INTERRELATED EFFECTS OF FOOD, TEMPERATURE, AND HUMIDITY ON THE DEVELOPMENT OF THE LESSER MIGRATORY GRASSHOPPER,

Melanoplus Mexicanus Mexicanus (Saussure) (Orthoptera)

by

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Pointing the Way
To Better Control of Grasshoppers—

The lesser migratory grasshopper, *Melanoplus mexicanus mexicanus* (Saussure), has caused tremendous crop losses in the United States. It was one of several destructive species in Oklahoma during the last grasshopper outbreak from 1936 to 1941.

Studies reported in this bulletin show how different foods, together with certain ranges of temperature and relative humidity, affect this insect, thus laying the scientific groundwork for more effective methods of preventing grasshopper damage in the future.

These studies also demonstrate the relationship between *M. mexicanus* and the Rocky Mountain locust which ravaged pioneer farms in the western plains area during the grasshopper plagues of the 1870's, and which since has seemingly "disappeared." Insects approaching the Rocky Mountain locust pattern were produced by rearing *M. mexicanus* under the proper combination of food, temperature, and humidity.

Disappearance of the Rocky Mountain locust seems to be in part explained by the greatly increased acreage of alfalfa west of the Mississippi River since 1900. *M. mexicanus* is strongly attracted to alfalfa, but the studies reported in this bulletin show that alfalfa is unsuited for the best development of this pest. Grasshoppers grown on alfalfa are comparatively small, and sometimes malformed. Historically, the disappearance of the Rocky Mountain locust appears to have coincided with the spread of alfalfa throughout its breeding grounds.

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INTRODUCTION

The lesser migratory grasshopper, *Melanoplus mexicanus mexicanus* (Saussure) is one of the insects most destructive to crops in the United States. The species as now constituted, is very plastic, occurring in different areas and under different climatic conditions in such a variation of form, size, color, and markings that it has been described under many names. Packard (22)[3] records that the first specimen to be named was collected by Thomas in Southern Illinois and sent to P. R. Uhler of Baltimore, in about 1860. The name *Caloptenus spretus* was assigned to this specimen. Grasshoppers from the same area were described by Thomas in 1865. Specimens from Kansas and Colorado which were described by Walsh (39) in 1866 were, however, more typical of the migratory form. In 1875 Riley (27) described *Caloptenus atlantis* as a new species which he distinguished from *C. spretus* by its smaller size, a more distinct separation of the dark mark running from the eyes onto the prothorax, and the pale line from the base of the wings to the hind "thigh" (femur). He described the "anal joint" in the male as tapering more suddenly in *atlantis* and the two lobes forming the notch as being less marked, the coloration as darker and more marbled with light parts a paler yellow.

In 1879 Scudder (33) replaced *Caloptenus* of Burmeister with *Melanoplus* of Stal. Hebard (12) in 1928 ascribed the name *M. mexicanus mexicanus* (Saussure) to the lesser migratory grasshapper, *M. atlantis* (Riley) and in 1931 (13) recognized the Rocky Mountain locust, *M. spretus* (Walsh) as a phase which he designated as *M. mexicanus* (phase) *spretus* (Walsh). Many racial or biologic forms have been described as new species by other authors. These are not considered in the present paper.

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[1] A thesis presented as partial fulfillment of the requirements for the degree Doctor of Philosophy in Entomology at Kansas State College.

[2] Acknowledgements. (See page 47.)

[3] Numbers in parenthesis refer to Literature Cited, page 48.

Differences in size and wing length between the Rocky Mountain locust and the lesser migratory grasshopper were discussed by Riley (28) in his eighth Missouri Report of 1876 as follows, "In defining the Rocky Mountain locust last year I endeavored to show that we have three closely related forms or so-called species, Viz: *spretus,* which is the devastating species of the west; *femur-rubrum,* a somewhat smaller, shorter-winged species common over the whole country, and *atlantis,* a still smaller species, but, except in size, approaching in general character nearer to *spretus* than *femur-rubrum.*

The similarities between these forms and Riley's conviction that they were distinct species appear as follows in his report, "I have a box full of each before me, and no one would for a moment hesitate to separate the typical diminutive, livid, mottled and strongly marked *atlantis* from the typical, large, pale, more uniform and voracious-looking *spretus.* Granted, as I freely have, that they approach each other through deviations from the average, as indeed most species do, I have yet to see the first specimen of *spretus* and *atlantis* that I could not properly separate; and when Mr. Scudder is more familiar with the true Rocky Mountain *spretus,* he will give up his notion that it occurs in different localities in the east."

Riley believed both *spretus* and *atlantis* to be descendents of *femur-rubrum,* with *atlantis* a transient form which would revert back to *femur-rubrum* when the climate changed.

Packard (22) considered *atlantis* to be a climatically dwarfed variety of *spretus* with *femur-rubrum* a separate species. He believed the specimen collected by Thomas in Southern Illinois and first assigned the name *spretus,* to be in actuality the small variety *atlantis,* which was a common form in that area.

A review of literature prior to 1940 revealed that no work had been done with *M. mexicanus* on the development of its nymphs and the resultant characters of the adults under controlled interrelated factors. Since any organism is the product of the interplay of physicochemical energies within the limits of its heredity and since the migratory grasshopper appeared to be capable of demonstrating great diversity of response, it was decided that such studies should be made concerning it. In 1940 this work was begun as a graduate thesis problem at the Kansas State College of Agriculture and Applied Science.

During 1943 it became a cooperative project between the Kansas and the Oklahoma Agricultural Experiment Stations and was continued as such until its conclusion in 1945.

History of Migratory Grasshopper Outbreaks in the United States

The earliest records [Packard (22)] of damage supposedly due to outbreaks of the Rocky Mountain locust were in 1818. By 1856 these insects had spread until nearly all of the North Central and Central States were affected. The outbreak peak apparently was reached in 1855 when Riley (27) found that, "The summers were exceedingly dry; the driest in fact that had been known for ten years."

During the period from 1857 until 1866 these plagues subsided until the insects were reported only from Colorado, Iowa, and Minnesota. Beginning in about 1867 the population again built up in the Central states and fanned out westward, northward, and southward. This reached outbreak proportions once again in the 1870's attaining its peak in 1876 when the devastation of crops became extreme. Settlers left their homes and many believed that agriculture in the Middle West would never be a possibility because of locust ravages. Since the 1880's, however, the Rocky Mountain locust seems to have disappeared from the face of the earth, leaving nothing but stories concerning the tragedy of its history.

Certain important findings were made during these "grasshopper years" which may well be considered. One of the most significant is that outbreaks reached their peaks during a succession of unusually hot, dry years. Although meteorological records from these early periods do not supply much information, there can be little doubt from the writings of competent observers that this was true. The phenomenon has been further verified by outbreaks of the lesser migratory grasshopper, *M. mexicanus mexicanus,* and other species, in more recent years of hot and dry periods. Urbahns (36) records four serious outbreaks in Oklahoma territory since it was opened to settlement in 1889. Grasshopper infestations were severe throughout the central and central-western portion of the state in 1912 and 1913 and again in 1919. In 1924 a serious outbreak occurred in the western part of the state, followed by another in the southwestern portion in 1925. The last state-wide outbreak of importance occurred during the years 1936 to 1938; however, serious damage was caused to crops in the Panhandle area in 1939 and 1940.

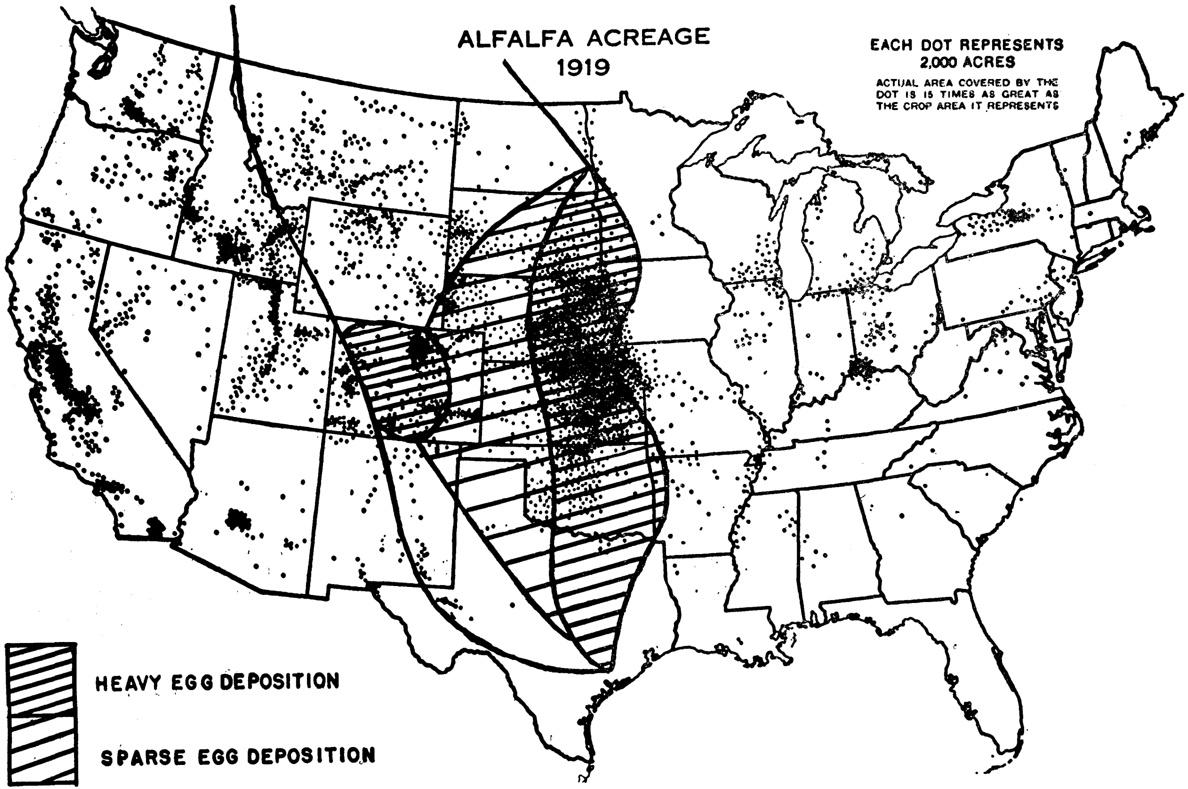


Fig. 1. Area invaded by the Rocky Mountain locust in 1876 [Riley (29)]. Map showing alfalfa acreage in 1919 is from the U. S. D. A. Year Book.

It appears that 1876 was a peak year of the worst grasshopper plague in the history of America. The total area affected at this time, as reported by Riley (29), is shown on the map in Figure 1. Riley, Packard, and Thomas (31) found the breeding grounds of these grasshoppers or "locusts" to be in plains and grasslands along streams and rivers from Texas into Canada. A key to the apparent disappearance of the locust was given by Doctor Packard in his statement, "It is evident that the breeding grounds of the locust are in those regions of the Rocky Mountains which will ultimately be taken up by settlers as farming and grazing lands; hence, when this region is settled, the prevention of locust injuries will be a problem of much easier solution than at present."

Agricultural plants introduced into the habitat of the grasshopper have brought about marked changes. It must be considered that in molding the pattern of development or the characteristics of the migratory grasshopper, each environmental factor would set up an interplay of influence with all the rest. If every element essential for the intensification of population vigor except one were present, the species would necessarily remain placid. Therefore it should be anticipated that grasshopper outbreaks would not infallibly accompany years with favorable climatic aspects. Kulagin (17) in a study of the mass outbreaks of Acrididae during the 18th and 19th centuries found that there was no definite periodicity. The most common periodicity for the two centuries was eight years for large regions and three to five for small areas. Outbreaks lasted two to three years and occurred during warm rather than cold years. Humidity was an important factor as well as food, temperature, and disease.

