus* | Single pod | 23.8 | 12.9 | 10.6 | 8.1 |
| *Dissosteira carolina* | do | 52.8 | 26.0 | 18.6 | 14.1 |

RECORDED AT BOZEMAN, MONT.

| Species | Sample | Average incubation period at— | | | | |
|---|---|---|---|---|---|---|
| | | 68° F. | 77° F. | 86° F. | 95° F. | 104° F. |
| | | *Days* | *Days* | *Days* | *Days* | *Days* |
| *Melanoplus bivittatus* | Single pod | 16.0 | 6.8 | 5.2 | 5.1 | 4.0 |
| Do. | 100 eggs | 13.1 | 8.6 | 7.7 | 4.5 | 4.4 |
| *M. differentialis* | Single pod | 36.7 | 20.7 | 10.7 | 11.0 | 10.2 |
| Do | 100 eggs | 37.1 | 22.5 | 18.1 | 11.2 | 10.9 |
| *Camnula pellucida* | Single pod | 33.9 | 13.5 | 7.2 | 7.9 | 6.4 |
| Do. | 100 eggs | 25.0 | 15.3 | 8.2 | 7.3 | 7.2 |
| *Dissosteira carolina* | Single pod | 46.9 | 22.0 | 12.2 | 10.9 | 10.0 |
| Do | 100 eggs | 40.5 | 27.3 | 12.7 | 11.9 | 12.0 |
| *Melanoplus mexicanus* | Single pod | 31.9 | 17.1 | 13.2 | 10.2 | 8.7 |
| *M. femur-rubrum* | do | 39.1 | 24.1 | 13.0 | 11.7 | 13.3 |
| *M. packardii* | do | 29.0 | 12.8 | 8.1 | 7.7 | 6.2 |

TABLE 14.—*Development in the spring of eggs of some economic grasshoppers: Correlation between rate and temperature, minimum effective temperature at which egg development begins, and number of developmental units required for completion*

| | Correlation coefficient | Minimum effective temperature | Developmental units [1] |
|---|---|---|---|
| | | *° F.* | |
| *Melanoplus bivittatus* | 0.8915±0.0069 | 62.2 | 322 |
| Do | .8054± .0060 | 59.4 | 153 |
| Do | .8627± .0067 | 59.2 | 167 |
| *M. differentialis* | .8367± .0090 | 63.5 | 280 |
| Do | .9210± .0046 | 59.0 | 425 |
| *M. mexicanus* | .8974± .0050 | 59.4 | 337 |
| *M. femur-rubrum* (from Tennessee) | .8672± .0075 | 62.2 | 365 |
| *M. packardii* | .8408± .0088 | 63.9 | 191 |
| *Camnula pellucida* | .9088± .0052 | 61.3 | 230 |
| Do | .9326± .0039 | 59.4 | 257 |
| *Dissosteira carolina* | .9563± .0046 | 65.1 | 540 |
| Do | .9127± .0050 | 62.4 | 328 |
| Do | .8438± .0057 | 61.5 | 380 |

[1] Developmental units are expressed in 1° F. 1-day units.

TABLE 15.—*Percentage of hatch at various constant temperatures based on the incubation at each temperature of 100 eggs selected at random*

| | Percentage of hatch at temperatures of— | | | | |
|---|---|---|---|---|---|
| | 68° F. | 77° F. | 86° F. | 95° F. | 104° F. |
| | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* |
| *Melanoplus bivittatus* | 28.0 | 34.0 | 11.0 | 25.5 | 22.2 |
| *M. differentialis* | 51.0 | 77.0 | 84.0 | 81.0 | 72.0 |
| *Camnula pellucida* | 95.0 | 89.0 | 70.0 | 68.0 | 70.0 |
| *Dissosteira carolina* | 70.0 | 94.3 | 74.4 | 63.0 | 79.5 |

In figures 7 and 8 the percentage of total development per day is plotted against temperature. The results agree with field observations.

In the outbreaks of 1931 and 1932 in South Dakota where *Melanoplus bivittatus* and *M. differentialis* were the two dominant species and about equal in numbers the former hatched from 2 to 3 weeks earlier than the latter. More recent field observations have supported these findings. By incubating the eggs of these two species under the same controlled temperatures it was found that the incubation period of *M. bivittatus* was shorter than that of *M. differentialis*. In other words, the slower rate of spring development of the eggs of *M. differentialis* is evidently the reason for its later appearance in the field. Two other species, *Dissosteira carolina* and *M. femur-rubrum*, also have a slower rate of spring embryonic development and they, too, appear later in the season than *M. bivittatus*. Correlation coefficients between length of spring development and temperature (table 14) are high for all species.

As shown in table 14 the minimum effective incubation temperature for most of the species is about 60° F. Several observations in the field have shown hatching to be suspended when soil temperatures descend to this point. Such a suspension was recorded for *Melanoplus mexicanus* in 1926.[10] A record was obtained in a laboratory experiment during January 1930 for eggs of *Dissosteira carolina* that had

[10] See footnote 6, p. 2.

been placed in the sand alongside the thermal unit of a soil thermograph. The temperature of the sand ranged from 35° to 85° F. during the period of the experiment. On January 12, newly hatched nymphs were observed at 10 a. m. The nymphs had reached the surface of the soil and 13 of them had cast their first skin. Three were on top of the ground, still in the vermiform stage, and inactive. The soil temperature at that time was 61° and according to the soil thermograph chart had steadily dropped from 74° since 4 p. m. the day

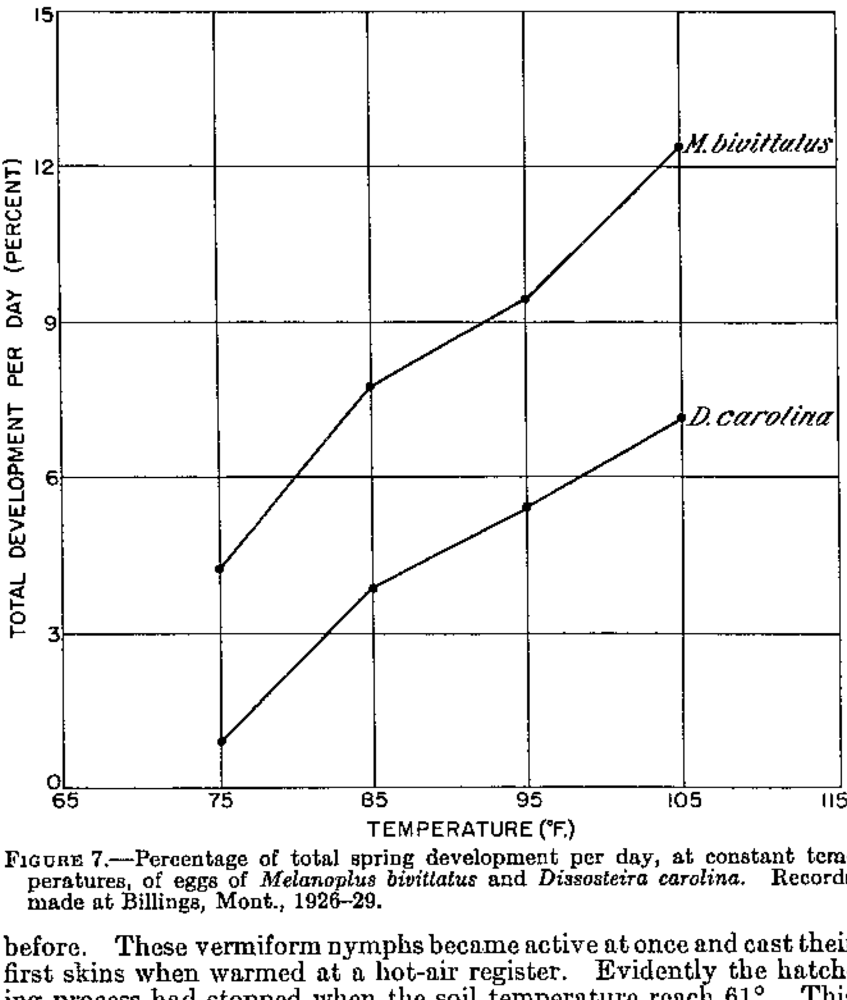



FIGURE 7.—Percentage of total spring development per day, at constant temperatures, of eggs of *Melanoplus bivittatus* and *Dissosteira carolina*. Records made at Billings, Mont., 1926–29.

before. These vermiform nymphs became active at once and cast their first skins when warmed at a hot-air register. Evidently the hatching process had stopped when the soil temperature reach 61°. This agrees with the other observation, and it appears safe to say that 60° F. is approximately the point below which no hatching takes place.

The percentages of hatch at various constant temperatures are given in table 15. It would seem that eggs of *Melanoplus bivittatus* were much less hardy than those of any of the others. A greater proportion of *Camnula pellucida* hatched at 68° F. than at any other temperature.

