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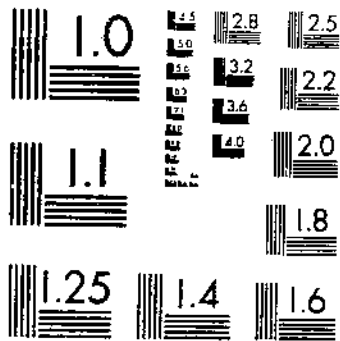
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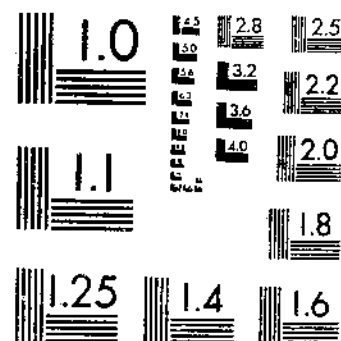
OBSERVATIONS ON MASS FLIGHTS AND OTHER ACTIVITIES OF THE MIGRATORY

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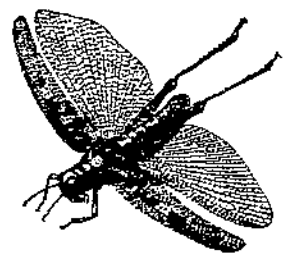
Observations on Mass Flights and Other Activities of the Migratory Grasshopper

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BY J. R. PARKER, R. C. NEWTON, AND R. L. SHOTWELL

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Common and Scientific Names of Plants Mentioned in This Bulletin

Alfalfa (<i>Medicago sativa</i>)	Peppergrass (<i>Lepidium</i> sp.)
Barley (<i>Hordeum vulgare</i>)	Rabbitbrush (<i>Chrysothamnus</i> sp.)
Bluegrass (<i>Poa</i> sp.)	Rose (<i>Rosa</i> sp.)
Bluestem (<i>Andropogon</i> sp.)	Russian-thistle (<i>Salsola kali</i> var. <i>tenuifolia</i>)
Brome (<i>Bromus</i> sp.)	Rye (<i>Secale cereale</i>)
Cactus (<i>Opuntia</i> sp.)	Sagebrush (<i>Artemisia</i> sp.)
Corn (<i>Zea mays</i>)	Sedge (<i>Carex</i> sp.)
Crested wheatgrass (<i>Agropyron cristatum</i>)	Skeletonweed (<i>Lygodesmia</i> sp.)
Dock (<i>Rumex</i> sp.)	Snowberry (<i>Symphoricarpos</i> sp.)
Flax (<i>Linum usitatissimum</i>)	Sunflower (<i>Helianthus</i> sp.)
Gramagrass (<i>Bouteloua gracilis</i>)	Sweetclover (<i>Melilotus</i> sp.)
Gumweed (<i>Grindelia</i> sp.)	Timothy (<i>Phleum pratense</i>)
Lambsquarters (<i>Chenopodium</i> sp.)	Western wheatgrass (<i>Agropyron smithii</i>)
Needlegrass (<i>Stipa</i> sp.)	Wheat (<i>Triticum aestivum</i>)
Oat (<i>Avena sativa</i>)	

Observations on Mass Flights and Other Activities of the Migratory Grasshopper¹

BY J. R. PARKER, R. C. NEWTON, AND R. L. SHOTWELL,
ENTOMOLOGISTS, ENTOMOLOGY RESEARCH BRANCH
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THE most spectacular and extensive mass flights of grasshoppers in the United States and Canada for over half a century took place during the summers of 1938, 1939, and 1940. The most recent previous flights exceeding them in density and distance occurred from 1874 to 1877, when great swarms of the Rocky Mountain grasshopper (*Melanoplus mexicanus spectus* (Walsh)) originated in the plains east of the Rocky Mountains in Montana, Wyoming, and Colorado and migrated eastward to the Mississippi Valley and southward to Texas. The species in the 1938, 1939, and 1940 flights was the migratory grasshopper (*M. mexicanus mexicanus* (Saus.)). Taxonomic workers in Orthoptera now believe that *mexicanus spectus* was an extreme gregarious phase of *mexicanus mexicanus* (Hebard 4, 5).² Since solitary and gregarious phases are not customarily considered distinct species or sub-species, *mexicanus spectus* is a synonym of *mexicanus mexicanus*. In this bulletin this grasshopper will be called *mexicanus*.