Riley (27) during the outbreaks of the 1870's observed that in the absence of grains Rocky Mountain locusts would feed on almost anything, including bark, paper, and dead animals, but that they preferred grasses or crops belonging to the grass family. He listed corn, wheat, rye, and oats in the order order of preference. Potatoes, tomatoes, sweet potatoes, castor-beans, butter beans, beet tops, carrot tops and celery were usually avoided.

High and long flights seldom occurred except when there was a fair wind. Riley stated that, "they move mainly with the wind and when there is no wind they whirl about like swarming bees. If a passing swarm suddenly meets with a change in the atmosphere, such as the . . . approach of a thunderstorm, or a gale of wind, they come down precipitately, seeming to fold their wings, and fall by the force of gravity, thousands being killed by the fall, if it is upon stone or other hard surface."

Byers in a letter to Packard (22) observed that, "the swarms settle down where there is fertility and vegetation," and that, "flights are governed by prevailing winds and temperature. A change of wind or a sudden even slight chill brings them quickly to the ground. Warm weather is favorable to flight."

During the warm years of its prevalence the "locust" developed two complete generations each season. The migration of adults of these generations, usually in opposite directions, created many interesting theories. Dodge, an entomologist at Glencoe, Nebraska, stated that the locust was double brooded, rearing the first brood in the South and the second in the North [Packard (22)]. Dawson (6) believed that "the young, due to instinct, while amenable to the migratory tendency, show a determination to exercise it in a direction exactly opposite of the preceding generation. This resulted in a migration back to the original breeding grounds at the end of two years." [Packard (22)]. Dawson (5) believed that "the young, due to during favorable seasons, to search for broad plains which would afford conditions for egg deposition and food.

Whatever the stimuli for migration may have been, it appears evident from the records that high temperature and winds were among the more important ones. Most of the early observers noted that egg deposition usually took place after a flight. Snow (35) in Kansas, observed the hatching of young locusts along the eastern border of that state in 1875, which were the progeny of parents that had arrived from the Rocky Mountain Plateau the previous summer. Riley (27) observed that those individuals which hatched from eggs after migrating did not copulate before their departure.

Corkins (4) studied flights of *M. atlantis* in 1920 which resembled closely those of *spretus*. Ordinarily the flights of *M. atlantis*, which were thought to be due to a lack of food or unpalatability, were low and of short duration. The flights in North Dakota, however, were strong. The grasshoppers rose out of succulent green crops and would settle in wheat from which they would probably leave the next day without doing much damage. Flights commenced during the heat of the day when there was a moderate breeze. The direction was with the wind and milling occurred during calms. Some inindividuals were collected at an altitude of 1650 feet. The rate of travel averaged about 20 miles per hour. No flights took place during cloudy, rainy or cool days.

The many differences and yet striking similarities that have existed between the two migratory grasshoppers, *M. spretus and M. mexicanus=(M. atlantis)* have created questions concerning their relationship throughout most of the history of our grasshopper plagues. Dr. George Dean of the Kansas Experiment Station has quoted the late Dr. Lawrence Bruner of the Nebraska Experiment Station as saying (during the early 1900's) that he would consider *spretus* a form of the lesser migartory grasshopper when he saw individuals of *M. atlantis* develop the long wings which were possessed by typical Rocky Mountain locusts.

Some explanation came with development of the theory of phases. Here was one of the important steps in opening a new and vital field of grasshopper research.

The Phase Theory

In 1921 Uvarov (37) proposed the phase theory which was based on his studies of *Locusta migratoria* L. While working in the Stavropol province of the Northern Caucasus in 1912, he studied swarms of *L. migratoria* coming from breeding grounds of the River Terek. Areas where they laid their eggs were mapped. In 1913 the progeny of these swarms appeared with many individuals resembling *Locusta danica* L., a solitary species which had little tendency to swarm. *L. danica* lives almost everywhere except in deserts and forests while *L. migratoria* is restricted to the reed beds of rivers and other comparable habitats. Structurally *L. migratoria* is distinguished from *L. danica* by being shorter, wider at the "shoulder" and constricted at the middle of the pronotum, with longer elytra and shorter hind femora. There is no apparent difference in the size of the sexes of *L. migratoria* while in *L. danica* the males are smaller than the females. The nymphs of *L. migratoria* are black in their early stages with orange and yellow appearing later. *L. danica* nymphs are usually uniformly green, fawn, grey, brown, or black. Plotnikov (25) produced these transformations in the laboratory. Crowding was the only factor found which would produce the variation. The embryo of *L. danica* developed uninterruptedly while that of *migratoria* demonstrated an embryonic diapause which was almost impossible to break.

Points brought out in Uvarov's concept of phases are: (1) that gregarious locusts are not stable in their morphological and biological characters; (2) extreme forms of the fluctuations are considered as phases; (3) there may be a striking difference between the swarming and the solitary phase; (4) specific character differences usually occur simultaneously in all individuals of a given locality and this is connected with the periodicity of outbreaks; (5) eggs of the swarming phase develop with a diapause, while those of the solitary phase can develop without it; (6) nymphs of the swarming phase are reddish, orange or yellow with well defined black markings and are inclined to wander in bands; (7) solitary nymphs vary in color, usually match their surroundings, and do not form bands; and (8) adults of the swarming phase do not develop sex products without a migratory flight, because of imaginal diapause, while solitary adults do not form bands and develop sexually without diapause.

Uvarov considers that a succession of favorable seasons or circumstances will make it possible for the solitary phase to build up a population in a given locality, overpopulation resulting in the swarming phase. Swarms will unite and large ones will migrate. The phenomenon of phases is most pronounced in warm climates.

Duck (7) in Oklahoma, demonstrated that the nymphs of *Schistocerca obscura* (Fabr.) showed marked differences in their coloration due to temperature and population density. Crowding had a greater effect than low temperatures in producing the darker forms. The phenomenon is discussed by Uvarov (38) in a few other species.

Faure (8) in his rearings of *M. mexicanus* at St. Paul, Minnesota, found the nymphal pattern equal to that described by the U. S. Entomological Commission (30) for *spretus*, when reared under crowded conditions, and equal to that of *mexicanus*, when isolated. He lists as the main points in distinguishing *gregaria* nymphs: (1) large black areas on the pronotum and hind femora, which are solid black in typical examples; (2) a strong contrast between the black and non-black areas of the head and pronotum; (3) the face black in the 2nd, 3rd and 4th instars; (4) in *solitaria*, subdorsal areas are not entirely black and are variable; (5) phase *transiens* is an intermediate form between *gregaria* and *solitaria*.

Husain and Mathus (15) reared *Schistocerca gregaria* nymphs in revolving wiregauze drums and somersault cylindrical cages. They demonstrated that an isolated nymph having *solitaria* tendencies at first would develop the coloration of *gregaria* when forced to move through a certain distance each day. They also found that association with other Orthoptera increased the activities of *S. gregaria* nymphs and produced *gregaria* coloration. It was found for this purpose, however, that the associates should be akin to the nymphs under experiment in their manner of habit and behavior. "The greater the likeness in this respect, the quicker is the response and the smaller is the number of associates required to bring about the color change." They concluded that the black pigment was produced as the result of physical muscular exertions.

Plotnikov (26) arranged silk brushes in such a way that areas where the color patterns should appear on *L. danica* would be stroked several minutes each day. His results with these tests were negative; also he found no effect on the black pattern from starvation or cannibalism.

Some Comparative Measurements of *M. mexicanus mexicanus* and *M. mexicanus* (phase) *spretus.*

Specimens of the Rocky Mountain locust which were collected between the years 1873 and 1879 were measured by Hebard (13). These were reported from a number of localities. He recorded a minimum length of the front tegmen as 23.6 mm. (for a male individual) and a maximum of 28 mm. (for a female individual). The average wing length of males was 25.2 mm., females 27 mm.

Faure (8) measured specimens of the Rocky Mountain locust which were in the U. S. National Museum. Of these, the front tegmen of the males averaged 24.78 mm. and the females 25.85 mm. In measuring adults of *M. mexicanus* under outbreak conditions in 1932 he recorded an average tegmen length of males taken at Lockhart, Minnesota, as 20.5 mm. and females as 21.45 mm. Males taken at Barnesville, Minnesota, averaged 21.37 mm. and females 21 mm. *M. mexicanus* reared by Faure on young wheat and corn leaves, under crowded conditions developed tegmina which averaged 17.1 mm. in the males and 17.13 in the females. Isolated individuals averaged 16.82 mm. in the males and 16.84 in the females. Measurements of the hind femora were also made and a comparable variation was found to exist.

Parker (24) observed that during the 1921-23 outbreak in Montana there was a definite tendency toward the migratory phase. He says, "the insects were noticeably longer winged and brighter colored than the typical *Melanoplus mexicanus* and, in localities where drought and high temperatures were most intense, numerous flights were observed, some of them extending 150 miles northward to the Canadian border."

Smith,[1] in 1935, observed swarms in which the grasshoppers flew at high altitudes, circled about and alighted in fields. Grasshoppers which he collected and measured from a flight at Minneapolis, Kansas, Sept. 30, 1935, had an average tegmen length of 21.7 mm. Nonswarming individuals from alfalfa insect collections were found to have an average tegmen length of 18.25 mm.

Nonswarming individuals collected from alfalfa in Oklahoma and Nebraska were measured by Brett during the years 1940 to 1945. Among these the tegmina ranged from 6 mm. to 22 mm. in length with the average below 20 mm. The posterior femora averaged 12.5 mm. and the pronotum 4.8 mm. in length.

Some specimens from an excellent collection of Rocky Mountain locusts taken by Bruner[2] at Turtle Mountains, South Dakota, in the early 1880's were measured by Brett. This large collection is in the possession of the Department of Entomology of the University of Nebraska and was made available for this study through the courtesy of Dr. H. Douglas Tate.[3] Length of the tegmina of these individuals ranged from 18 mm. to 28 mm. It averaged 24.4 mm. for the males and 26.1 mm. for the females. A male individual from this collection is shown in Figure 2, top, for comparison with a typical male *M. mexicanus,* Figure 2, center, collected from alfalfa in Oklahoma in 1944. Figure 2, bottom, shows the appearance of small *M. mexicanus* individuals with undeveloped organs of flight which were reared on alfalfa under conditions of low temperature and high humidity in the present experiment. Similar forms often occur in alfalfa fields during late, cool falls. Photographs of a pair of *M. mexicanus* (phase) *spretus* from the Bruner collection are shown in Figure 17.

[1] Unpublished notes of Dr. Roger C. Smith, Head of the Department of Entomology, Kansas State College, Manhattan, Kansas.

[2] Bruner was a field agent in Entomology of the U. S. D. A. from 1880-82, employed to help in surveys on the Rocky Mountain locust. Later, he served as Head of the Department of Entomology at the Unievrsity of Nebraska and became one of the most distinguished American Entomologists.

[3] Head of the Department of Entomology, University of Nebraska, Lincoln, Nebraska, at the time.