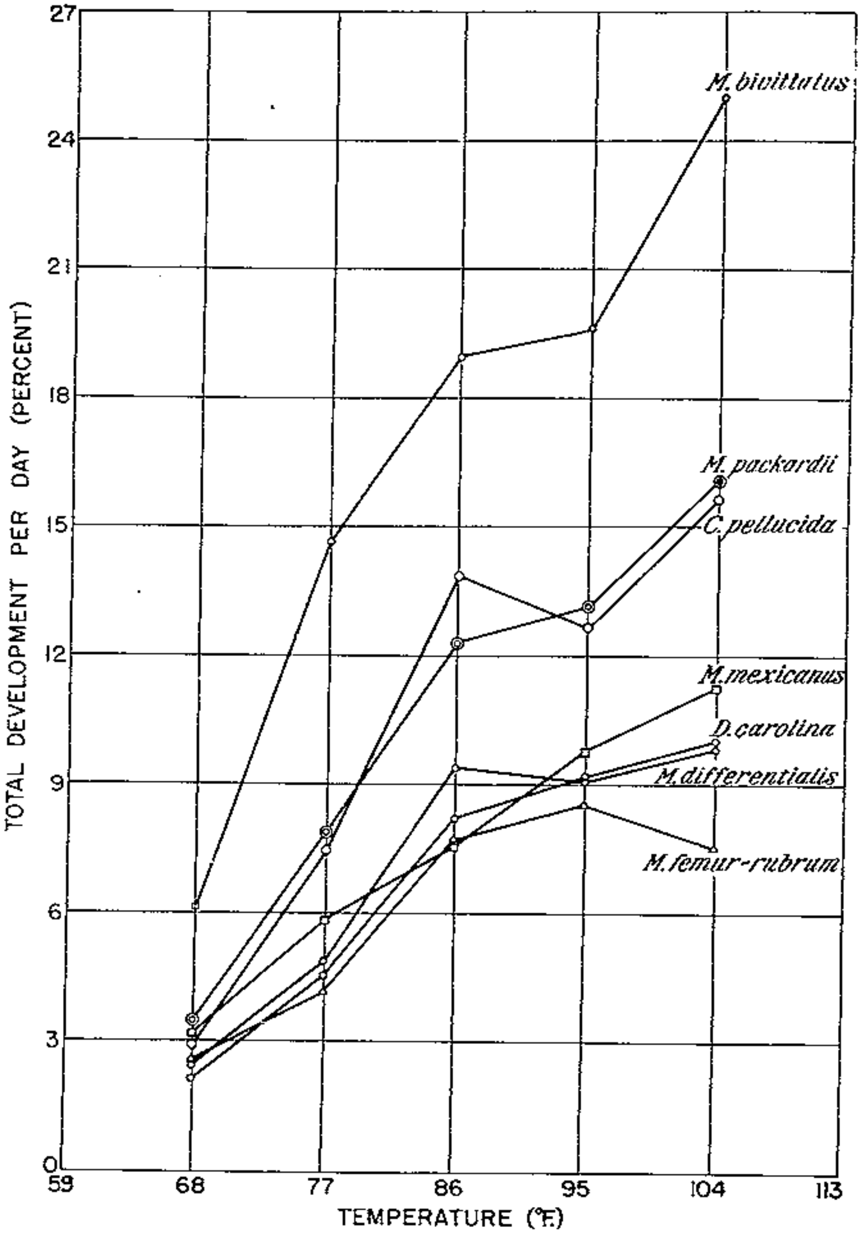



FIGURE 8.—Percentage of total spring development per day, at constant temperatures, of eggs of *Melanoplus bivittatus*, *M. differentialis*, *Camnula pellucida*, *Dissosteira carolina*, *M. mexicanus*, *M. femur-rubrum*, and *M. packardii*. Records made at Bozeman, Mont., 1931–34.

## Effect of Temperature on Nymphal Development

In 1930 Parker [11] published time-temperature curves of the nymphal development of *Camnula pellucida*, *Melanoplus mexicanus*, *M. packardii*, and *M. femur-rubrum* based on the rearing of these at constant temperatures of 71.6°, 80.6°, 89.6°, and 98.6° F. The present work considers these and five additional species—*M. bivittatus*, *M. differentialis*, *M. dawsoni*, *Phoetaliotes nebrascensis*, and *Dissosteira carolina*. The method used is practically the same as Parker's except that the regression line showing the relationship between temperature and rate of development was determined statistically as described on page 25.

The average numbers of days required to complete nymphal development at various constant temperatures are given for each species in table 16 and the percentages of total development per day of the western species are plotted against temperature in figures 9 and 10.

Table 16.—*Average number of days required by various grasshoppers to complete nymphal development at constant temperatures*

RECORDED AT BILLINGS, MONT.

| Species | Period of nymphal development at temperatures of— | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 70° F. | 75° F. | 80° F. | 85° F. | 90° F. | 95° F. | 100° F. | 105° F. |
| | *Days* | *Days* | *Days* | *Days* | *Days* | *Days* | *Days* | *Days* |
| *Melanoplus bivittatus* | 51.2 | 45.7 | 32.7 | 29.0 | 22.7 | 20.5 | 22.7 | 20.3 |
| *M. differentialis* | 55.1 | 52.1 | 40.1 | 33.7 | 26.0 | 24.8 | 26.5 | |
| *M. femur-rubrum* | | 45.3 | | 27.9 | | 19.5 | | 20.3 |
| *M. packardii* | 70.0 | | 36.6 | | 24.7 | | 24.6 | |
| *Phoetaliotes nebrascensis* | | | | 31.7 | | 22.5 | | 19.6 |
| *Dissosteira carolina* | 70.0 | | 39.3 | 41.9 | 22.4 | 22.1 | 20.2 | 21.2 |

RECORDED AT BOZEMAN, MONT.

| Species | Period of nymphal development at temperatures of— | | | | |
|---|---|---|---|---|---|
| | 68° F. | 77° F. | 86° F. | 95° F. | 104° F. |
| | *Days* | *Days* | *Days* | *Days* | *Days* |
| *Melanoplus bivittatus* (from Montana) | 61.3 | 39.2 | 25.0 | 22.1 | 23.0 |
| *M. bivittatus* (from Minnesota) | 59.6 | 47.1 | 26.1 | 25.0 | 24.1 |
| *M. differentialis* | 71.1 | 50.6 | 29.1 | 27.7 | 25.3 |
| *M. femur-rubrum* (from Tennessee) | 78.7 | 72.6 | 33.1 | 27.2 | 21.6 |
| *M. packardii* | 67.8 | 47.2 | 25.7 | 24.1 | 27.5 |
| *M. dawsoni* | 66.0 | 40.5 | 21.7 | 20.8 | 21.5 |
| *M. mexicanus* | | 33.4 | 24.7 | 19.9 | 17.7 |
| *Dissosteira carolina* | 74.3 | 52.3 | 25.8 | 22.0 | 23.3 |
| *Camnula pellucida* (from Minnesota) | | 37.7 | 21.7 | 18.6 | 17.4 |

The curves for *Melanoplus differentialis* and *M. bivittatus* are emphasized because of their close connection with, and importance in, some of the recent outbreaks in the northern Great Plains and because these are the two outstanding species of grasshoppers of the solitary type. Not only the eggs but also the nymphs of *M. bivittatus* make more rapid development at all temperatures than do those of *M.*

[11] See footnote 5, p. 2.

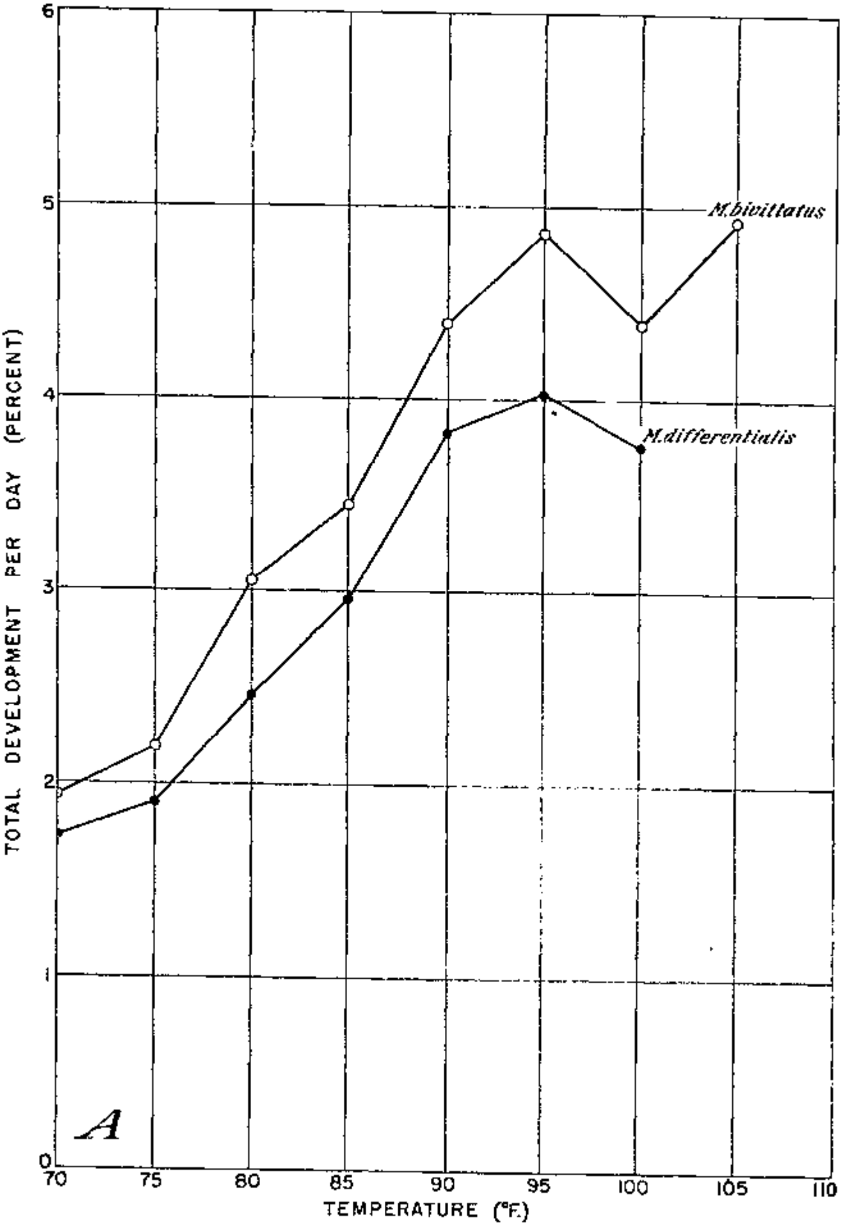



FIGURE 9.—*A*, Percentage of total nymphal development per day, at constant temperatures, of *Melanoplus bivittatus* and *M. differentialis*.