Most of the 1938 flights originated in north-central South Dakota. The heaviest flights were to the northwest into western North Dakota, eastern Montana, and southern Saskatchewan; to the north into north-eastern North Dakota, northwestern Minnesota, and southern Manitoba; and to the southwest into southwestern South Dakota, northwestern Nebraska, and eastern Wyoming. Flights in 1939 started within the areas invaded by the 1938 swarms, and for the most part were in the same general directions as in the previous year. Sporadic flights from areas invaded by 1939 migrants occurred in 1940, but were of less importance than the flights in 1938 and 1939.

During the years when these flights occurred extensive data on the seasonal development and habits of *mexicanus* were gathered by the Bureau of Entomology and Plant Quarantine. A summary of these data, together with information supplied by entomologists in the

¹ Submitted for publication September 9, 1954.

² Italic numbers in parentheses refer to Literature Cited, p. 46.

States and Canadian Provinces where flights took place, is presented in this bulletin.³

The zones where flights originated, the main migration routes, and the areas where eggs were deposited in greatest numbers are shown in figure 1.

METHODS OF OBTAINING DATA

The long-distance mass flights of 1938 were unexpected and were not studied in detail because of other work in progress. Data regarding them are therefore of a general nature, consisting for the most part of reports of flights, areas invaded, and extent of damage. No attempt was made to classify the 1938 flights, and such terms as "light," "moderate," and "heavy" merely reflect the impressions of the persons reporting them. In the fall of 1938 surveys were conducted to delimit the areas where migratory swarms laid eggs and to determine the habitats most commonly selected for egg laying, and in 1939 and 1940 studies were made of *mexicanus* flights in several States.

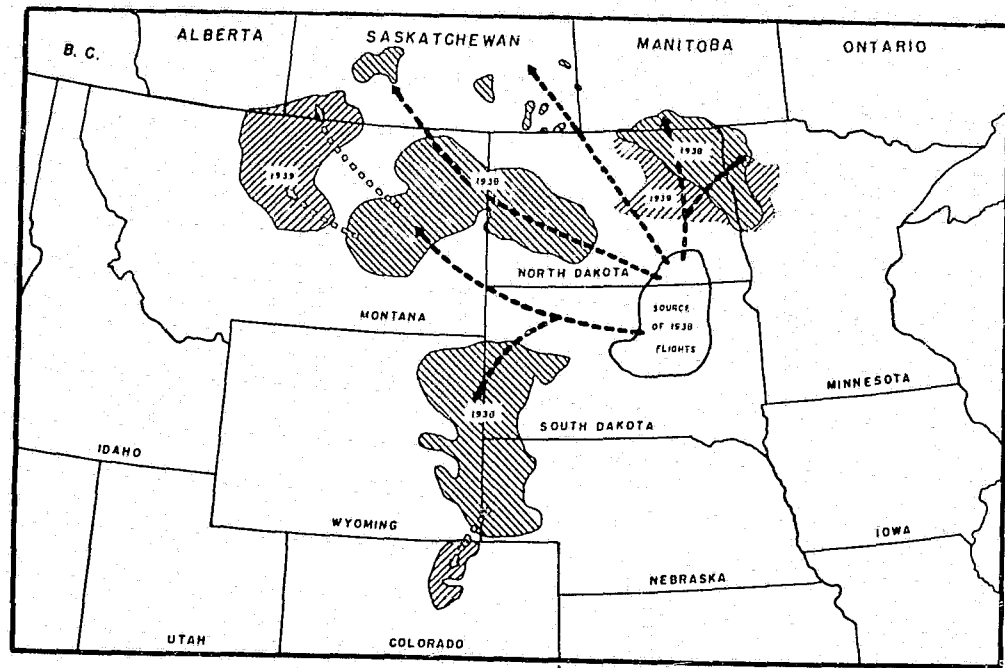
In 1939 and 1940 areas known to be heavily infested with eggs laid by invading swarms of the previous year were assigned to individual workers for the season. Repeated observations were made at fixed stations throughout each area to obtain data on egg, nymphal, and early adult populations, seasonal development, behavior, and prevailing conditions. All flights observed were recorded, together with information on location, date, hour, temperature, sky conditions, wind direction, type and direction of flight, and other pertinent data.