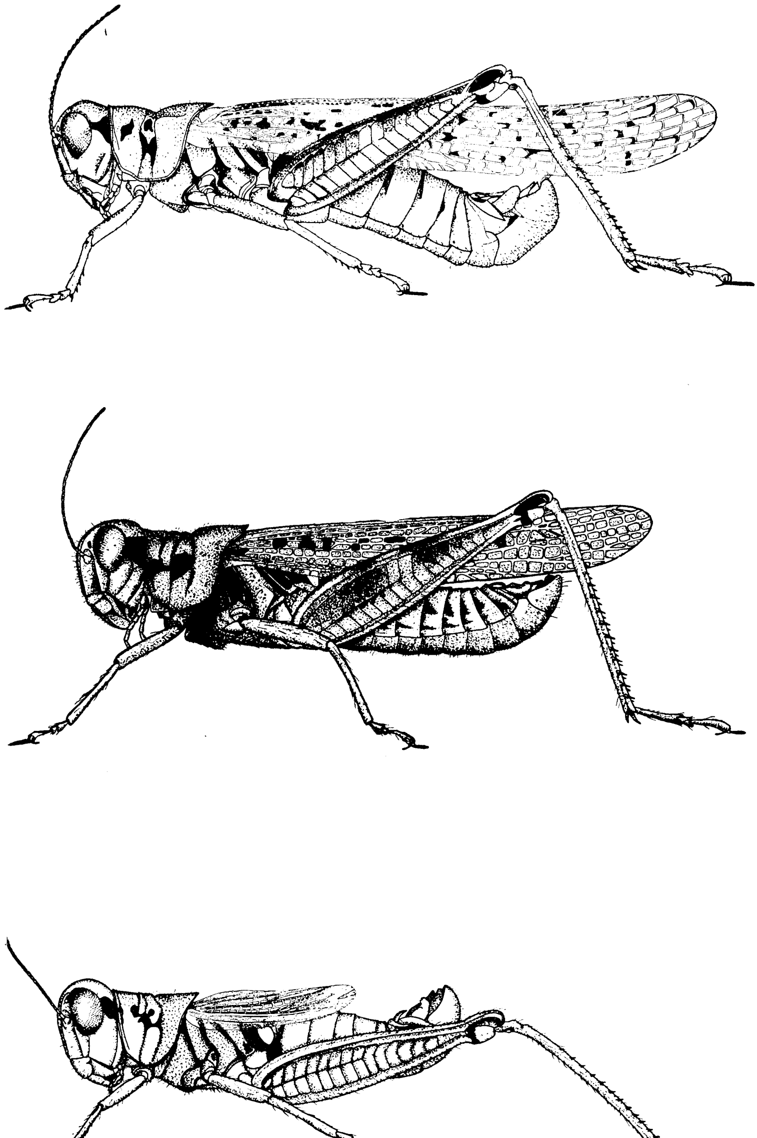


Fig. 2. Top, male, **Melanoplus mexicanus** (phase) **spretus** showing the characteristic long tegmina with many small, scattered melanic spots. Center, male **M. mexicanus mexicanus,** collected from alfalfa. The tegmina are shorter and the melanic spots fewer, larger and located near the center line. Bottom, male, **M. mexicanus mexicanus**, reared on alfalfa at 75° F. and 65 percent relative humidity.

METHODS OF PROCEDURE

Rearing Methods and Apparatus Used

Grasshoppers reared in these experiments were hatched from eggs deposited by gravid females collected during the middle of October. These individuals were placed in screen cages 9″ x 11″ x 7″ and fed head lettuce, dandelions, white clover, alfalfa, and lambs quarters, foods which were available and palatable to the insects.

Wide-mouthed bottles 1.75″ x 1.75″ were filled with washed sand which had been sterilized with heat. The sand was kept moist by adding distilled water which contained tincture of iodine at the rate of one drop per pint of water. Shortly after egg deposition, the jars were transferred from the cages to the incubator and held at a constant temperature of 80.6° F. which had been found by Parker (23) to be the point of most rapid development. Newly hatched nymphs were transferred from the incubator to the rearing cages on the day of their hatching. Individuals were captured by placing the large opening of a thistle tube over them. As soon as they hopped inside of the tube it was immediately transferred to a rearing cage and gently tapped in order to stimulate the nymphs moving into the cage.

Two types of cages were used. The large cages measured 9″ x 11″ x 14″ and were partitioned in the middle in order to serve as two cages, each 9″ x 11″ x 7″. Twenty-five newly hatched nymphs were placed in each cage. The small cages measured 4″ x 4″ x 12″ and were each partitioned, forming two cages 4″ x 4″ x 6″. The small cages were used for rearing grasshoppers under solitary and crowded conditions. Fifty individuals were placed in each cage for crowded rearings.

All cages had been sterilized several days before the newly hatched grasshoppers were placed in them, by spraying them with 70 percent alcohol and allowing them to stand in the sun. Fresh food was placed in each cage daily and was always available. Debris was removed each day.

Rearing cages previously mentioned were constructed with a wood floor. The ends were also of wood and each had a hinged door which fastened shut with a screen door hook. A wood partition was attached at the center of the floor in order to make the unit serve as two cages. Brass 18-mesh screen was tacked over the frame formed in this manner. Screen door stripping made a complete seal along all edges.

The rearing compartments measured 26″ x 20″ x 20″ and were constructed of ½″ insulation board. The single door on front measured 19″ x 14″ and was equipped with a double glass window for viewing the temperature and humidity recording apparatus which was mounted just on the inside of this window.

At one end of the compartment was attached a smaller outer compartment which measured 18″ x 16″ x 17″. This served as a housing space for the apparatus used in controlling temperature and humidity. The general arrangements of these units can be seen in Figures 3 and 4. All of the control assembly was enclosed except the mercury switch unit, which is shown on top of the housing compartment.

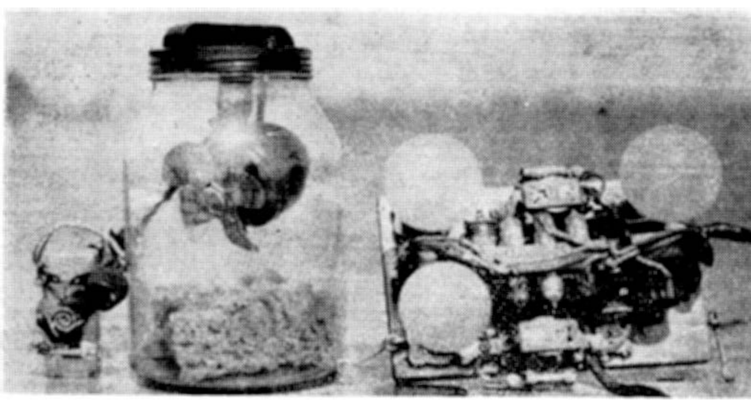


Fig. 3. Unassembled humidity control unit showing hygrostat, humidifying apparatus, and mercury switch assembly.

Temperature was regulated by means of a standard snap contact thermostat and a 60-watt electric heating coil. The apparatus for controlling relative humidity has been previously described by Brett (1). This consists principally of a moisture sensitive coil from a mechanical hygrometer which has been adapted for carrying an electrode between two circuits which operate through a set of mercury switches. By means of this device an electric fan is turned on and off. The fan increases the relative humidity of the rearing compartments by circulating air over warmed distilled water.

In order to maintain uniform conditions throughout the entire inner space of the rearing compartment, a fan was placed between it and the compartment which housed the regulating apparatus as is shown in Figure 4. This fan was in continuous operation.

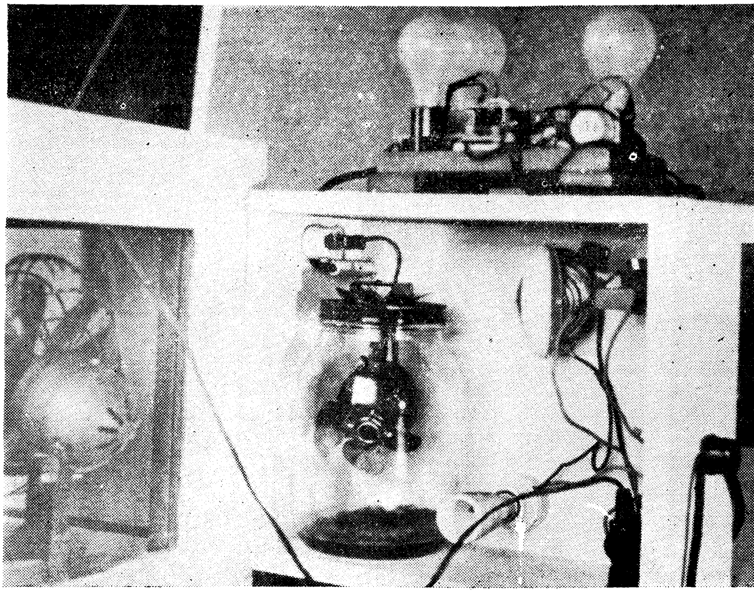


Fig. 4. Assembled humidity and temperature control units in compartment hinged to the rearing compartment.

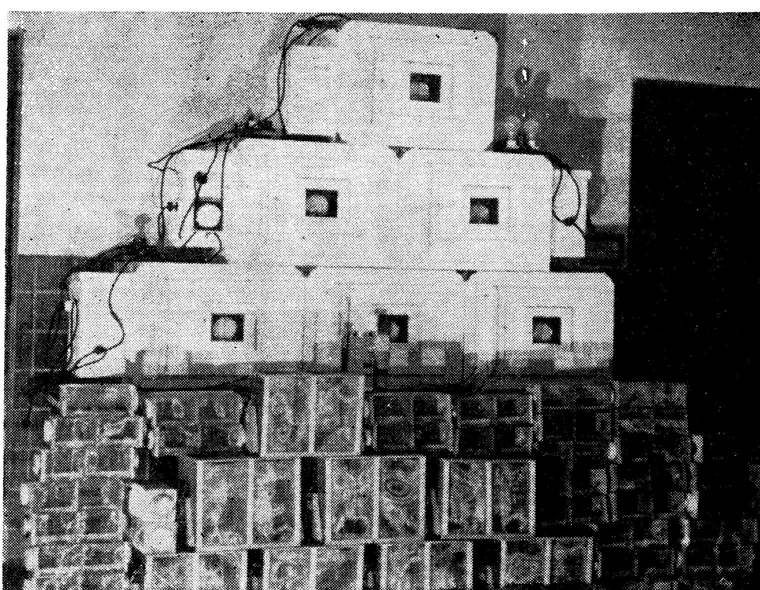


Fig. 5. Rearing compartments and cages.

The rearing compartment was lined with white oilcloth which was wiped clean from time to time in order to prevent undue development of mold and to reduce moisture collection at high humidities. Six compartments were constructed (Figure 5). Four of these were used for rearing grasshoppers. Two served as incubators.

Methods of Making Biometric Measurements

About one week after reaching the adult stage each grasshopper was killed with cyanide and weighed on an analytical balance. This measurement was made in milligrams as soon as the insect died in order that there would be no great loss of weight due to drying.

Body measurements (20) of adult grasshoppers were made in accordance with the recommendations of the Fourth International Locust Conference held in Cairo, Egypt, April 22, 1936.

The apparatus used, for measuring with maximum accuracy in a minimum time, consisted of a 4" reading lens permanently mounted in a wood frame and held above a transparent millimeter rule which had been calibrated under a microscope. Measurements were made down to .1 mm.

INTERRELATED EFFECT OF DIFFERENT FACTORS ON THE DEVELOPMENT OF THE MIGRATORY GRASSHOPPPER

Tables showing measurements of the individual grasshoppers were not included in this publication. They are available in copies of the thesis at the Kansas and Oklahoma Agricultural Experiment Stations. Averages from the tables appear in Figures 6 to 14 inclusive. Upon examining the graphs in these figures, it should be noted that each bar is divided at the top. The left hand side of the bar represents the average for male and the right hand side the average for female grasshoppers.

Langford (18) found that light had no effect upon the rate of growth of grasshoppers. This factor was not considered in the present work except that it was uniform throughout. A 30-watt electric bulb located in the top of each compartment and wired in series with the 60-watt circulator fan supplied some illumination.