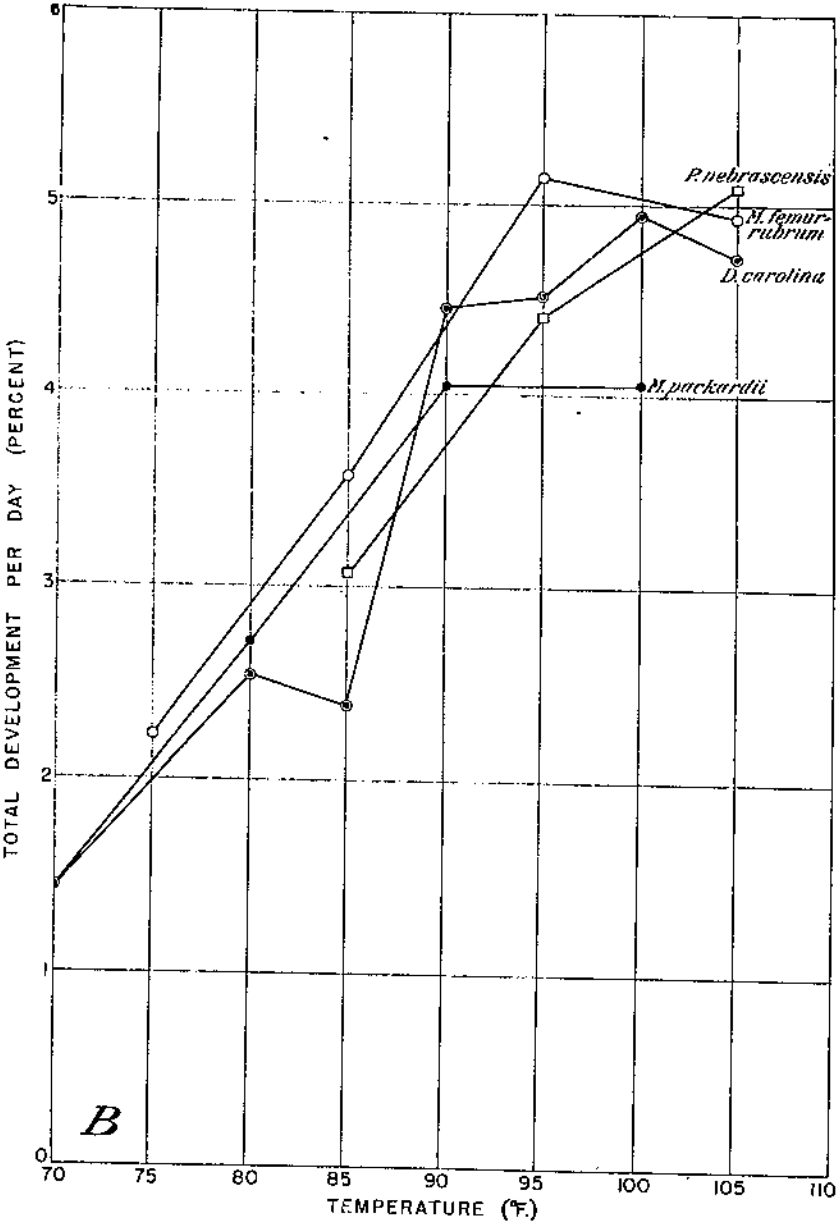



FIGURE 9.—*B*, Percentage of total nymphal development per day, at constant temperatures, of *M. femur-rubrum*, *Dissosteira carolina*, *M. packardii*, and *Phoetaliotes nebrascensis*. Records made at Billings, Mont., 1925–30.

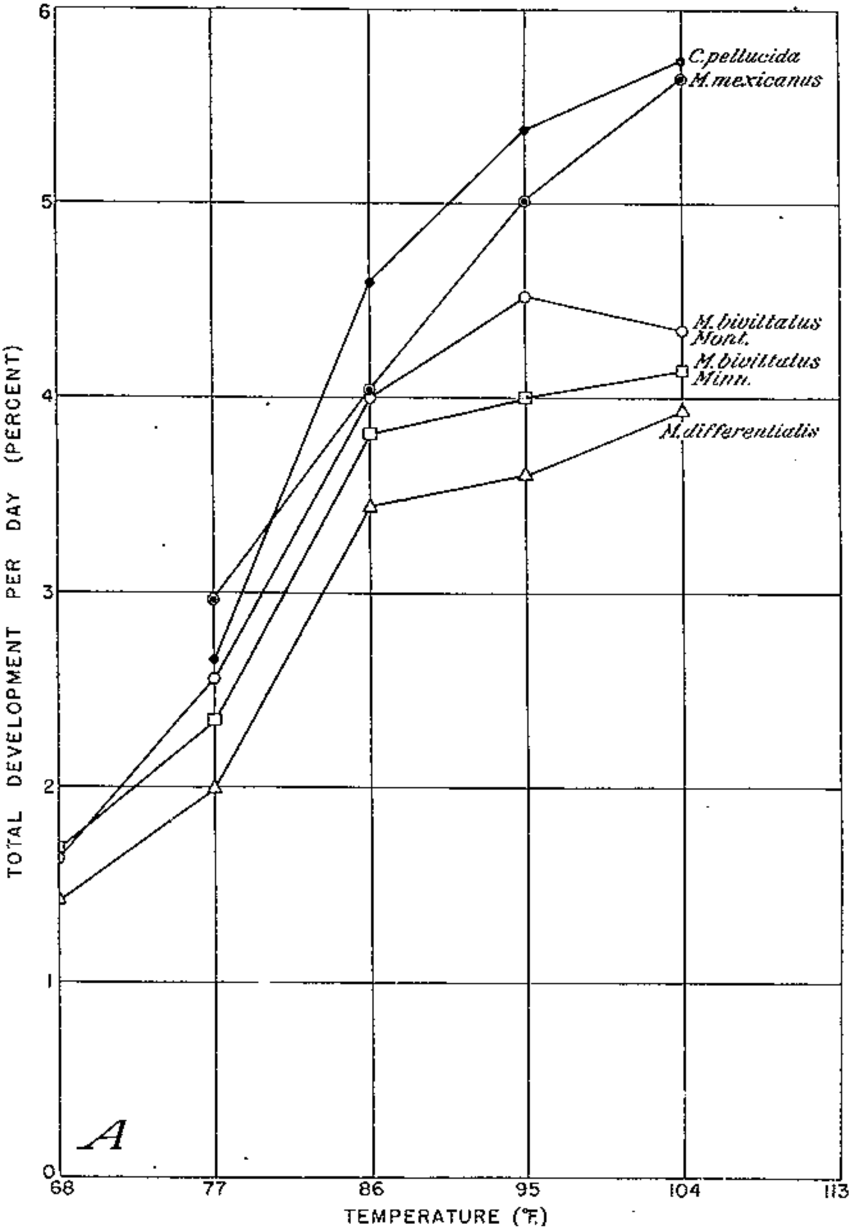



FIGURE 10.—*A*, Percentage of total nymphal development per day, at constant temperatures, of *Melanoplus mexicanus*, *Camnula pellucida*, *M. bivittatus* (from Montana and Minnesota), and *M. differentialis*.