The point of the compass toward which most members of a swarm were traveling was recorded as the flight direction. When there was no uniform direction and many individuals flew in circles close to where they took off, the flight was recorded as milling.

Flights were classified as low or high according to whether the grasshoppers were flying less or more than 25 feet above the ground, and flight density was rated as light, moderate, or heavy. To determine the density of flight an observer cupped his hands over his eyes, glanced at the edge of the sun, and made a rough estimate of the number of grasshoppers he could see without further movements of the hands or head. Ratings for the number seen were as follows: Less than a hundred, light; several hundred, moderate; and many hundred, heavy.

As soon as mass flights started in a certain study area, observation stations were set up in advance of the flights and at right angles to their general direction. Counts of adults were made at these stations

³ The following persons supplied some of the information used in this bulletin: Field notes and reports—J. M. Brennan, F. D. Butcher, A. W. Buzicky, Roy Chamberlain, Stewart Clare, E. G. Davis, D. G. Denning, W. E. Dove, J. A. Gillett, Albert Mihelic, F. A. Morton, F. E. Skoog, L. A. Spain, H. S. Telford, E. R. Tinkham, and Claude Wakeland of the former Bureau of Entomology and Plant Quarantine; correspondence from State entomologists in Minnesota, Montana, Nebraska, North Dakota, and South Dakota—T. L. Aarnodt, O. A. Bare, Gray Butcher, Wayne Colberg, C. I. Gilbertsen, H. B. Mills, and H. C. Severin; and correspondence from Canadian entomologists about *mexicanus* flights in Alberta, Manitoba, and Saskatchewan—R. D. Bird, K. M. King, L. G. Putnam, and H. L. Semans. The authors are also grateful to A. B. Gurney and Claude Wakeland for reviewing the manuscript.



AREAS OF HEAVIEST EGG LAYING 1938  1939 



GENERAL DIRECTION OF FLIGHTS 1938  1939 

FIGURE 1.--Main migration routes and areas of heaviest egg laying by *mexicanus* in 1938 and 1939.

before flights reached them, and any sudden increase thereafter indicated the arrival of an invading swarm. As soon as one line of observation stations was reached by flights, another was established a known distance in advance and across the general direction of the last migration observed. In this way it was possible to measure population increases due to flights and the time taken by swarms to cover known distances. This method was particularly effective in Montana, where adult numbers before flights were very low.

Nymphal, adult, and egg-pod populations were classified as normal, light, threatening, severe, or very severe, as shown in table 1 (Shotwell 9).

TABLE 1.—Classification of nymphal, adult, and egg-pod populations of grasshoppers in large fields

Classification	Nymphs per square yard	Adults per square yard	Egg pods per square foot
Normal.....	0-9	0-3	0-0.4
Light.....	10-19	4-7	.5-.9
Threatening.....	20-39	8-15	1.0-1.9
Severe.....	40-79	16-31	2.0-3.9
Very severe.....	80+	32+	4.0+

CHANGES IN DISTRIBUTION AND POPULATION DENSITY PRECEDING 1938 FLIGHTS

The general area in which mass flights of *mexicanus* originated in 1938 included the northeastern counties of South Dakota and the southeastern counties of North Dakota, east of the Missouri River and between U. S. Highways Nos. 10 and 14. Normally this species is of minor economic importance in this area, and in the 1934 survey it composed only 17 percent of the adult grasshoppers in crops and 20 percent of those in range vegetation. In 1935 *mexicanus* began to increase, and in that year composed 56 percent of the grasshoppers found in crops. The percentage in rangeland remained about the same as in 1934. By 1936, 60 percent of the grasshoppers in crops and 40 percent of those in range vegetation were *mexicanus*. Severe infestations developed in Beadle, Faulk, Hand, and Hyde Counties in South Dakota, and threatening infestations were found elsewhere.