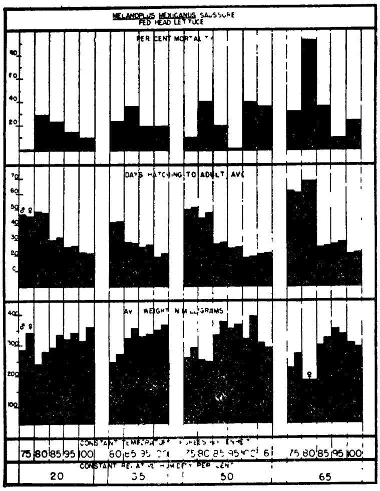
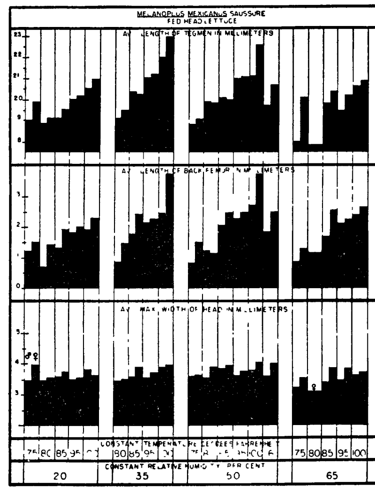


Fig. 6.



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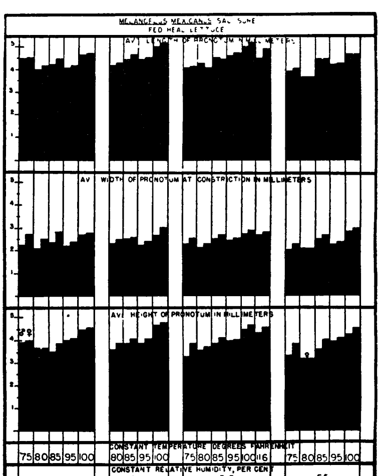
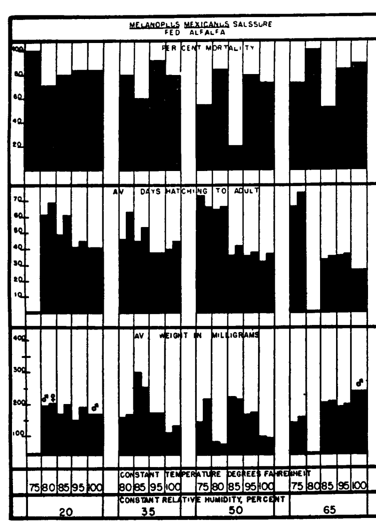


Fig. 8.



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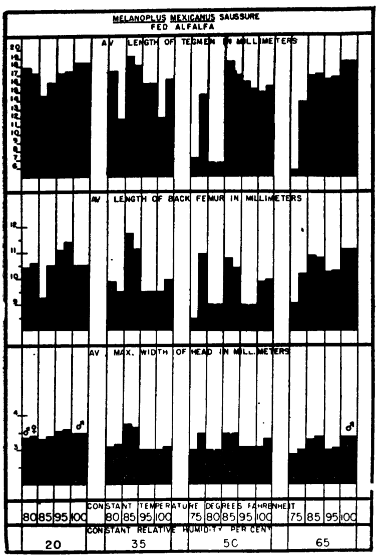

Fig. 10.

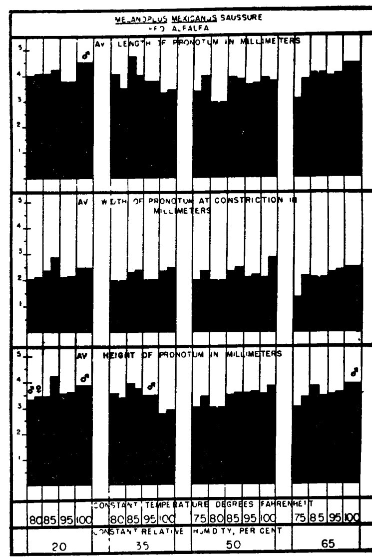

Fig. 11.

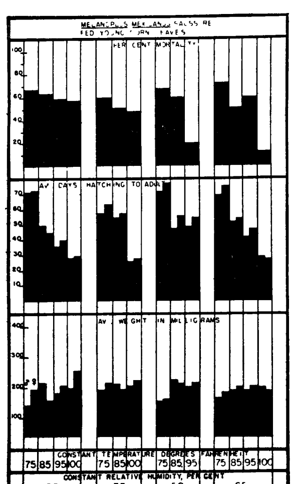

Fig. 12.

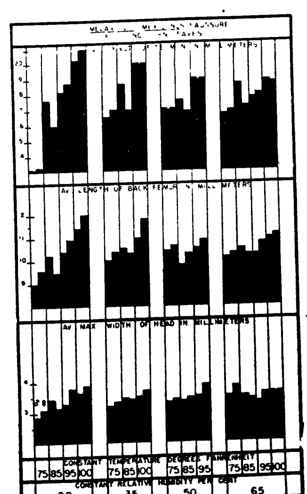

Fig. 13.

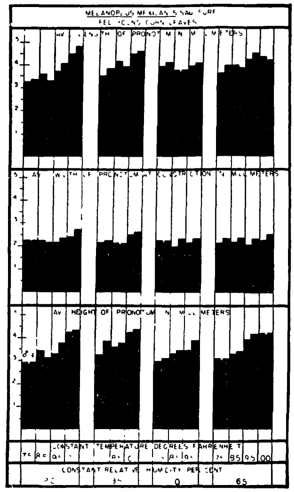

Fig. 14.

Grasshoppers Reared on Head Lettuce

Fresh leaves of head lettuce were placed in each cage daily. The entire head was utilized. The leaves averaged 93.1 percent water by weight. The grasshoppers fed more often and consumed greater quantities of head lettuce than any of the other foods. Although head lettuce is not normally available to the insects in nature, it serves very well in the laboratory for demonstrating food potentialities in relation to grasshopper development.

EFFECT ON MORTALITY AND RATE OF NYMPHAL DEVELOPMENT. The least mortality occurred among grasshoppers fed head lettuce. Irregularity in the percentage of mortality of the nymphs being reared under different conditions of temperature and humidity is shown in Figure 6. The general picture is one of high mortality at low temperatures and high humidity, with a low mortality under the reverse of these conditions. The greatest mortality, 92 percent, occurred at 80° F. and 65 percent humidity. This was mostly due to bacteria. Nymphs became discolored and sluggish. In about two days after the onset of symptoms, death resulted. Fungous attacks were more prevalent at slightly higher temperatures than those most favorable for bacteria, but both types of organisms were usually present at the same time.

An individual dying from bacterial infection turned black. Sometimes only a part of the body would appear to be diseased. This part would discolor and become useless. One grasshopper lived several days, apparently healthy except for a black, functionless hind leg.

Individuals attacked by fungi became sluggish but died without undergoing discoloration. The body appeared dry rather than more or less liquid as when affected by bacteria. There was no appearance of external conidiophores on the dead grasshoppers in the cages; however, when they were placed in stoppered test tubes and held at about 60° F.-65° F. the conidiophores appeared in from one to two weeks. Walton and Fenton (40) observed that although internal hyphal bodies were present, external conidia did not appear on grasshoppers in the field nor under laboratory temperatures of 70° F, 80° F, or 90° F. Dr. Winfield Ray found,[1] however, that external mycelium appeared when diseased specimens were placed on a moist blotter and held in a refrigerator for about three weeks. Temperature is an important factor to consider in the problem of difficulty in culturing the grasshopper fungous, *Empusa grylii,* under laboratory conditions. A review by Smith (34) of literature concerning the fungous and bacterial organisms attacking grasshoppers shows that the field and laboratory observations of many writers agree that disease outbreaks, due both to bacteria and fungi, occur during wet periods, especially when it is cool.

At extreme high temperatures mortality is usually due to desiccation or rigor. Grasshoppers developed quite successfully at 100° F., few of them dying at any of the different humidities. Grasshoppers in one cage were reared at 116° F. and 50 percent humidity. The mortality of 48 percent which resulted under these conditions shows a tolerance for high temperatures where other conditions compensate. Twelve nymphs fed head lettuce survived a temperature of 125° F. and a humidity of 50 percent during a four-day exposure, but were extremely nervous. It is very probable that in the nervous twitchings of individuals caged at high temperatures lies a fundamental reason for the taking off of grasshopper swarms. Since such "take offs" are generally made during the heat of the day this would seem to be further verified.

The maximum time for reaching maturity on head lettuce was 76 days. This was a female at 80° F. and 65 percent humidity. Undoubtedly the disease factor entered here. The minimum time required in reaching maturity was 18 days.

[1] Unpublished notes in the Department of Botany, A. and M. College, Stillwater, Oklahoma.

This occurred with one male at 100° F. and 35 percent humidity and three males and two females at 100° F. and 50 percent humidity.

It can readily be seen on the chart in Figure 6 that fewer days are required for reaching maturity when the temperature is increased. This is in accordance with well established facts regarding temperature effects. Upon examining the chart, however, it will be seen that humidity influences this rate. The time required for development is greater for the same temperature at high humidities and this variation becomes more noticeable at the lower temperatures. Thus it is generally true, as is shown on the chart, that development is slowest at low temperatures and high humidities and most rapid at high temperatures and low humidities. It would appear that fungi and bacteria play a part in the retarding of development at low temperature and high humidity. Uvarov (38) believes that *Coccobacillus acridiorum* d' Herelle normally plays a useful part in the physiology of grasshoppers but that under certain conditions (notably at low temperatures and high humidities) the bacteria increase in numbers and become dangerous parasites. This would seem very probable from the results of the present experiment and could explain the effect which occurred at the extremes of temperature and humidity.

EFFECT ON THE SIZE OF THE ADULT. Body weight of grasshoppers reared on head lettuce ranged from 125 mg. for a female matured at 80° F. and 65 percent humidity to 470 mg. for a female reared at 85° F. and 35 percent humidity. Figure 6 shows a general average increase in weight with increases in temperature; however, at 50 percent humidity the average weight of grasshoppers reared at 116° F. was 296 mg. for the males and 280 mg. for the females as compared with 318.7 for males and 396.5 for females at 100° F. There was also a decrease in size when the temperature was raised from 95° F. to 100° F. at 65 percent humidity. The heaviest average weights occur at high temperatures with humidities of 35 percent and 50 percent. The lightest average weights occur at the low temperatures and high humidities.

The most remarkable variation in any of the body proportions was in wing length. Figure 7 shows an increase in wing length as the temperature was raised. The greatest lengths were attained at 100° F. and 35, 50, 20, and 62 percent relative humidities in that respective order. The individual with the longest wings was a male reared at 100° F.and 35 percent humidity. Its tegmina measured 24.6 mm., which is equal to the average for *spretus*. Three females under these conditions developed wings which measured 24 mm. or more in length. The shortest winged grasshopper was a female reared at 75° F. and 65 percent humidity. The tegmina measured 15 mm.

Grasshoppers reared at 50 percent humidity developed longer wings at 100° F. than at 116° F. This indicated the possibility that wing length might be increased somewhere between these two temperatures. On this assumption 50 grasshoppers were reared at 105° F. and 35 percent humidity and 50 at 105° F. and 50 percent humidity. There was a 22 percent mortality among these individuals. Their tegmina ranged in length from 20 mm. to 24 mm., averaging but a fraction over 22 mm. Thus it appears that for grasshoppers fed head lettuce maximal wing development was attained at 100° F. and 35 percent humidity. Perhaps some other food such as a grass or a combination of foods would supply ingredients which would extend the tegmina length another 2 or 3 millimeters. Individuals reared under the above conditions developed tegmina equivalent in length to those of *spretus*. Rearings made at 105° F. are not shown in the graphs.