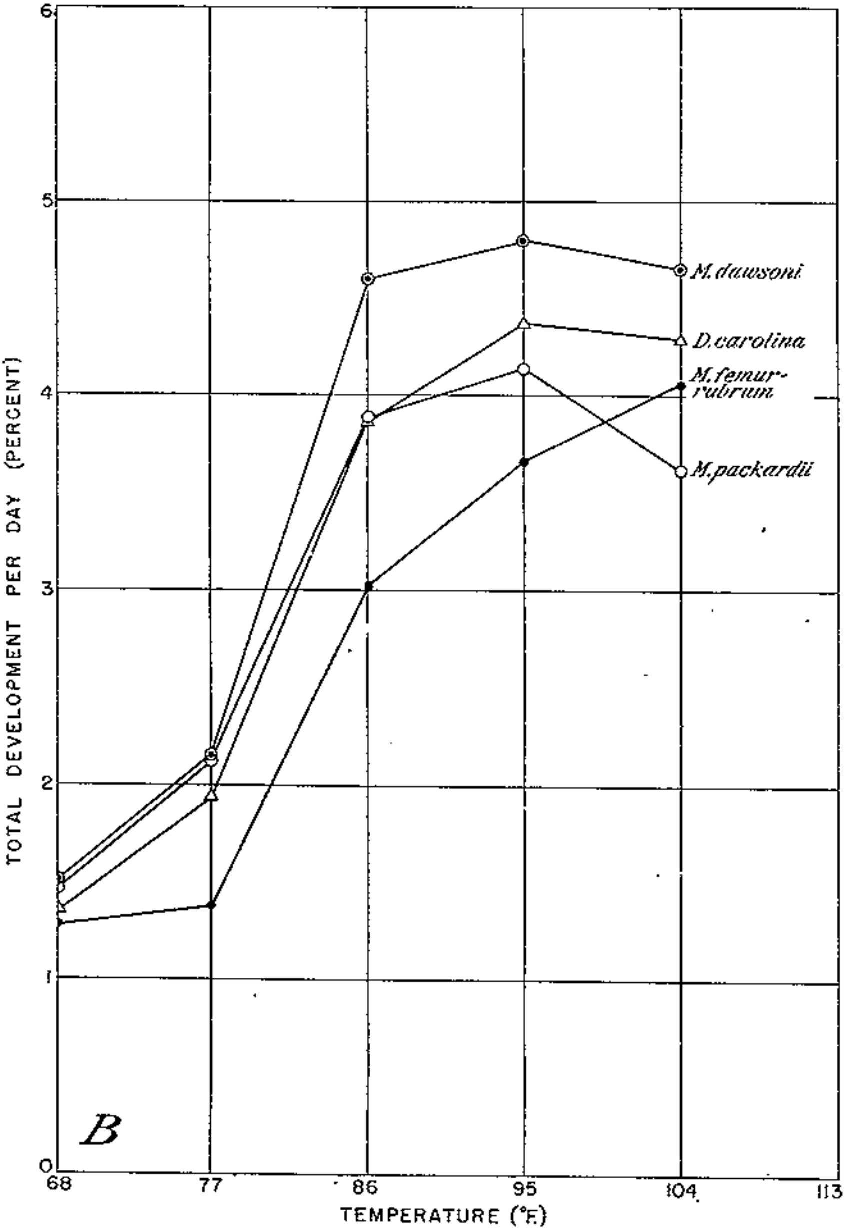



FIGURE 10.—*B*, Percentage of total nymphal development per day, at constant temperatures, of *M. dawsoni*, *Dissosteira carolina*, *M. femur-rubrum*, and *M. packardii*. Records made at Bozeman, Mont., 1931–34.

*differentialis*, as shown in figures 9, *A*, and 10, *A*. The combination of an earlier hatch and a more rapid nymphal development enables *M. bivittatus* to develop into outbreak numbers in latitudes much farther north than those at which *M. differentialis* can do as much damage.

*Melanoplus differentialis* is not well established north of parallel 47°, which is close to Washburn, N. Dak., whereas *M. bivittatus* occurs in outbreak numbers north into Canada. For years *M. differentialis* has been fairly well established around Mandan, N. Dak., but not in outbreak numbers. Under the exceptional conditions of long, hot summers of 1932, 1933, and 1934 this species increased greatly and extended its limits northward and westward more than 100 miles, but it did not become well established in these additional areas. In these years it was collected as far north as Williams County, N. Dak., and Sheridan County, Mont. In 1933, north of Washburn, *M. mexicanus*, *Cammula pellucida*, and *M. bivittatus* were in the adult stage and were mating and ovipositing in the last week of July, while among them *M. differentialis* was numerous but still in the last, or sixth, nymphal stadium.

The year before, owing to favorable conditions, adults of *Melanoplus differentialis* migrated north into this area and laid a large number of eggs which hatched in the spring of 1933. Nothing came of this infestation. It could not establish itself permanently because lateness in hatching and slower nymphal development require a longer growing season than that prevailing in this part of the country. Southward from Bismarck, N. Dak., into central and southern South Dakota *M. differentialis* becomes increasingly abundant and important. Here the mean annual temperature is from 5° to 6° F. higher than at Bismarck. In 1932 and 1933 there were great flights of this species in all directions, for they were particularly numerous in the New England, Mott, and Mandan areas of North Dakota. Owing to the extreme and early drought of 1934 there was a marked reduction in the numbers of both this species and *M. bivittatus* throughout the northern Great Plains area.

Referring again to figure 10, *A*, *Melanoplus mexicanus* makes a rapid nymphal development, showing an adaptation to a short growing season. *Camnula pellucida* develops faster than any of the others and this may explain why it is found abundant in, and is limited to, higher elevations or more northern latitudes. *M. dawsoni* is fairly abundant in Montana, North Dakota, and northeastern Wyoming, but not so common in South Dakota except in mountainous areas where the growing season is short. Its nymphal development is more rapid than that of *M. bivittatus*. *Dissosteira carolina* is a heat-loving grasshopper and its whole life history is carried out at higher temperatures than any of the others. It prefers the hot, dusty road when most of the other species have collected in the cool shade of weeds and grasses.

A number of *Melanoplus femur-rubrum* eggs were obtained from Tennessee, and specimens hatched from these were reared in Montana at constant temperatures. The *M. femur-rubrum* curve in figure 10, *B*, is that of the Tennessee specimens. In figure 11 this rearing is compared with the results obtained by Parker and the writer working with *M. femur-rubrum* from Montana. The Tennessee specimens were slower in their rate of nymphal development than those from Montana. It has already been pointed out that most of the Tennessee specimens exhibited six instars whereas those from Montana had but five.

It was also found that nymphs of *Melanoplus bivittatus* from eggs collected in Bridger Canyon near Bozeman, Mont., developed faster

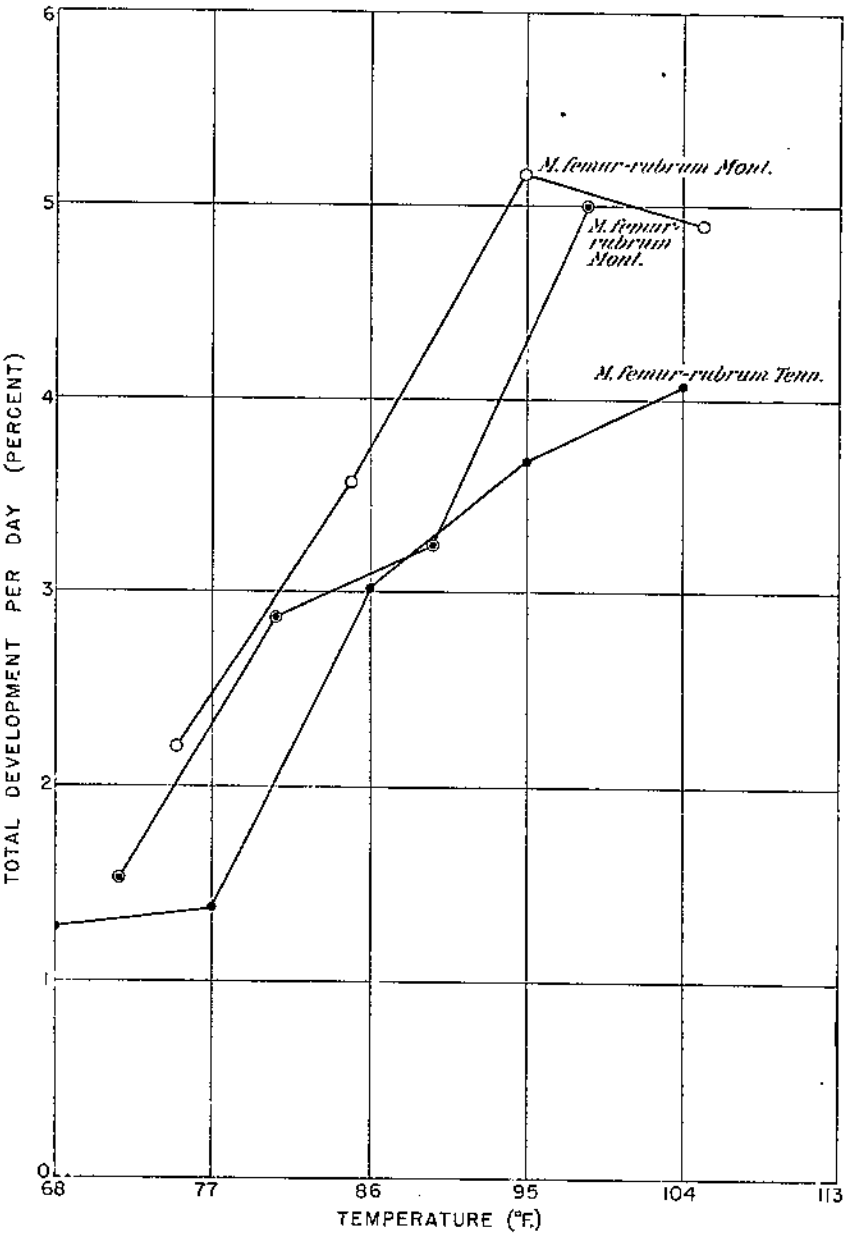



FIGURE 11.—Daily percentage of the total nymphal development, at constant temperatures, of *Melanoplus femur-rubrum* from Montana and from Tennessee. Records made at Bozeman, Mont.

than those from eggs gathered at Crookston, Minn. (fig. 10). The difference in rate of development between these is probably due to adaptations to the length of the growing season and the temperatures prevailing in the respective localities. A slower rate of nymphal development is manifested by species or specimens from places having a longer growing season and a faster rate by those from places having a shorter growing season. The difference between the rate of development of the Bridger Canyon and Crookston individuals of *M. bivittatus* may perhaps be explained by a study of the differences between the mean monthly temperatures at these two places for the spring and summer months (table 17). Bozeman records are used for Bridger Canyon temperatures, but as these are somewhat higher than those occurring in the canyon the difference would be still greater.