In the spring of 1937 very severe infestations of nymphs hatched at many spots throughout Beadle, Brown, Clark, Day, Faulk, Hand, Hyde, Spink, and Sully Counties in South Dakota. Ground dispersal of these heavy early-instar concentrations resulted in high late-instar populations throughout these counties. Light local flights and ground dispersal early in the adult stage resulted in a spread to surrounding counties previously only lightly infested. By late summer adults were present in threatening numbers throughout most of northeastern and north-central South Dakota and in a few adjacent counties in North Dakota. In collections at this time *mexicanus* made up 70 percent of the populations in crops and 56 percent of those on rangeland.

The general spread of adults throughout the area was followed by unusually warm weather in September and October. This was highly favorable for egg laying and consequently very severe egg-pod infestations were deposited throughout 33 counties east of the Missouri River. In a survey in which five 1-square foot samples were taken in each of 264 fields, egg pods were found in 15 out of every 16 samples examined.

The upsurge in *mexicanus* populations from 1934 to 1938 is thought to have been due to drought. Native grasses were greatly reduced and became interspersed with annual weeds, and much land formerly in small grains was left idle after crop failures and became weedy. Depleted range and weedy idle land are favored habitats of *mexicanus*, and the increased acreages of both during the drought provided many more places suitable for feeding and egg laying. Dry, warm weather in the spring and early fall was favorable for the survival of newly hatched nymphs and for heavy egg deposition.

FLIGHTS IN 1938

Seasonal Development and Habits Before Flights

As predicted by the egg survey in the fall of 1937, *mexicanus* hatched in enormous numbers in the north-central counties of South Dakota and in adjacent counties of North Dakota in the spring of 1938. Hatching began in the last half of April, when daily maximum temperatures ranged from 82° to 89° F. for several days. The main hatch continued throughout May, when the temperature and precipitation were about normal. Hatching was about 80 percent complete by June 1 and practically ended by June 15. By May 20 nymphs were numerous enough to damage crops. Adults were first noticed about June 10, but on June 20 most of the population was still in the fourth and fifth nymphal stages. High temperatures during the last 10 days of June accelerated the development of nymphs and by July 1 nearly all were adults.

Nymphs hatched in greatest numbers in small grains, field margins, idle land, and depleted range. Patches of peppergrass in idle land and depleted range contained the heaviest concentrations, which sometimes reached 1,500 to 8,000 per square yard.

Mass movements from range and idle land to nearby crops made it necessary to rebait many fields in which the initial infestation had been controlled. Baiting only partially stopped the invading nymphs. Sufficient numbers survived to cause serious crop damage, and large numbers of nymphs transformed to adults in and around cropped land. However, only a small portion of the nymphs that hatched in range and idle land moved into crops. The others fed on weeds and grasses and after becoming adults were the main source of flights.

Adults took to the air in low dispersal flights on the first hot days after getting their wings. Many such flights were reported from June 15 to 24. One of the authors saw several of them on June 21 while driving through Hand, Hyde, and Sully Counties in north-central South Dakota. Crops as well as vegetation in range and idle land were beginning to suffer from drought, and all vegetation had

been greatly reduced by the feeding of grasshoppers during very severe infestations. The day was hot, the temperature reaching 90° F. at 10 a. m. By that time the shady sides of fence posts were black with grasshoppers trying to escape the hot sun. Weeds, grass stems, and grain stems were bending from the weight of grasshoppers trying to get as far as possible above the hot ground. Most of them were fourth- and fifth-instar nymphs, but approximately 25 percent were recently transformed adults. At 11:30 a. m. with the temperature at 99° a light breeze started to blow. Adults immediately swirled out of the drying vegetation and flew in all directions from 1 to 25 feet above the ground. As soon as the breeze died down, they settled to the ground and then climbed as high as possible on vegetation or sought the shady side of fence posts. Only a few could be seen high in the air against the sun. Several similar local flights were seen the same day. All of them started when a light breeze rippled vegetation and stopped when the wind died down.