The general tendency of the females to develop longer wings than the males can be seen on the graph in Figure 7. An important relationship between wing length and body weight, brought out by these data, is that body weight does not increase in the same proportion as wing length. Maximum weights are attained at temperatures of 80° F. to 95° F. They level off or decrease at higher temperature. Wing length continues its increase throughout this scale. The result is that the long-winged grasshoppers appear to have smaller bodies than the short-winged ones. Actually the body may be the same size or only slightly smaller, the effect being one of optical illusion.

Length of the back femora varies with temperature in a pattern similar to that for wing length. The greatest length occurred on a female reared at 100° F. and 35 percent humidity. The femora of this individual were 15 mm. long, which is 0.44 mm. greater than the average length for *spretus* females which were measured for comparison.

Uvarov (38) found that the wings of *Locusta migratoria* were longer and the femora shorter than those of *L. danica*. A comparison of the wing and femur length of *M. mexicanus* and *M. mexicanus* (phase) *spretus* however, shows both the wings and femora of *spretus* to be decidedly longer than those of *M.*

mexicanus. *Spretus* proportions are very similar to those of the *M. mexicanus* individuals reared at 100° F. and 35 percent humidity.

Variation in the maximum width of the head capsule shows little effect from temperature and humidity. The graph in Figure 7 indicates that individuals reared under conditions that favor a considerable increase in the length of the tegmina and femora do not show a proportional increase in the width of the head. This would heighten the illusion of *spretus* as having a slender form. Specimens in the Bruner collection show the average width of the head capsule for *spretus* males to be 3.7 mm. and females 3.8 mm., which is not greater than that of *M. mexicanus*. The width of the head capsule was the least variable of any of the body parts measured.

Proportions of the pronotum developed under different conditions of temperature and humidity are shown in Figure 8. Uvarov (38) found that the pronotum of *Locusta migratoria* was more constricted than that of *L. danica*. A study of the graph for *M. mexicanus* shows that such is not the case for this species. There is a slight increase in width, length and height of the pronotum as temperatures are raised. This variation is in a pattern similar to that for the tegmina and femora but is not so pronounced. The size of the prothorax of the long-winged individuals may be slightly greater than those with short wings but will not appear to be so by general observation. This seems to also be true of specimens collected in the field.

Grasshoppers Reared on Alfalfa

For these tests common alfalfa was grown from inoculated seed, in large wooden boxes or in the earthen bed of a greenhouse. Fresh leafy stems from plants about two-thirds mature were cut at their bases and placed in the grasshopper cages daily. These plants averaged 81.1 percent water by weight.

The influence of different kinds of food on the development of *M. mexicanus* is demonstrated in a comparison of individuals reared on alfalfa plants with those reared on head lettuce. Grasshoppers fed alfalfa were less active and were darker colored than those fed head lettuce. They also consumed less food during the daily period and required a longer time for reaching maturity.

Although alfalfa appeared to be unfavorable to a vigorous development of *M. mexicanus,* the grasshoppers are nevertheless attracted to it in the field. Hebard (14), in his studies of ecologic habitats in Oklahoma, recorded *M. mexicanus* as occurring more abundantly in alfalfa than anywhere else except in cotton.

Specimens collected from alfalfa are often unusually small. It is not a rare thing during late September and October to find second generation adults which are diminutive and have the organs of flight greatly reduced. Hebard (14) describes a female of this type which was collected at Chickasha, Oklahoma. Such a type is shown in Figures 2, bottom, and 18.

Grasshoppers reared on alfalfa in the laboratory were not only reduced in their body size but had also less fecundity. Paired individuals seldom copulated. The few pods which were deposited contained but five or six eggs each and were mostly composed of froth. Grasshoppers reared on head lettuce copulated readily and deposited more and larger clusters of eggs.

Since much of the valley grassland, which was originally the breeding grounds for *spretus,* has been turned into cultivation, the food habitat for grasshoppers in these areas has changed. Alfalfa is now grown extensively in such regions. This is shown in Figure 1. Perhaps this is one of the basic causes for the disappearance of *spretus*. Liebermann (19) observed that depredations of *Dichroplus arrogans* (Stal), in the valley of Uspallata, Mendosa, were terminated by the fields of alfalfa.

The removal by man of native food plants which he replaced, to a considerable extent, with alfalfa, may be part of a gigantic biological control of the Rocky Mountain phase. Sanderson (32) observed that a major shift from cotton to soy beans in Northeastern Arkansas since 1933 was a factor in the increased population of *Melanoplus differentialis* (Thomas). Undoubtedly the type of food which is available for the development of grasshoppers is of great importance in regard to their economic status.

EFFECT ON MORTALITY AND RATE OF NYMPHAL DEVELOPMENT. The percentage of mortality was extremely high among those grasshoppers fed alfalfa (Compare Figures 6 and 9). The lowest was at 85° F. and 50 percent humidity. Twenty percent of these grasshoppers died before reaching maturity. One male and four females succumbed to bacterial disease shortly after reaching the adult stage. All of the nymphs died at 75° F. and 20 percent humidity and 80° F. and 65 percent humidity. Figure 9 shows that the mortality was generally high at 20 percent humidity. This was probably due to a moisture factor. Attempts to rear grasshoppers on dry alfalfa plants were unsuccessful either at low or high humidities.

At 100° F. and 20 percent humidity grasshoppers fed fresh alfalfa plants daily, which were not placed in bottles of water, incurred a mortality of 88 percent. Grasshoppers supplied with alfalfa which had its stems in bottles of water incurred an 80 percent mortality. The latter also developed in a shorter period of time and were larger than the former. The difference in moisture content of the food under these two conditions was small, yet its influence was detectable in the results. Grasshoppers supplied daily with fresh cuttings incurred a mortality of 88 percent at 105° F. and 35 percent humidity. At 105° F. and 50 percent humidity only 40 percent of the nymphs died. This again is probably due to the moisture factor. The tegmina ranged from 15 mm. to 18 mm. in length and the duration of the nymphal stage from 31 to 45 days. Rearings at 105°F. are not shown on the graphs.

The lowest percentage of mortality incurred among grasshoppers fed alfalfa was at 50 percent humidity. Fewer grasshoppers died at 85° F. than at any other temperature. The shortest period of time required to complete nymphal development was 24 days. This was a male at 100° F. and 65 percent humidity. The longest period of time required was 104 days. This was a female at 75° F. and 65 percent humidity. An explanation for this appears in the graph in Figure 9. Here it is shown that as humidity increases there is a greater variation in the time required for nymphal development at each end of the temperature scale; that is, low temperatures result in a greater period while high temperatures resulted in a shorter period of time for development than that which is required for the same temperatures at low humidities.

EFFECT ON THE SIZE OF THE ADULT. The graph in Figure 9 shows that in general the heavier grasshoppers were produced at high temperatures and high humidities while the lighter adults matured at low temperatures and high humidities. This is not, however, without exception. The lightest adult grasshopper, a male which weighed 80 mg., was reared at 75° F. and 50 percent humidity. The heaviest adult was a 350 mg. female reared at 85° F. and 35 percent humidity.

Little indication of the influence of temperature and humidity on the length of the tegmina is shown by the graph in Figure 10, except at low temperatures and high humidities where they are in some instances greatly shortened. Unusually long-winged forms did not appear under any of the conditions. No individuals developed wings comparable to those of *spretus*.

The probable reason for the lack of effect from temperature and humidity on wing development is that alfalfa acts as a critical factor and limits the growth of the tegmen in accordance with Liebig's law.[1] For the same reason there is little apparent influence of temperature and humidity on the length of the femora.

Temperature and humidity are negligible in their effects upon the width of the head (which shows the least variation) and the proportions of the prothorax of grasshoppers reared on alfalfa. There was some irregular variation in the size of these structures, but it was not great. No constriction of the thorax occurred.

Grasshoppers Reared on Corn

Fresh leaves of Reid Yellow Dent corn were cut from plants growing in the greenhouse when they reached a height of about 8 to 18 inches. These were placed in the grasshopper cages each day. The leaves averaged 86.5 percent water by weight.

Development among those individuals which fed on corn was somewhat intermediate between those reared on head lettuce or alfalfa. The adults were mostly typical *M. mexicanus mexicanus* in their general size and color. Nymphs developing on corn were yellowish in varying intensities, sometimes with even an orange tint. Faure (8) recorded such a color for nymphs developing on corn under crowded conditions.

Grasshoppers feeding on alfalfa showed more of a gray or slaty color and were darker than those feeding on head lettuce or on corn. Head lettuce resulted in very little background color in the nymphs. Some were even white at the higher temperatures, especially when reared under solitary conditions. Crowding would, however, bring out the black melanic pattern in an intense contrast against the light body color as is shown in Figure 16. The yellow-orange color also occurred in nymphs and adults of some *M. differentialis* which were fed corn. This same species reared on head lettuce was a lighter yellow.

When adults of *M. mexicanus* which had been reared on corn were paired, they copulated and produced egg pods.

EFFECT ON MORTALITY AND RATE OF NYMPHAL DEVELOPMENT. Mortality among grasshoppers feeding on corn was intermediate between those feeding on head lettuce and on alfalfa. The graph in Figure 12 shows the lowest mortality occurring at high temperatures and high humidities. Low temperature or low humidity or both appear to be quite unfavorable to development. Bacterial and fungous diseases were not as prevalent as among those grasshoppers fed alfalfa, being

[1] Liebig considers that when there is a multiplicity of factors and one is near the limits of toleration, this one factor would be the controlling one.

evident only occasionally at low temperatures and high humidities. The lowest mortality incurred (20 percent) was among grasshoppers being reared at 100° F. and 65 percent humidity. Seventy-two percent of the grasshoppers reared at 75° F. and 65 percent humidity died. This was the highest mortality.

A few individuals reached maturity in 24 days at 100° F. and 20 percent and 35 percent humidities. This was the shortest period of time for those fed corn. The longest period required for development was 82 days. This was a female reared at 75° F. and 50 percent humidity. Rate of development showed a greater variation at the extremes of temperature and humidity for those individuals fed corn, in the same manner as was described for grasshoppers reared on alfalfa and head lettuce.

EFFECT ON THE SIZE OF THE ADULT. Low temperature, as can be seen on the graph in Figure 12, is not conducive to the development of large size among grasshoppers fed corn. The smallest individual was a male reared at 75° F. and 20 percent humidity. This insect weighed only 80 mg. However, other individuals under the same conditions were more than twice as heavy. The heaviest adult was a female which weighed 345 mg. and matured at 100° F. and 20 percent humidity. In general, weight was least at low temperatures and low humidities and greatest at high temperatures with low humidities. Extremes in the variation of size, due to temperature, was somewhat leveled off by higher humidities.

Wing length was most strongly influenced by temperature variation at low humidities and least affected at high humidities. At 20 percent humidity a male reared at 75° F. developed tegmina only 6 mm. long. The maximum wing length for any individuals reared on corn was 22 mm. This occurred in a male and a female at 100° F. and 20 percent humidity. Tegmina of this length are equal to those of *spretus*.

Maximum width of the head capsule was increased somewhat from low to high temperatures at 20 percent humidity. The variation decreased as humidity was increased until no temperature effects were in evidence at 65 percent humidity.

Grasshoppers Reared on Sorghum

A few individuals were reared on fresh cut leaves of Atlas sorgo. The plants were propagated in wooden boxes filled with earth. Leaves were cut from them when they were 6 to 8 inches tall. All of the grasshoppers died at 85° F. and 20 and 65 percent relative humidities. Eighty-four percent of the grasshoppers died at 85° F. and 50 percent humidity. Only ten grasshoppers were placed at 95° F. and 50 percent humidity. Four of these died before reaching maturity. Adults reared on sorghum were small with comparatively long slender wings.