TABLE 17.—*Comparison of the mean monthly temperatures at Crookston, Minn., and Bozeman, Mont.*

| Place | Mean monthly temperatures for— | | | | | |
|---|---|---|---|---|---|---|
| | April | May | June | July | August | September |
| | °*F.* | °*F.* | °*F.* | °*F.* | °*F.* | °*F.* |
| Crookston | 41.7 | 55.9 | 63.3 | 68.9 | 66.0 | 58.1 |
| Bozeman | 40.2 | 49.0 | 57.0 | 64.0 | 62.7 | 54.0 |
| Difference | 1.5 | 6.9 | 6.3 | 4.9 | 3.3 | 4.1 |

Nymphs hatched from eggs of the same species from the same locality show considerable variation in their rates of development. In the case of those whose nymphal development was prolonged, a shorter growing season would reduce their opportunity for oviposition and reduce the numbers of their offspring.

Correlation coefficients between the rate of nymphal development and temperature within the limits of the straight-line relationship are high for all species (table 18). Hot summers, if not too dry, are conducive to more rapid development and subsequent longer oviposition periods, thus tending to give greater opportunity for reproduction and increase.

TABLE 18.—*Correlation coefficients between rate of development of grasshopper nymphs and temperature, and the minimum effective temperatures for nymphal development*

| Species | Correlation coefficient | Minimum effective temperature |
|---|---|---|
| | | °*F.* |
| *Melanoplus bivittatus* | 0.9049±0.0049 | 62.1 |
| *M. bivittatus*, (from Montana) | .8766± .0070 | 53.6 |
| *M. bivittatus*, (from Minnesota) | .8735± .0038 | 54.1 |
| *M. differentialis* | .8801± .0062 | 58.3 |
| *M. differentialis* | .9329± .0030 | 54.1 |
| *M. femur-rubrum*, (from Montana) | .9823± .0013 | 60.8 |
| *M. femur-rubrum*, (from Tennessee) | .9426± .0033 | 64.9 |
| *M. packardii* | .7369± .0177 | 62.9 |
| *M. packardii* | .8186± .0069 | 57.4 |
| *M. mexicanus* | .5880± .0022 | 63.3 |
| *M. dawsoni* | .8814± .0067 | 50.0 |
| *Phoetaliotes nebrascensis* | .9596± .0030 | 55.1 |
| *Dissosteira carolina* | .8681± .0090 | 66.2 |
| *D. carolina* | .9040± .0055 | 58.5 |
| *Camnula pellucida*, (from Minnesota) | .8571± .0059 | 64.9 |

Above 95° F. the rate of development of *Melanoplus bivittatus*, *M. packardii*, *M. dawsoni*, and *Dissosteira carolina* is not greatly accelerated and in some instances is actually retarded. On the other hand, that of *M. differentialis*, *M. femur-rubrum* (from Tennessee), *M. mexicanus*, and *Camnula pellucida* tends to be accelerated up to a temperature of 104°. The most notable of these latter was *M. femur-rubrum* from Tennessee. It increased its rate up to and including 104° F.

## Survival of Nymphs at Constant Temperatures

Records were kept of the total number of specimens subjected to the various constant temperatures and the number that died before reaching maturity. This gave percentages of nymphal survival for each species at each temperature as summarized in table 19. At 59° F. it was impossible to rear any species through to maturity. Evidently this is too low a temperature for complete development. At 68° F. no specimens of *Camnula pellucida* reached maturity, while *Melanoplus differentialis*, *M. packardii*, and *Dissosteira carolina* proved hardier at this temperature than *M. bivittatus* and others. All the species reached their peak of survival at 86° to 95° excepting *M. differentialis* and *M. femur-rubrum* from Tennessee. This latter showed an increasing percentage of survival or decreasing death rate up to and including 104°. Perhaps this was due to its adaptation to the warmer conditions of a southern climate. *Dissosteira carolina* showed a higher percentage of survival at high temperatures than did any other species. In the field it is usually found under conditions of higher temperatures than are the other species. *Camnula pellucida* showed a narrower range of temperature at which it survives, but at these temperatures it made a more rapid development than did the others. Perhaps this is due to its adaptation to a shorter growing season with the limited range of temperature such as occurs in the higher altitudes of mountain parks where this species is often dominant and numerous.

Table 19.—*Survival of grasshopper nymphs at various constant temperatures*

| Species | Proportion of nymphs surviving at indicated constant temperatures | | | | | |
|---|---|---|---|---|---|---|
| | 59° F. | 68° F. | 77° F. | 86° F. | 95° F. | 104° F. |
| | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* |
| *Melanoplus bivittatus*, from Montana | 0 | 15.8 | 53.3 | 73.7 | 68.4 | 31.6 |
| *M. bivittatus*, from Minnesota | 0 | 34.4 | 63.0 | 67.8 | 83.0 | 44.8 |
| *M. differentialis* | 0 | 78.6 | 90.0 | 72.2 | 73.7 | 45.0 |
| *M. packardii* | 0 | 61.9 | 80.0 | 89.5 | 85.7 | 68.4 |
| *M. femur-rubrum*, from Tennessee | 0 | 14.3 | 33.3 | 30.4 | 68.4 | 83.3 |
| *M. dawsoni* | 0 | 9.1 | 22.2 | 54.5 | 83.3 | 20.0 |
| *Dissosteira carolina* | 0 | 52.9 | 94.1 | 90.0 | 100.0 | 94.4 |
| *Camnula pellucida* | 0 | 0 | 10.5 | 70.0 | 83.3 | 57.9 |

## Effect of Cold on Subsequent Development of Newly Hatched Nymphs

Newly hatched nymphs of *Melanoplus bivittatus* were subjected from 1 to 22 days to temperatures of 50° and 59° F. immediately after hatching. They were then brought to a favorable temperature to complete their development. From 1 to 6 days' subjection to these temperatures retarded the rate of development and caused a mortality of 60 to 96 percent. Those held at 50° for 9, 10, and 11 days all died, and at 59° all held over 10 days died (table 20). Early spring hatching periods are usually accompanied by inclement weather which subjects newly hatched nymphs to several days of such temperatures. In some cases this has wiped out infestations and in all cases it at least has tended greatly to reduce the numbers of grasshoppers. The temperature range of 50° to 59° F. approximates the theoretical minimum effective temperature for nymphal development.

TABLE 20.—*Effect of cold on Melanoplus bivittatus hatched February 2, 1933, held from 1 to 22 days, inclusive, at 50° and 59° F. immediately thereafter, and then brought to 77°*