Time, Origin, and Directions of Flights

There is general agreement that the first long-distance mass flights of *mexicanus* in South Dakota in 1938 occurred during the last few days in June. The only reference to flights on a particular date during this period was found in an unpublished report of G. I. Gilbertsen, South Dakota State leader in grasshopper control for 1938, which contains the following statement: "There was a substantial migration of *mexicanus* from our State in a northwesterly direction on June 28." Since temperatures from June 25 to 27 were below those later found favorable for flights, it seems probable that June 28 was the date of the first major flight.

On July 1 swarms of *mexicanus* borne on winds from the southeast were seen at Mandan, Dickinson, and Beach in southwestern North Dakota and in the southeastern counties of Montana. The approximate air miles from Highmore in the South Dakota area where flights started on June 28 to points where incoming flights were seen on July 1 are as follows: Mandan 165; Dickinson 220; Beach 265; and Fallon County, Mont., 240. Using the 265 miles to Beach as the longest distance traveled in 4 days gives an average of 66 miles per day. This is faster than the progress of more closely observed later flights in 1938 and 1939, but it could have been accomplished by 5 hours of daily flying with favorable winds of 10 to 15 miles per hour on all 4 days.

Mass flights out of north-central South Dakota occurred whenever weather was favorable during July and the first 2 weeks in August. The boundaries of the zone in which they originated are not well known but are approximately those shown in figure 1. All of one county and parts of five adjacent counties in North Dakota were very severely infested before flights started in South Dakota and have been included within the zone where flights originated. There are no records of flights out of them before the arrival of swarms from South Dakota, but it is known that flights occurred later and that local populations were greatly reduced because of them.

Once a heavily infested locality was invaded by migrants it became impossible to determine the composition of departing swarms, but it seems certain that *mexicanus* adults from many localities must have

joined the migrants. It is known that the more mature grasshoppers were continually dropping out, and if their numbers had not been replaced swarms could not have progressed for hundreds of miles without marked decreases in size.

There were many general reports that 1938 flights occurred on very warm days and that swarms were carried by prevailing winds. Definite data on the effect of wind direction and temperature were obtained by Munro and Saugstad (7). On July 17, 1938, they released about 100,000 marked grasshoppers, most of which were *mexicanus*, in southeastern North Dakota. During the next 29 days specimens were recovered in northern and northwestern parts of the State, some of them having traveled at least 215 miles. Winds from the south and southeast prevailed during 18 days of the period, and the average daily maximum air temperature was 89.9° F. For the remaining 11 days, which included 7 in July and 4 in August, prevailing winds were from the north and northwest and the average daily maximum temperature was 79°, or 10.9° cooler than when the wind was blowing from the south and southeast.

The prevailing wind directions and the average daily maximum temperatures for Huron on the eastern edge of the South Dakota flight zone from July 1 to August 14, when most of the flights from that area took place, are shown in table 2.

TABLE 2.—*Prevailing wind directions and average daily maximum temperatures at Huron, S. Dak., from July 1 to August 14, 1938*

Wind direction	Duration	Average daily maximum temperature
	Days	° F.
North.....	10	87.3
Northeast.....	1	84.0
East.....	1	78.0
Southeast.....	11	93.0
South.....	8	98.3
Southwest.....	5	89.8
West.....	5	89.2
Northwest.....	4	86.7

The prevalence of winds from the south and southeast on 19 days when temperatures were highest and flights were most likely to occur explains their general direction to the north and northwest. This does not mean that individual swarms traveled in only one direction. Swarms in South Dakota traveling northwest toward southeastern Montana could have been diverted to Wyoming by northerly winds or to western and central North Dakota by winds from the south or southwest.

Swarms of *mexicanus* from the source in north-central South Dakota and south-central North Dakota, flying north and northeast, reached the northeastern counties of North Dakota in the last 2 weeks

of July and moved into northwestern Minnesota and south-central Manitoba in the first 2 weeks of August.

South-central Manitoba municipalities bordering Rolette, Towner, Cavalier, and Pembina Counties in North Dakota were most heavily invaded. Severe to very severe infestations, attributed to flights, were found throughout the Pembina River system in surveys conducted by Canadian entomologists.