Sorghum does not supply the nutritional factors which favor vigorous development of the migratory grasshopper, but like corn and perhaps other plants of the grass family it nurtures the development of long slender wings at high temperatures. The longest-winged individual was a female with tegmina 16.5 mm. long. This did not approach *spretus,* but considering the small size of the grasshopper such a wing was relatively long.

Brunson and Painter (3) found that grasshoppers were not attracted to sorghums as they were to corn. Sorghum fields which were almost uninjured were often adjacent to corn which was eaten to the ground. Undoubtedly this selectivity exists for many species of grasses and other plants in nature.

SOME COLOR AND PATTERN RELATIONSHIPS

One of the most noticeable ways in which the migratory grasshopper reflects its environmental pattern is in the deposition of melanic substances. These include the products of oxidized amino acids and toxic phenols which arise as breakdown products of metabolism. Such pigments are generally incorporated in the substance of the cuticle. When ecdysis occurs these metabolic wastes are eliminated with the exuviae and a whole new melanic pattern can be set up by the insect for each succeeding instar [Wigglesworth (41)]. Thus it is that investigators experimenting with grasshoppers of different species have found the *solitaria* type nymph changing to *gregaria* and vice versa, depending upon the influences to which it is subjected. Results of the present study support the findings of others regarding the appearance of melanin.

Regardless of the type of food consumed, grasshoppers were darker colored at low temperatures than at high ones. Melanic patterns of broad black markings were superimposed upon a darkened background when hoppers matured at low temperatures. Under such conditions the black spots in the tegmina of *M. mexicanus* were large and comparatively few in number. As temperatures were raised the background color began to lighten. The black pattern marks became smaller in size and broke up into a speckling. Spots in the tegmina became small, numerous and scattered. Colors appeared in the background. This continued until at very high temperatures the melanin had almost entirely disappeared. The nymphs and adults became white with only a few minute black spots scattered about the body. Once a pattern was set, it did not change unless the insect underwent ecdysis. Humidity played no such a part as temperature in the setting of melanic patterns in *M. mexicanus.* The variation between individuals reared at low and high humidities at a given temperature was not evident so far as melanism was concerned.

In the present experiment it was observed that nymphs being reared at 116° F. were very nervous. They twitched and moved about constantly. *M. mexicanus* nymphs are normally quiet for long periods of time when temperatures are more tolerable. The individuals at this high temperature were feeding on head lettuce and their background color was nearly pure white. Most of them had just a few splotches of black on their bodies. However, four of them developed the melanic pattern of phase *gregaria.* This may have been the result of physical activity stimulated by high temperature.

General body color varies in accordance with the type of food consumed and the resulting pigments, depending partially upon heredity, environmental influence, and the physiology of the individual. Scudder (33), in his observations of grasshoppers in many regions of the United States, found that in the color of the caudal tibiae of *M. mexicanus,* red predominated over blue and green. Hebard (10) found that glaucous tibiae were more common on individuals from Mexico than those in the United States. In South Dakota Hebard (11) found that grasshoppers in arid regions had a predominance of glaucous tibiae while those in humid regions had a predominance of red tibiae.

In the present study an attempt to relate the color of tibiae to certain influencing factors revealed that of those insects fed alfalfa, 38 had red tibiae, 33 glaucous, and 16 pale. It is assumed that the paleness is due to a lack of pigment, since the intensity of the red, blue or green varies considerably. Of those insects reared on corn, 86 had red tibiae, 39 glaucous and 28 pale. This suggests a food relationship which may be similar to the yellow or orange body color of grasshoppers fed corn. Of the insects reared on head lettuce, 198 had red tibiae, 103 glaucous, and 112 pale. This also indicates the food factor. Depth of color was greatest among those individuals fed corn.

Considering only grasshoppers with red or glaucous tibiae it was found that of the adults reared at 20 percent humidity (disregarding other factors), 60 percent had red tibiae. Of those reared at 65 percent humidity, 69 percent had red tibiae. This shows a slightly higher percentage of adults with red tibiae, under humid conditions, and is in accordance with Hebard's field observations.

Among grasshoppers reared under the various humidities on corn and head lettuce, 53 percent had red tibiae at 75° F. as compared with 62 percent at 100° F., which indicates that warm moist conditions should favor the appearance of the red color. In studying this factor it was found that 45 percent of the adults had red tibiae at 75° F. and 20 percent humidity, while 70 percent had red tibiae at 100° F. and 65 percent humidity.

Adults collected from alfalfa in October, during several years, near Lincoln, Nebraska, showed a predominance of glauous tibiae. The was probably due to food and climatic factors. The grasshoppers were small and dark colored.

This evidence indicates that when adults develop on certain grasses or other plants during periods of high temperature, where at least the microclimates could be somewhat humid, they would be large and light colored, with the black markings on the body and tegmina small and scattered. The color of the caudal tibiae would be predominantly red. An examination of 100 specimens of *M. mexicanus* (phase) *spretus* in the Bruner collection at the University of Nebraska revealed that 85 percent had red tibiae while 15 percent had glaucous or pale tibiae. This, with the general color and body markings, is very much the same as for those adults of *M. mexicanus* reared on head lettuce at 100 F. and 35 percent humidity. Figure 17 shows a comparison of these forms. Ninety-four percent of 100 grasshoppers reared at 105° F. and 35 percent and 50 percent humidities had red tibiae.

In considering all of the adults for which records were made, except those reared at 105° F., it was found that 49 percent of them had red tibiae. Red occurred more often than the glaucous coloration but the presence of such color must be largely physiological, with food, temperature, and humidity acting as influencing factors.

EFFECTS OF CROWDING

Grasshoppers to be reared under crowded conditions were placed in a small cage at the rate of one grasshopper for every two cubic inches. They were fed head lettuce and reared at 100° F. and 50 percent humidity. Thirty-eight percent mortality occurred due largely to cannibalism on individuals undergoing ecdysis. Twenty-eight percent of the nymphs were typical *gregaria*. The adult males developed tegmina which averaged 20.5 mm. with a maximum of 21.5 mm. The females developed tegmina which averaged 20.8 mm. with a maximum of 22.2 mm. This equals minimum measurements for *spretus*.

Grasshoppers reared under solitary conditions at 100° F. and 50 percent humidity were divided into two groups. Ten individuals were fed both head lettuce and fresh alfalfa. Ten were fed head lettuce only. Among those fed head lettuce and alfalfa the males developed tegmina which averaged 20 mm. with a maximum of 20.5 mm. The females developed tegmina which averaged 22 mm. with a maximum of 23 mm. When head lettuce was fed alone the male tegmina averaged 21.11 mm. with a maximum of 21.6 mm. and the female tegmina averaged 23.7 mm. with a maximum of 24 mm., the latter being approximately the average length of *spretus* tegmina.

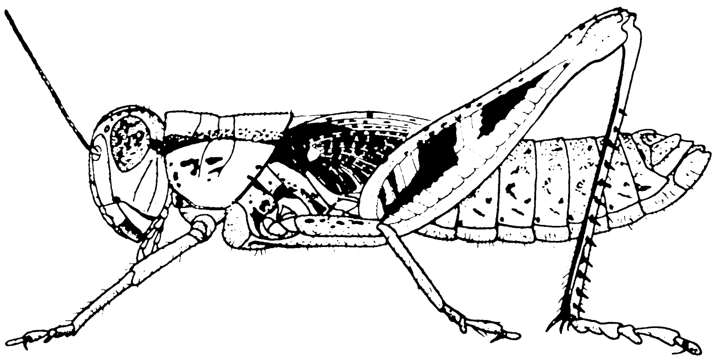

Fig. 15. **Melanoplus mexicanus mexicanus**, fifth instar nymph reared under solitary conditions on head lettuce at 100° F. and 50 percent humidity. Phase **solitaria.**

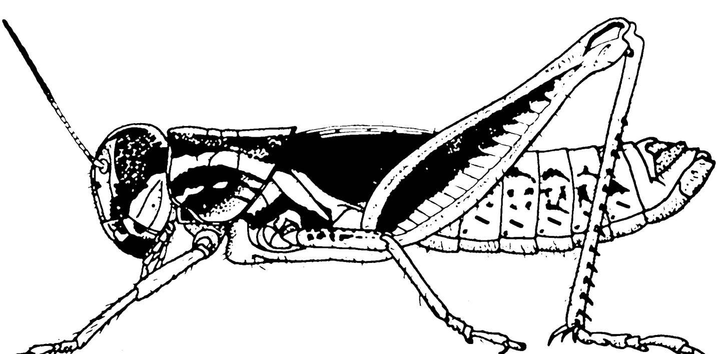

Fig. 16. **M. mexicanus mexicanus**, fifth instar nymph reared under crowded conditions on head lettuce at 100° F. and 50 percent humidity. Phase **gregaria.**

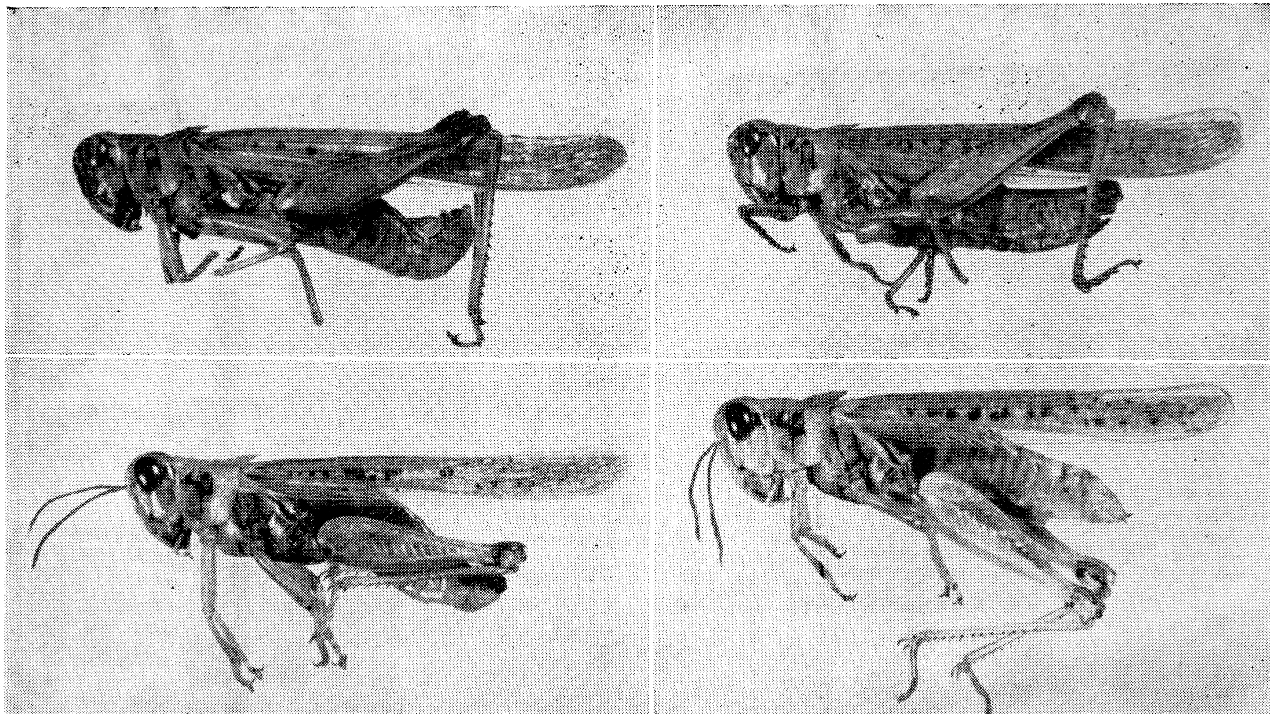

Fig. 17. Upper left, **M. mexicanus** (Phase) **spretus** collected by L. Bruner in the early 1880's at Turtle Mountains, South Dakota. Male x 2. Upper right, **M. mexicanus** (Phase) **spretus** collected by L. Bruner in the 1880's at Turtle Mountains, South Dakota. Female x 2. Lower left, **M. mexicanus mexicanus** reared on head lettuce at 100° F. and 35 percent humidity. Male x 2. Lower right, **M. mexicanus mexicanus** reared on head lettuce at 100° F. and 35 percent humidity. Female x 2.