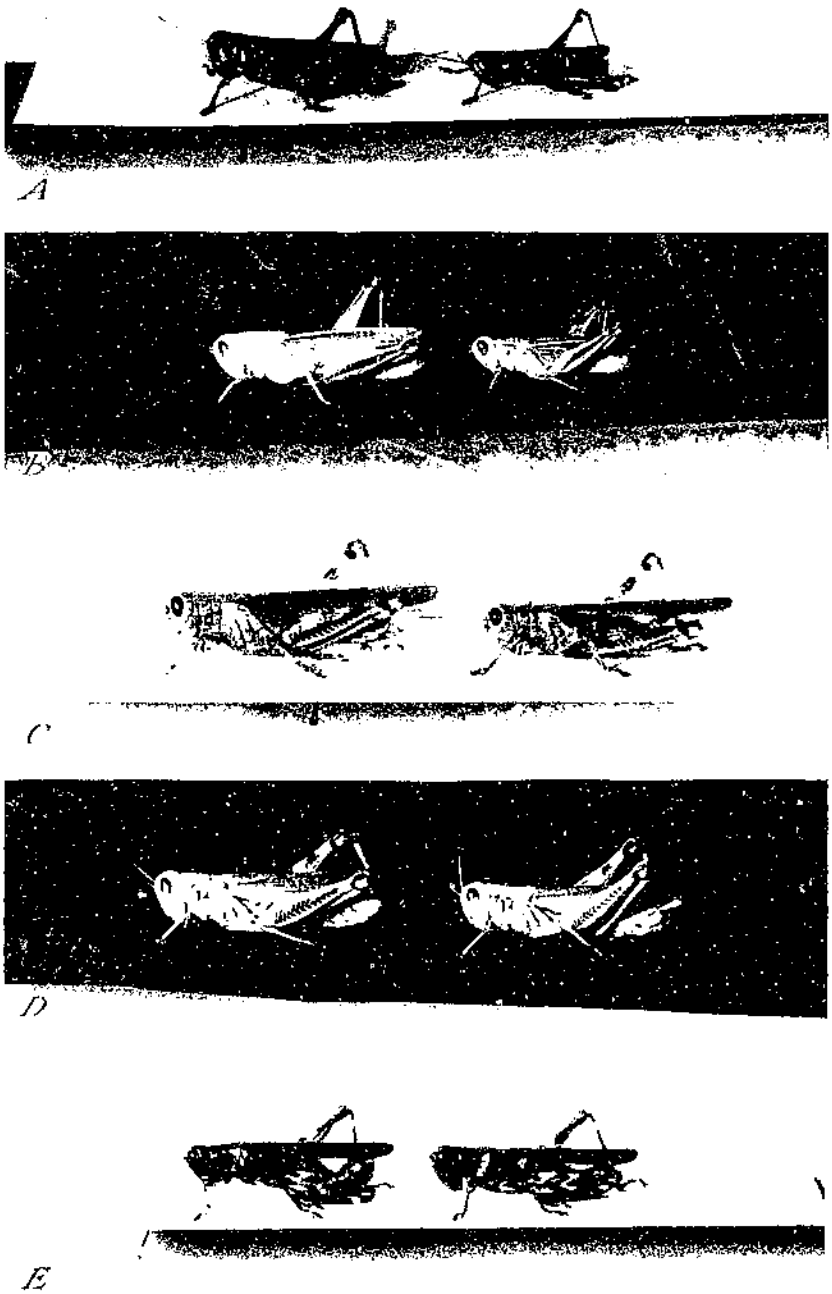
| Period of exposure (days) | Date of maturity or death of last survivors | Survival | Total developmental or survival period |
|---|---|---|---|
| EXPOSED TO 50° F. | | | |
| | | *Percent* | *Days* |
| 1 | Apr. 14 | 24 | 71 |
| 2 | Mar. 26 | 12 | 52 |
| 3 | Mar. 23 | 32 | 49 |
| 4 | Mar. 23 | 24 | 49 |
| 5 | Feb. 16 [1] | 0 | [2] 14 |
| 6 | Mar. 22 | 4 | 48 |
| 7 | Mar. 21 | 8 | 50 |
| 8 | Mar. 23 | 28 | 49 |
| 9 | Feb. 12 [1] | 0 | [2] 10 |
| 10 | Feb. 13 [1] | 0 | [2] 11 |
| 11 | Feb. 15 [1] | 0 | [2] 13 |
| 12 | Mar. 9 | 4 | 35 |
| EXPOSED AT 59° F. | | | |
| 2 | Mar. 23 | 24 | 49 |
| 4 | Mar. 14 | 4 | 40 |
| 6 | Mar. 19 | 40 | 45 |
| 8 | Apr. 11 | 4 | 68 |
| 10 | Mar. 20 | 8 | 46 |
| 12 | Feb. 16 [1] | 0 | [2] 14 |
| 14 | Feb. 13 [1] | 0 | [2] 11 |
| 16 | Feb. 23 [1] | 0 | [2] 21 |
| 18 | Feb. 19 [1] | 0 | [2] 17 |
| 20 | Feb. 19 [1] | 0 | [2] 17 |
| 22 | Feb. 16 [1] | 0 | [2] 14 |

[1] Died before reaching maturity.
[2] Length of survival period.

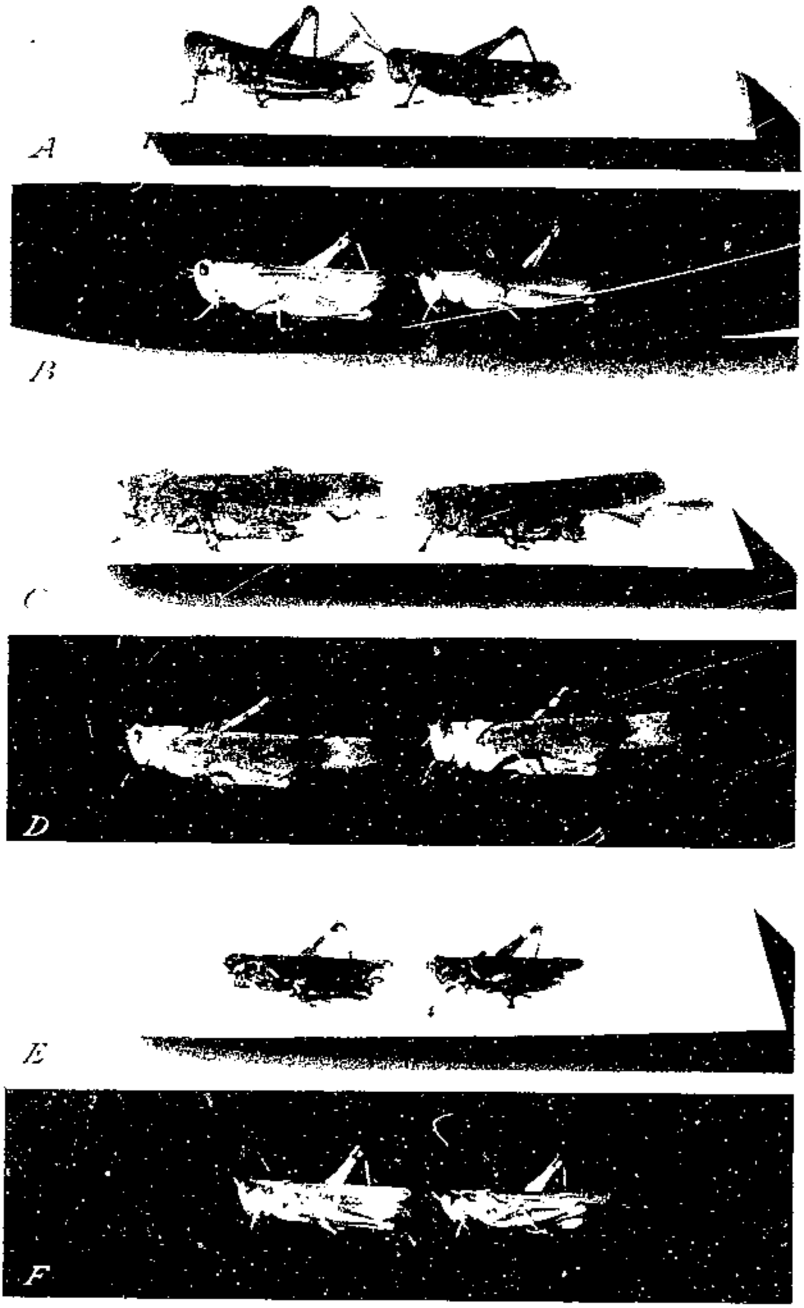
## EFFECT OF HIGH TEMPERATURES ON COLOR IN GRASSHOPPERS

Plates 8 and 9 reproduce photographs of several species of grasshoppers taken to show the effect of high temperatures on intensity of coloration. Each specimen shown was reared at the constant temperature indicated in the legends.

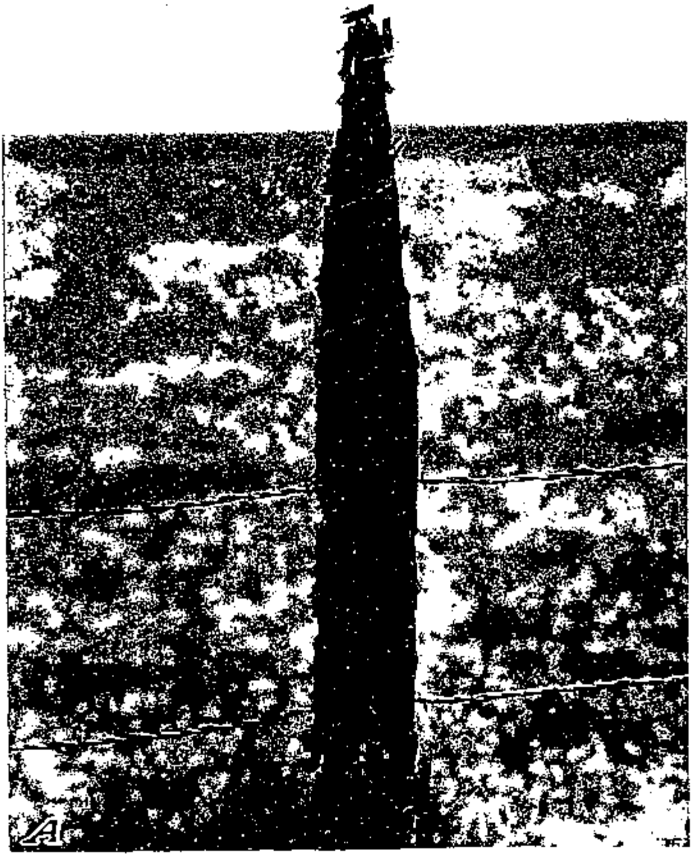
At high temperatures the color patterns fade or become more contrasting, and specimens of *Dissosteira carolina* lose almost all their color. This is probably owing to the more rapid oxidation of the pigment. A whole collection containing several species taken from a hot, stony creek bottom in Wyoming in 1924 was much lighter in color than collections from other, cooler places. During the hot summers of recent years many species of grasshoppers have shown the effect of high temperatures on coloration.




Effect of high temperature on the coloration of grasshoppers reared at constant temperatures: *A*, *Melanoplus bivittatus* reared at 75° F.; *B*, *M. bivittatus* reared at 95°; *C*, *M. differentialis* reared at 85°; *D*, *M. differentialis* reared at 95°; *E*, melanic form of *M. differentialis* reared at 100° F.