Other swarms traveled across northwestern North Dakota and entered southwestern Manitoba and southeastern Saskatchewan. Flights reached halfway to the international boundary by July 10. Canadian entomologists reported heavy flights into southwestern Manitoba on July 15, 23, 25, 29, and August 1. These flights progressed about 100 miles farther north during the first 2 weeks in August and left severe infestations of adults in the southwestern municipalities of the Province. The swarms entering southeastern Saskatchewan at the same time continued northward for about the same distance.

Swarms moving through southwestern North Dakota entered Montana on July 1 and produced very severe infestations in the eastern counties. Their progress across eastern Montana has been described by Mills (6), whose map is reproduced in figure 2.

Some of the swarms that entered eastern Montana continued their flights into Saskatchewan. They began crossing the Canadian border on July 17, and when flights terminated about August 15 they had reached the South Saskatchewan River Valley.

The swarms that entered Saskatchewan from Montana and North Dakota left moderate to very severe infestations in all the municipalities south of the South Saskatchewan and Qu'Appelle Rivers except in the southwestern corner of the Province.

The distance to the South Saskatchewan River from the place the flights started in South Dakota is approximately 575 miles, which is the greatest known distance traveled by swarms in 1938.

Data on distances flown by *merriami* adults in 1938 have been reported by Willis (12), who released 18,500 painted grasshoppers at three points in eastern Montana and one point in northwestern North Dakota during the flight period of July 19-24. Fourteen were recovered 30 to 230 miles from the points of release; 8 traveled northwest, 3 northeast, 2 southwest, and 1 north. Three were recovered in southern Saskatchewan 230, 200, and 180 miles from release points, after 15, 16, and 9 days, respectively. One specimen released at Wibaux, Mont., was captured the next day 30 miles to the northeast at Beach, N. Dak. Another, released at Williston, N. Dak., was taken 6 days later 200 miles to the southwest at Jordan, Mont.

Large swarms of *merriami*, presumably originating in north-central South Dakota, came into the Black Hills of western South Dakota and the northeastern counties of Wyoming during the first 2 weeks of July and were followed by smaller swarms on favorable flying days during the remainder of the month. These grasshoppers did not continue across Wyoming, but flew south to settle in large numbers throughout the Black Hills, the extreme eastern counties of Wyoming, and in smaller numbers in the extreme western counties of Nebraska.

The wind-direction data for Huron, S. Dak., presented in table 2 show only 2 days from July 1 to August 14 when the wind was from the east or northeast. It therefore does not seem likely that swarms