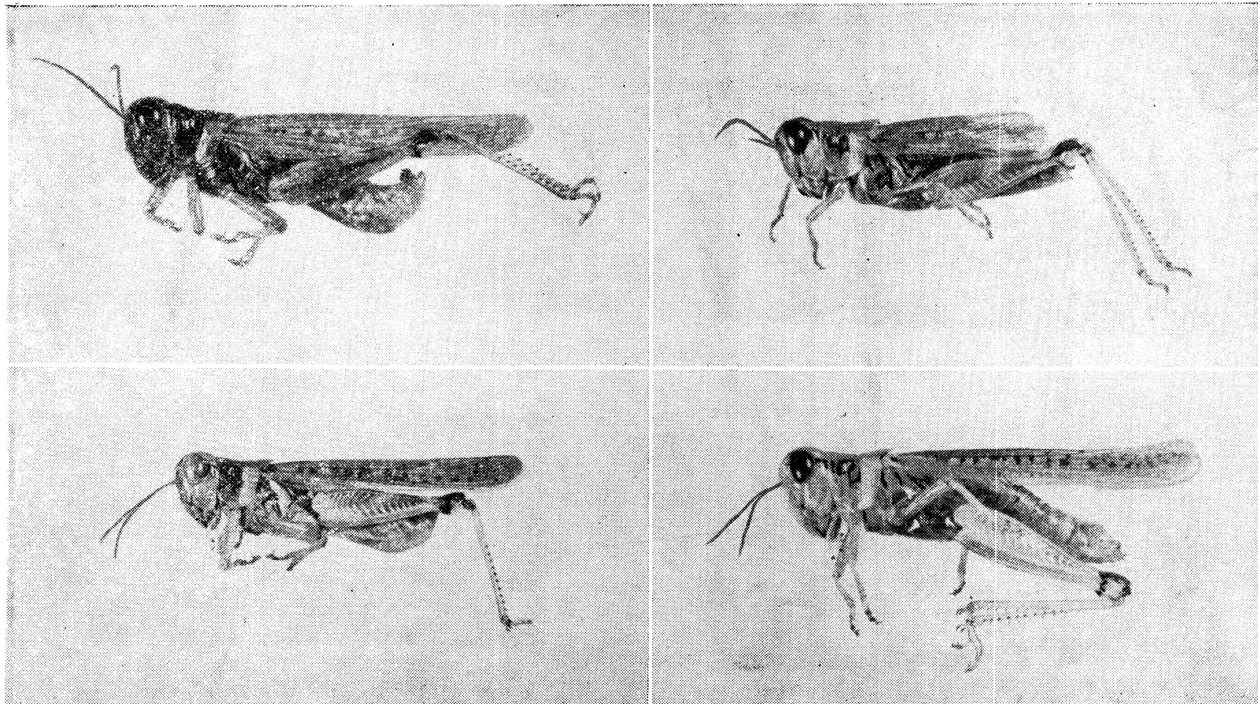

Fig. 18. Upper left, **M. mexicanus mexicanus** reared on head lettuce at 75° F. and 20 percent humidity. Male x 2. Upper right, **M. mexicanus mexicanus** reared on alfalfa at 85° F. and 65 percent humidity. Female x 2. Lower left, **M. mexicanus mexicanus** reared on corn at 85° F. and 20 percent humidity. Male x 2. Lower right, **M. mexicanus mexicanus** reared on corn at 100° F. and 20 percent humidity. Female x 2.

These figures show a reduction in the length of the tegmina of grasshoppers fed both alfalfa and head lettuce as compared with those fed head lettuce alone. The wings of adults reared under solitary conditions were somewhat longer than those reared under crowded conditions. From these records it appears that crowding had no effect on increasing the length of the tegmina and that actually the tegmina may be longest, at certain conditions of temperature and humidity, among individuals reared under solitary conditions.

Appearance of the melanic pattern on grasshoppers due to physical activity during their maturation is usually the result of crowding or high temperature or both and so it is that during the presence of food and climatic factors which favor their development, grasshoppers increase in numbers to an extent where crowding or temperature effects become evident in the color pattern. The same factors of food and climate which are conducive to this situation stimulate the insects in their growth and adults produce tegmina of unusual length. *Gregaria* nymphs and long-winged adults are associated only in this way. Thus, as has been shown, solitary forms may develop the long wings of *spretus* while crowded forms may produce tegmina which are shorter than the average *M. mexicanus*. Figure 16 illustrates the typical pattern of *gregaria* reared under crowded conditions as compared with *solitaria* (Figure 15) reared under solitary conditions. These sketches were made of nymphs developing at 100° F. and 50 percent humidity.

Riley (27) in describing the nymphs of *M. spretus* stated that, "with each succeeding stage the broad and pale streaks of the prothorax intensify. The black face of the first molt is quite characteristic and often endures to the pupa state. On each side of it the anterior part of the prothorax is black, relieved below by a conspicuous arched pale line, and this again with a more or less distinct dark lateral mark beneath." He described *M. atlantis* nymphs as having more obsolete black marks on the prothrax and a more speckled appearance. It is interesting to note that Riley's description of *M. spretus* nymphs showed their resemblance to *M. mexicanus* reared under crowded conditions (Figure 16). His description of *M. atlantis* nymphs quite characterized those of *M. mexicanus* reared under solitary conditions (Figure 15). This is also in agreement with the findings of Faure (8) concerning the melanic pattern of *M. mexicanus* nymphs reared under crowded and solitary conditions. Faure referred to *transiens* as being an intermediate stage between *gregaria* and *solitaria*.

Grasshoppers reached maturity in a slightly shorter period of time when reared on head lettuce under crowded conditions, requiring an average of 23.8 days for both males and females, as compared to 23.7 days for males and 25 days for females fed only head lettuce, under solitary conditions.

Body weight was greatest among those individuals reared under solitary conditions except for males fed both head lettuce and alfalfa. Duarte (6) in studying the effects of crowding on the growth of *Locusta migratoria* (Sauss.), concluded they were greater in sex differentiation than in phase differentiation.

It would appear from all of the evidence thus far that nymphs of *M. mexicanus* show color phase differentiation but the adults do not.

INFLUENCE OF HEREDITY

Heredity undoubtedly plays an important role in the development and characteristics of *M. mexicanus*. The variation among individuals reared under the same controlled conditions is evidence of this. In considering the variation among grasshoppers under each of the various combinations of factors it will be found that where conditions are highly favorable to the insect's development, for example 95° F. and 50 percent humidity with head lettuce as the food, the range of variation, for any unit measured, is narrow. Here, there was no mortality. The minimum number of days required for development was 23 as compared with a maximum of 27. The minimum weight was 310 mg. as compared with a maximum of 410 mg. and the minimum tegmen length was 20.7 mm. as compared with a maximum of 21.5 mm.

Under conditions which approach the limits of tolerance, individual variation, which is probably due to hereditary plasticity, becomes greatly amplified and the range for the units measured is wide. Thus at 75° F. and 65 percent humidity, 72 percent of the nymphs fed alfalfa died. The minimum time required for development was 62 days as compared with a maximum of 104. The minimum weight was 90 mg. as compared with a maximum of 195 mg. and the minimum length of the tegmina was 6 mm. as compared to the maximum of 18 mm.

Nabours (21) in his extensive work on the grouse locust, *Apotettix eurycephalus* Hancock, demonstrated the inheritance of a number of characters, especially in color, and color pattern. Good (9) in a paper concerning the genetics of the grouse locust *Tettigidea parvipennis* Harris, states that "the long and short wing alleles are of particular interest since they are in contrast with findings in *Paratettix texanus* and *Apotettix eurycephalus,* the wing length of these two species being conditioned by the season of the year."

In order to study the extent of variation between insects reared under the conditions of the present experiment, due to different parent stock, parallel rearings were made, under the same conditions, of progeny from adults collected near Lincoln, Nebraska, and adults collected near Stillwater, Oklahoma. The results of this test show little difference between the adults reared from Oklahoma stock as compared with those reared from Nebraska stock under the same conditions.

At 80° F. and 20 percent humidity, Oklahoma male progeny matured in 50.33 days as compared with 48 days for those from Nebraska. They weighed 215.5 mg. as compared with 231.37 mg. for those from Nebraska and the tegmina measured 19.41 mm. compared with 18.12 for those from Nebraska. At 80° F. and 35 percent humidity male progeny from Oklahoma stock matured in 42.18 days as compared with 42 days for those from Nebraska. They weighed 210.5 mg. as compared with 242.65 mm. for those from Nebraska. The tegmina measured 19.5 mm. as compared with 18.7 mm. for those from Nebraska.

Differences among female grasshoppers were similar to those of the male and so slight as to be well within the limits of normal variation. The range among individuals from different parent stock was not sufficiently great to account for the variation which occurred between groups reared under the different combinations of influencing factors.

DISCUSSION

A few species of grasshoppers have been studied concerning their food preferences. One of the most interesting and enlightening works on this subject was done by Isely (16) who grouped phytophagous grasshoppers in accordance with their mandibular structure, the principal types of mandibles being forbivorous and graminivorous. Normal vigor of the species depends upon the availability of food for which the mandibles are developed. *M. mexicanus* possesses mixed feeder mandibles and is a forbs-grass feeder. However, it is considered that even with such a species there would be optimum subsistence and reproductivity diets.

Considering that the effect of any single factor would be conditioned by other interrelating influences, the present work has expanded its approach in evaluating food and physical energies as they are related to development of the migratory grasshopper. In the initial environment, energy and matter are held together in an orderly fashion and function in accordance with natural laws. An organism exists as an internal and external adjustment of energy molded by every law and property. An insect, or any other form of life, is a reflection of its environment complexes within the limits of heredity and these heredity limits have been established over long periods of time by environmental energy complexes.

The total or interrelated effect of different energies cannot be measured fully as separated factors. To relate them, however, multiplies the complexity of the experiment by the number of factors involved. In the present work it has been found that different types of food greatly affect the rate of growth, physical proportions, size, disease susceptibility, and fecundity of the migratory grasshopper, but the effect of any given food is considerably different for varying combinations of influencing physical energies. In considering the value of a given diet it would be quite necessary to take into account the character of physical factors affecting the insect while it was utilizing this food, for example, mortality may be high or low and certain body proportions may be greatly increased or decreased by exactly the same food but with a variation of influencing physical energies.

A number of investigators have shown that temperature will bring about an increase in the rate of metabolic processes and development of insects and other animals in accordance with certain laws. This was true in the present experiment. It has been shown additionally that humidity conditions this rate. Extremes of temperature or humidity or both tend to exaggregate the total effect, that is, to increase the rate more than it would be for a single factor if the other was stabilized, or to decrease the rate to a greater extent than it would be for a single variable. The effects of such interrelationships were demonstrated especially in the unusual increase or decrease in length of the tegmina and posterior femora. Among individuals fed head lettuce and reared at 100° F. and 35 percent humidity, growth was accelerated to such an extent that progeny of *M. mexicanus* developed wings, legs, pronota and other body structures to a magnitude equalling that of the larger Rocky Mountain locust, *M. mexicanus* (phase) *spretus*. This development was also approximated under certain other conditions.