Effect of high temperature on the intensity of coloration of grasshoppers reared at constant temperatures: *A*, *Melanoplus packardii* reared at 80° F.; *B*, *M. packardii* reared at 100°; *C*, *Dissosteira carolina* reared at 80°; *D*, *D. carolina* reared at 100°; *E*, *M. femur-rubrum* reared at 85°; *F*, *M. femur-rubrum* reared at 95° F.



*A*, Adults of *Melanoplus bivittatus* and *M. differentialis* roosting on a fence post during the heat of the day; *B*, grasshoppers feeding on bran mash on piepans in feeding experiments.

## Temperature and Nymphal Activities

There are definite movements of the nymphs of *Melanoplus bivittatus* and *M. differentialis* which are more or less governed by certain temperature limits. The first of these occurs daily. During the night both adults and nymphs roost on the plants above the surface of the soil. As the rays of the rising sun penetrate to the ground and the air temperature rises to 68° F. and above there is a general movement of both stages toward the ground and from plant to plant. A second general movement occurs when the air temperature reaches about 90° or the surface-soil temperature reaches 113°. In this second movement the grasshoppers leave the ground and roost on the shady sides of plants, fence posts, telephone poles, or buildings. On small plants they will roost at least 2 inches above the ground and on taller plants or objects they will climb up as far as possible (pl. 10, *A*).

There is a gradual movement of first and second instars from the hatching grounds into the adjacent crops. Later there are definite migratory movements from field to field. Most of these migrations begin at air temperatures of from 75° to 80° F. The insects are not congregated in bands during these migrations but individually participate in a general movement in the same direction. A detailed description of one nymphal migration will suffice to describe this movement from field to field. On June 16 and 17, 1931, there was observed at Hamill, S. Dak., a migration of nymphs from an alfalfa field in the northwestern quarter of one section to a barley field and garden tract in the southeastern quarter of the section located westward across the road. They had practically destroyed the alfalfa, and there was little else for them to do but move out. The direction of the migration was southwestward against a strong south wind. Adjoining this alfalfa field to the southward, in the southwestern quarter of the same section, was a field of corn that was from 4 to 6 inches high. The young grasshoppers migrated across the northwestern corner of this, stripping bare a triangular patch of corn from the corner in the path of the migration.

During this movement individuals were closely watched to determine their behavior. As they passed through the corn, they would deviate from 2 to 4 feet from the line of migration to clamber up on the young corn, take a few nibbles, climb down, and pass on again with the migrating horde. Apparently they knew where they were going and why, and stopped only long enough to take a bite before continuing their journey. They may have been following up the moisture-laden stream of air coming from the green barley field. This movement continued for 2 days, during the periods of normal activity. Not all nymphal migrations are due to lack of food, however. Grasshoppers have been seen to leave one perfectly good barley field for another apparently not any better.

## Temperature and Adult Activities

From July 16 to 26, 1931, inclusive, daily observations were made near Winner, S. Dak., on movements of adults of *Melanoplus bivittatus* and *M. differentialis* in relation to temperature. During this period the maximum daily air temperatures rose above 90° F. on most of the days. A heavily infested cornfield was watched during a whole day while records were made of air and surface soil temperatures at which certain activities began and ceased.

The first movement of the grasshoppers was to become active and feed at 68° F. As with the nymphs, there was also a general movement toward the ground and from plant to plant. When the air temperature reached 90° they became restless and began making short flights in all directions. At first a grasshopper here and there would pop up, fly a short distance, and alight. The frequency of this movement increased with rising temperatures until the air over the field was thick with grasshoppers rising and circling 20 to 30 feet above the corn. The number of circling insects and the height of movement increased until the air as far up as could be seen contained large numbers of flying grasshoppers. If there was no wind the movement would be in all directions, but when there was a wind the movement became general with the wind. At this time the shady side of fence posts (pl. 10, *A*), telephone poles, buildings, etc., were covered with grasshoppers. This kind of activity cannot be considered as truly migratory because the insects were evidently trying to escape from the hot ground and in this endeavor were being caught and carried along by the wind.

Other movements of these species of a more definitely migratory nature were observed at this time. On July 16, 1931, at seven different places near Winner, S. Dak., migrations of adults were observed in which the grasshoppers were moving against the wind in the direction of green cornfields. The actions of individuals were observed closely. Adult grasshoppers were making low, flying jumps in their advance toward the corn. When they rose too high off the ground, the wind, which was fairly strong at times, would carry them back. They would then alight and start over again. *Melanoplus differentialis* appeared in all these migrations to be more active and a stronger flier than *M. bivittatus*. The cause of these movements is believed to have been the moisture-laden air from the cornfields, giving an upwind direction to the migration. It has been observed that grasshoppers located from 30 to 40 feet away and to the leeward of a pan of wet bait or the moist body of a person will move upwind toward these objects when at the same time there is no such movement of grasshoppers from any other direction. It seems reasonable to believe that this particular movement is their reaction to the current of moist air which is being blown toward them.

Another of the general movements of both adults and nymphs is that from cut or harvested fields toward others of standing crops. Probably one of the saddest experiences of the farmer in grasshopper campaigns, after he has destroyed the insects in his own fields by dint of hard work and patient application of control methods, is to find them in July, when adjacent small grain is being cut, moving in from all directions and either completely destroying or seriously damaging the standing crop. In the past the prospect of such a catastrophe has been one of the worst bugbears to those otherwise willing to cooperate in a community control campaign. Their complaint is, "What's the use of making a fight when your neighbor's 'hoppers will take your crop anyway?" Some entomologists have fostered this attitude by assuming that control measures are useless when applied after grasshoppers have become adult. Their point seems a practical one in that the farmers are busy with the harvest and do not then have time for any more control work. Nevertheless the control of this movement from the cut to the uncut crops is of vital importance to a well-rounded campaign. At this period the food supply of the insects becomes greatly reduced, the ground is dry, native grasses and weeds are more or less dried and unpalatable, and wet bait, as well as the succulent crop, is attractive to the hungry and thirsty grasshoppers. If farmers would take a little time each day to scatter bait across the path of migrating grasshoppers, a large amount of late damage could be prevented and a great many possible progenitors of future outbreaks destroyed.

### Effect of Temperature on Feeding

Observations have been made by the laboratory staff from time to time over a period of 10 years on the numbers of grasshoppers during a whole day attracted to baits placed on boards or in piepans on the ground (pl. 10, *B*). Counts of these were made at 10-minute intervals from 6:00 a. m. to 6:00 p. m. At half-hour intervals observations were made and recorded of the air and soil-surface termperatures and sky and wind conditions. There are about 150 days' observations in all on file for the years 1923, 1924, 1925, 1931, and 1932. These were made during the 3 summer months in the north-central and Yellowstone Valley areas of Montana and in south-central South Dakota, where the dominant species were *Melanoplus mexicanus*, *M. bivittatus*, and *M. differentialis*. The maximum air temperatures for the days during which these observations were made ranged from 65° to 105° F.

The data thus obtained were analyzed as follows: The total number of grasshoppers feeding at the pans was summarized for each hour of each day, together with the mean hourly air and soil temperatures. The number feeding during each hour was then reduced to a percentage of the total for the entire day to reduce all the observations for all days and localities to a uniform scale of measurement. These records were then classified according to maximum air temperatures for the days of observation, and the average percentages feeding during each hour of the day were determined. Only whole-day observations were included, and the results are presented graphically in figure 12.

In all but the 60°–70° F. class the means of the curves occur before noon. Between the maxima of 70°–90° the means of the curves lie within the narrow range of 46 minutes between 11:20 a. m. and 12:06 p. m. Above 90° the means are successively earlier.

On days when the maximum air temperatures range from 60° to 70° F. the feeding is evenly divided between the morning and afternoon. With a maximum of 71°–90° the bulk of the feeding is in the morning, although enough feeding is continued into the afternoon to warrant poisoning up to 3:30 p. m. Above 90° the feeding period is earlier and shorter. For maxima of 91°–95° the poisoned bait must be scattered before 10:30 a. m., and for 96° and above, before 9:30 a. m. The data indicate that the average feeding period is about

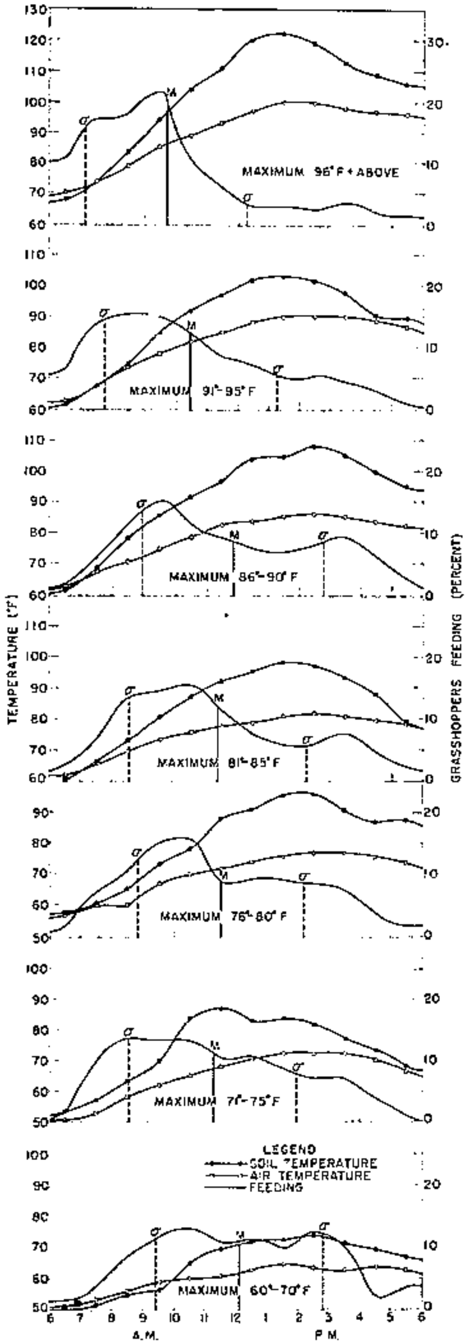



FIGURE 12.—Daily feeding of grasshoppers grouped according to maximum air temperatures for the days included in each graph and showing the percentages feeding at bait pans at different hours. *M*, mean; σ, standard deviation.

the same each day for the classes ranging from 71° to 90°. Observations have shown that activity on the ground occurs within about this temperature range. It is not advisable to put out poison when air temperatures are below 70° or above 90° F., even though grasshoppers have been observed feeding on pan baits at temperatures as low as 59° and above 96°.

In table 21 are shown the daily feeding periods for 5 consecutive days of observations at Hamill, S. Dak., when the air temperatures rose from below 70° to above 90° F. The beginning of feeding, the maximum feeding, and the end of feeding are given, together with the air and soil-surface temperatures on a mean hourly basis. On the first 3 days feeding began when the temperature reached about 70°. On the last 2 days it was close to 80° before feeding began, but the hours are different. The fourth day was hot early in the morning, but grasshoppers did not come down to feed until the sun's rays penetrated to the ground. It was cloudy until 7:00 a. m. on the fifth day. For the maximum feeding hour the mean air temperatures ranged, on the different days, from 78° to 85.1°. In three instances the end of the feeding period came when the air temperature reached 90°; but in one instance, on the second day, it ended at 83.3°, for the surface soil temperature had reached 113°. It has been regularly observed that grasshoppers leave the ground when the surface temperature reaches 113°. Of course there is scattered feeding below and above these temperatures, but only the main feeding period is considered in this discussion.

TABLE 21.—*Daily optimum period for feeding of adult grasshoppers, Melanoplus bivittatus and M. differentialis, on poisoned bran mash in a cornfield, July 22 to 26, 1931, Hamill, S. Dak.*

| Date | Beginning of feeding | | | Maximum feeding | | | End of feeding period | | |
|---|---|---|---|---|---|---|---|---|---|
| | Time | Air temperature | Soil temperature | Time | Air temperature | Soil temperature | Time | Air temperature | Soil temperature |
| | | °F. | °F. | | °F. | °F. | | °F. | °F. |
| July 22 | 6-7 a. m. | 68.6 | 69.8 | 9-10 a. m. | 82.4 | 98.6 | 10-11 a. m. | 88.1 | 102.8 |
| 23 | 6-7 a. m. | 68.0 | 68.3 | 8-10 a. m. | 78.0 | 95.6 | 10-11 a. m. | 83.3 | 113.0 |
| 24 | 6-7 a. m. | 71.2 | 70.7 | 11-12 a. m. | 85.1 | 82.4 | 12-1 p. m. | 90.2 | 89.6 |
| 25 | 5-6 a. m. | 77.6 | 72.5 | 6-7 a. m. | 79.3 | 75.6 | 8-9 a. m. | 90.7 | 95.3 |
| 26 | 7-8 a. m. | 81.1 | 75.6 | 7-8 a. m. | 81.1 | 75.6 | 10-11 a. m. | 90.2 | 97.1 |

Parker, in 1923,[12] found that the maximum feeding period for *Camnula pellucida* occurred when the air temperature first reached 73°–77° F. In a later bulletin [13] he states that *Melanoplus mexicanus* under Montana conditions feeds sparingly on bran-mash baits at air temperatures of 55°–63° and soil-surface temperatures of 70°–94°, more actively at air temperatures of 64°–67° and soil-surface temperatures of 95°–103°, and most actively at air temperatures of 68°–78° and soil-surface temperatures of 104°–112° F.

Both Parker's work and the writer's indicate that grasshoppers may feed at temperatures as low as 55° to 60° F., but this is unusual. Such low temperatures usually occur early in the morning, and the pan of bait offers a good roosting place for grasshoppers to sun themselves. Wet bait being handy, they nibble on it. In spite of this the data from the pan-bait method have proved valuable in determining the relationship between temperature and feeding.

## SUMMARY

The two species of solitary grasshoppers *Melanoplus bivittatus* and *M. differentialis* were wholly responsible for the destruction of 25 to 75 percent of the crops in an area of 30,000 square miles in South Dakota and northeastern Nebraska in 1931. Since then these two species have been prominent and often dominant in most of the outbreaks between the Mississippi River and the Rocky Mountains.

Grasshoppers feed on trees and shrubs, showing a preference in the following order: Mulberry, apple, Chinese elm, honeylocust, caragana, boxelder, willow, spruce, and poplar. The green ash seems immune. Of the small grains, the grasshoppers seem to prefer barley, oats, wheat, and rye, in the order named. They feed only sparingly on the sorghums.

During the period from 1923 to 1936, inclusive, the date of first hatching of grasshopper eggs in the northern Great Plains area ranged from April 20 to June 6, a difference of 47 days. The date when the first adults were observed ranged from May 30 to July 12, a difference of 43 days.

For individuals of *Melanoplus bivittatus* living under the same conditions of soil and weather, the hatching period may extend over 6 weeks.

[12] See footnote 4, p. 2.
[13] See footnote 5, p. 2.

Low temperatures, lack of moisture, and hardness of soil may retard the hatching of grasshopper eggs.

The greatest number of eggs counted in one pod of *Melanoplus bivittatus* was 104, and the greatest number of pods laid by one female of *M. bivittatus* was 4. Forty females of *M. differentialis* deposited an average of over 300 eggs per female.

Grasshopper populations are constantly shifting, not only from field to field but from one part of a field to another. Over a period of 6 days, populations ranged in one plot from 52 percent of the original numbers to 245 percent.

Generally speaking, *Melanoplus bivittatus*, *M. differentialis*, and *Camnula pellucida* prefer grass roots with good drainage and a maximum of sunlight for egg deposition. Their egg pods are concentrated in spots. *M. mexicanus*, *M. packardii*, *M. femur-rubrum*, and *Dissosteira carolina* tend to scatter their pods in more open ground. *M. mexicanus* often deposits its pods somewhat in masses in sandy hummocks, roots of wheat stubble, or crowns of alfalfa. *Dissosteira carolina* seldom oviposits among grass roots.

*Melanoplus bivittatus*, *M. mexicanus*, *Dissosteira carolina*, and *Camnula pellucida* go through either five or six instars in their nymphal development. The rule is five, with a tendency towards six instars much more pronounced in the females than in the males. *M. femur-rubrum* from Montana developed five instars, whereas the same species reared from eggs collected in Tennessee went through six. *M. differentialis* regularly has six instars.

The most noticeable changes in structure that take place during nymphal development are in the thoracic segments. The wing pads and tegmina point ventrad in the first three instars of the five-instar individual and the first four instars of the six-instar individuals. In all the species studied the wing pads and tegmina are turned dorsad in the last two instars.

The cerci of both males and females are very prominent in the first instar. They become less and less prominent in the females as these develop to the adult. In the males they flatten and take on certain specific characters useful in taxonomy.

The minimum temperature for hatching of the eggs was approximately 60° F. for most species. *Melanoplus bivittatus* hatches earlier in the season than *M. differentialis*, *Dissosteira carolina*, or *M. femur-rubrum*.

*Camnula pellucida* developed faster than any of the others. *Melanoplus femur-rubrum* from Montana completed nymphal development faster than *M. femur-rubrum* from Tennessee. *M. bivittatus* reached maturity in a shorter time than *M. differentialis*. All the stages of *Dissosteira carolina* make their optimum development at temperatures higher than those favorable for the other species.

In the laboratory no nymphs survived a constant temperature of 59° F. The rate of development increased as the temperatures were raised from 70° to 100°, but above 100° mortality increased rapidly.

Nymphs of *Melanoplus bivittatus* died that were subjected to a constant temperature of 50° F. for more than 8 days immediately after hatching.

High temperatures bleach out the color patterns of grasshoppers, probably by rapid oxidation of the pigment.

Both nymphs and adults roost on plants during the night. When the rays of the rising sun penetrate to the ground through the plant foliage and the air temperature reaches 68° F. there is a general movement toward the ground and from plant to plant. When air temperatures reach 90°, or surface soil temperatures 113°, the grasshoppers leave the ground and either take to the air or roost in the shade on plants, fence posts, poles, etc.

When the air temperatures are between 70° and 90° grasshoppers remain on the ground and may feed on the poisoned bait during such times.

Both nymphs and adults have been observed migrating against the wind toward fields of green grain or corn. The adults accomplished this by low, flying hops. It is believed that they follow up the stream of moist air coming from these green fields. The same reaction may be caused by a pan of wet bait or a person wet with perspiration.

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