Since the advent of Uvarov's phase theory concerning the development of plastic species of grasshoppers from sedentary solitary forms into long-winged migratory forms, much interest has been centered on factors which might cause these changes. Originally it was considered that crowding, during the insect's development, was the only contributing factor. This caused an increase of melanin to be deposited in the cuticle and a subsequent darkening of the body color pattern. Reds and yellows occurred more often and more intensely. Later experiments demonstrated that melanic patterns of grasshoppers under such conditions were due to the effects of physical activity and that crowding was simply a means of creating activity. There has never been any separation made, however, between the causes of color patterns and the size of the adult insects. The long-winged, large, melanic form has come to be known as phase *gregaria,* while the smaller, short-winged, lighter colored form is known as phase *solitaria.*

In the present experiment it has been demonstrated with ***M. mexicanus,*** that large body size and long wings are the result of temperature and humidity relationships and that the effects of these physical factors are much more pronounced when certain types of food are available. The magnitude in size is entirely separate from the coloration phase. It is evident, however, that factors which would produce large, long-winged individuals would be similar to these which would produce the colored gregarious phase. So it is that high temperatures, low humidities, and succulent nutritious foods which create large long-winged grasshoppers, do so because of an accelerated utilization of energy. By these same circumstances grasshoppers would mature in a shorter period of time, complete more generations, produce more eggs, and finally reach a stage wherein there would be such numbers that crowding would result. The increasing numbers, during a favorable period would concentrate in valleys, along streams, and near ponds, since only in these places during dry hot years would there be succulent food to nurture them. As this food becomes gradually diminished, due to heavy feeding, the insects would begin to appear in many small bands, continuously coming together and forming large bands. The disturbances due to such crowding would produce the coloration of phase *gregaria*. Evidence in the present experiment indicates that such crowding may actually impair maximum body and wing development; however, climatic and food factors are the more effective determiners.

About the time individuals developing under such conditions reach maturity, the season may be very hot. It was observed during this experiment that high temperature created a nervous physical activity which produced gregarious coloration. Disturbance among the grasshoppers, resulting from their crowded state, combined with the stimulation of high temperatures, could cause them to make short take-offs. Intensifications of this influence could stimulate area populations to rise as swarms, high into the air, where, as has been observed by many persons, they remain, milling about unless carried along by winds. Upon encountering cool masses of air, the driving heat stimulation is lost and the insects settle quickly. The availability of food at the point of "settling" may be no criterion, for swarms have been reported alighting on nearly barren prairie. It is possible, however, that fields of green succulent crops may create a coolness in the air which might precipitate a swarm from flight.

Removal of any one of the energy factors essential to the development of such physical specialization in grasshoppers would reduce or prevent it. There is presented in the data of this experiment a partial explanation for the disappearance of the Rocky Mountain locust, based on food relationships. No single individual being reared on alfalfa, under any conditions, developed the large physical proportions of *spretus*. At the same time we know that alfalfa in the field is very attractive to *M. mexicanus* and that the native grassy areas in the valleys and prairies within its geographical limits have been largely placed under cultivation. During the 1820's alfalfa, which had been raised for centuries in Europe, was introduced into the United States. The Agricultural Year Book in 1875 reported it as growing successfully in California and experimentally in Texas. The 1889 year book stated that alfalfa was being raised successfully in California and some of the western and southern states. After this time there was much experimental work regarding its propagation. In 1903 the year book reported that a general introduction of alfalfa was being made. By 1919, as is shown in Figure 1, this crop was well established in the valley lands and over much of the dry prairie region of the middle and western states.

There is a correlation between the appearance of alfalfa throughout the area inhabitated by phase *spretus* both in space and time, the attractiveness of this food for the migratory grasshopper, its inhibiting effect on the maximal development of the insect, as shown both by field observations and in the results of this experiment, with the disappearance of locust plagues such as occurred prior to 1890. Perhaps other food plants are also of such an influence. The probability of climatic and food factor combinations which would favor development of *M. mexicanus* physically and numerically to the magnitudes attained during the nineteenth century thus may have been greatly lessened.

The comparative development of the migratory grasshopper under different influencing factors is illustrated in Figures 17 and 18. Figure 17 shows the Rocky Mountain locust, *M. mexicanus* (phase) *spretus*. These specimens were collected by L. Bruner during the 1880's and are typical of this large, long-winged form. In comparison, are shown a male and female which are progeny of *M. mexicanus mexicanus* parents. These two individuals were reared on head lettuce at 100° F. and 35 percent humidity and can readily be seen to approximate the proportion and size of *spretus*. Figure 18 shows a male reared on head lettuce at 75° F. and 20 percent humidity. It has shorter wings and is much smaller. Also a female reared on alfalfa at 85° F. and 65 percent humidity and the comparison of a male reared on corn at 85° F. and 20 percent humidity with a female reared on corn at 100° F. and 20 percent humidity. The high temperature effects are shown in greater body size, increased wing length, and lighter color. Grasshoppers reared on corn are seen to be smaller than those reared on head lettuce.

Coloration of the posterior tibiae was shown by this experiment as having been due to the intereffects of food, temperature, and humidity. Both head lettuce and corn produced a predominance of red color, alfalfa did not. High humidity and high temperature also produce a predominance of red. This is in accordance with observations made in the field and the few published records concerning tibial coloration. It is also supporting evidence regarding the origin of *spretus* since this phase was very predominantely red-legged.

No single factor, studied alone, either in nature or quantitatively in the laboratory, can give the key to the rise and fall of grasshopper populations and phases. Such things have been shown to be complex in their source and relationship. "Locust plagues" or "bad grasshopper years" would not necessarily follow cycles in rainfall or temperature since they are dependent upon a combination of many factors occurring as energy complexes which are reflected by grasshoppers in their color, size, and prolificacy. Swarms of locusts, of such magnitude as to stagger the imagination, may deposit tons of eggs, but the shifting play of energies to which they are subjected may seal their fate in a kaleidoscopic pattern of influence.

Perhaps an intimate study of the picture which these energies create on the developing insects would help map local areas of potential outbreaks. It is suggested that the color pattern and abundance of the grasshoppers, dates for the appearance of the first adults, and measurements of the adults would give us the warning needed to know where and when extensive control programs should be started, or perhaps an ecological study of the food plants available in such areas would enable us to remove a factor and replace it with another which would retard development of the insect.

Tests conducted by Brett and Rhoades (2) using hexachlorocyclohexane dust in fields of alfalfa heavily infested with grasshoppers, showed this material to hold great promise as a means of destroying outbreak centers. The development of synthetic insecticides will perhaps afford a new era in grasshopper control.

SUMMARY

This study of the lesser migratory grasshopper, *M. mexicanus mexicanus* (Saussure), was concerned with measuring the interrelated effect of food, temperature and humidity on the insect's development. Using but one type of food for a group of insects during their development, they were reared on leaves of head lettuce, common alfalfa, and Reid Yellow Dent corn, at 75° F., 80° F., 85° F., 95° F., and 100° F. With each of these temperatures they were reared at humidities of 20, 35, 50, and 65 percents. Additional rearings were made on head lettuce at 105° F. and 35 and 50 percent humidities. Under certain of these conditions they were also fed Atlas sorgo, a food which proved to be inadequate for vigorous development. Individuals were also caged under crowded and solitary conditions at 100° F. and 50 percent humidity.

Adults were measured as to weight in milligrams, length in millimeters of the tegmen, posterior femur, and pronotum, width of the pronotum at the constriction, height of the pronotum, and maximum width of the head. A record was made of the days required for nymphal development, mortality percentage, and color of the posterior tibiae.

Among individuals reared on head lettuce and corn, body size increased as the temperature was raised. However, grasshoppers reared at 116° F. were smaller than those reared at 100° F. This increase was not proportional for all body parts, being least for head width and greatest for tegmen and posterior femur length. Head lettuce afforded greater development of the grasshoppers than corn. The influence of temperature was further conditioned by humidity, which at the extremes was retarding in its effect.

The largest adults were matured on head lettuce at 100° F. and 35 percent and 50 percent humidities. One of these, a male, produced tegmina 24.6 mm. in length. Several other

individuals possessed tegmina 24 mm. or more in length. This is equal to the average for the Rocky Mountain locust, *M. mexicanus* (phase) *spretus*. All of the individuals reared under these conditions and at 105° F. possessed tegmina which were within a measurement range which could be ascribed to *spretus*.

It is shown both by the data of this experiment and that collected from field observations that as conditions become more favorable to the development of the migratory grasshopper it increases somewhat in body size and the wings lengthen considerably. Phase *spretus* exemplifies the maximum of its physical development and is seen in specimens collected from flight under outbreak conditions, apparently having reached its greatest development during the 1870's.

Grasshoppers reared on alfalfa were comparatively small, never reaching *spretus* dimensions, and a high percentage of them were affected by bacterial disease. When subjected to cool, humid conditions, the organs of flight were often undeveloped. The tegmina of many individuals attained a length of only six mm. Effects of temperature and humidity on body development were not as pronounced as among insects reared on corn and head lettuce, indicating that alfalfa functioned as a critical factor. Individuals reared on corn and head lettuce had a predominance of red over glaucous and pale tibiae. This was not true of those reared on alfalfa. The red coloration, so characteristic of *spretus,* was further increased by high temperature and humidity.

Succulence of food was an important factor. Two hundred nymphs were placed on dry head lettuce or dry alfalfa leaves under both high and low humidities at temperatures which were favorable to development. None of the insects survived more than a few days. Wilted leaves were noticeably less palatable to the grasshoppers than fresh leaves and were less favorable to their development.

Conditions most favorable to the maximum physical development of the migratory grasshopper were, as shown in the data of this experiment, type of food, succulence of food, high temperatures (about 100° F.), and low humidities (about 35 percent).

Fifty-two percent of the grasshoppers reared on head lettuce at 116° F. and 50 percent humidity reached the adult stage. A few nymphs which were fed head lettuce and exposed to 125° F. and 50 percent humidity for four days, survived without mortality. At the highest temperatures, all individuals twitched nervously and were continuously active, indicating the probable importance of temperature in stimulating swarm "take offs." At lower temperatures the insects were quiet, remaining motionless for long periods of time.

Grasshoppers being reared under crowded conditions, on head lettuce, at 100° F. and 50 percent humidity developed the black melanic pattern of phase *gregaria*. Solitary grasshoppers did not show this. The pattern also appeared on nymphs developing at 116° F., probably as a result of their continual physical activity which is considered to be the cause for *gregaria* coloration.

Adult grasshoppers which had developed under crowded conditions showed no colors or patterns which would distingish them from those reared under solitary conditions. Individuals produced under crowded conditions were slightly smaller and shorter winged than the solitary ones. Factors responsible for the development of large, long-winged adults of *M. mexicanus* are not the same as those which produce the color pattern of *gregaria;* however, the circumstances in nature which will produce one will probably result in the other.

Evidence in the data of this experiment supports the contention that *spretus* is a phase of *M. mexicanus* and that this form would appear under favorable climatic conditions in areas where the proper type of food was available. Supplementing such food with a type unfavorable but attractive to the species such as alfalfa would prevent development of the migratory form, bringing about biological control. This appears to have resulted from the cultivation of land in the breeding areas of the Rocky Mountain locust. Alfalfa is one food which could have this effect and is now grown extensively in these regions (Figure 1). It is among the foods most attractive to the migratory grasshopper, yet it appears, from the results of this experiment and a study of the history of grasshopper years, that it has had much to do with the leveling off of migratory grasshopper populations. It appears to be an important factor in preventing great physical development such as occurred during some of the historical "plague" years; however, it may hold the population level above that of the low points reached before alfalfa was introduced, thus preventing extreme population fluctuations.

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Footnote on introduction page.

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