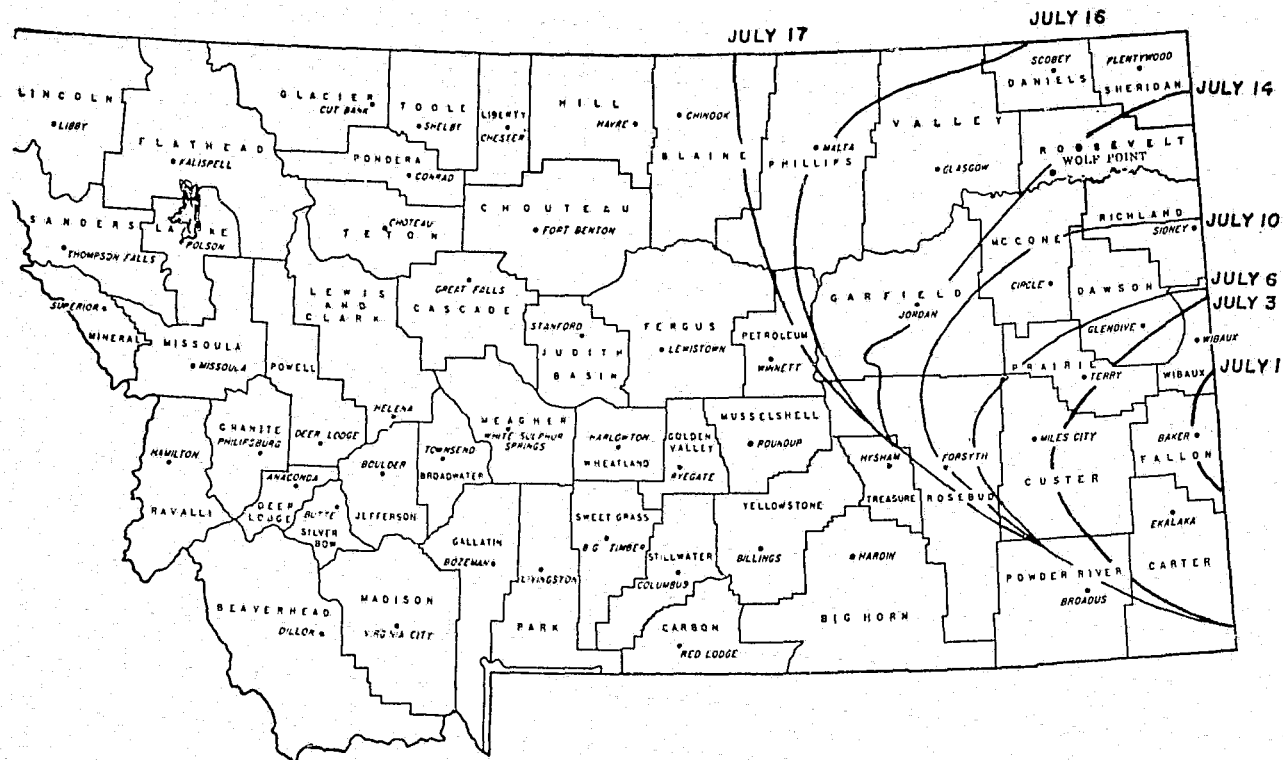


FIGURE 2.—Progress of invading swarms of *mexicanus* across eastern Montana in July 1938 (after Mills 6).

entering the Black Hills, eastern Wyoming, and western Nebraska could have followed a direct westerly or southwesterly route. It seems more probable that they had been carried from north-central South Dakota to southwestern North Dakota on winds from the southeast and had then encountered northerly winds, which diverted them to the south.

Apparently few large swarms traveled any great distance directly east or south from their origin. No reports of flights in these directions were made by field supervisors of the Federal grasshopper control project or by entomologists in the States that would have been invaded if such flights had extended beyond their borders. At Huron, S. Dak., there were 8 days favorable for flight to the east and south from July 1 to August 14. The wind was favorable from the west on 3 days and from the north on 5 days when maximum daily temperatures ranged from 90° to 98° F.

That some flights to the east and south did occur, at least within South Dakota, is indicated in correspondence from H. C. Severin, entomologist for the South Dakota Agricultural Experiment Station.

Since the egg survey in the fall of 1938 did not show any heavy infestation of *mexicanus* eggs directly traceable to eastern or southern flights from north-central South Dakota, it seems evident that they were of minor importance compared with flights to the north, northwest, and west, which were followed by heavy egg deposition in the areas where gravid females finally settled.

Changes in Local Populations Due to Flights

Only a few estimates of changes in local *mexicanus* populations due to 1938 flights are available. Localities in the path of sustained mass flights underwent repeated shifts in numbers. Normal and light infestations of 1 to 5 per square yard were often suddenly increased to very severe infestations of 32 or more by the first invading swarms. If conditions were favorable for flying, these swarms moved on within a few days, leaving only slight increases over the original numbers. Later invading and departing swarms also caused local populations to fluctuate throughout the flight period. The permanent increases were greatest near the end of the flight, when many females ceased flying and began egg laying.

One of the authors spent several days in eastern Montana when the first flights of 1938 were in progress. Grasshopper infestations before invasion were noneconomic, and crops were good. Incoming swarms were observed in the late afternoon settling in fields of well-headed wheat in numbers sufficient to bend many stems to the ground and populate entire fields with several hundred grasshoppers per square yard. If such dense swarms moved on the next day, damage to crops was slight; if they remained for several days or were followed immediately by other incoming swarms, crops were often completely destroyed.

Changes in populations on study areas were recorded at Mandan, Dickinson, and Beach in southwestern North Dakota. These areas were 4 miles long by 2 miles wide, and included farm, pasture, and range lands. They were repeatedly invaded by swarms of *mexicanus* from the south and southeast during July. The observations are

summarized in table 3. These figures represent average populations for the entire 8 square miles of each area, but do not show the heavier concentrations in small grains, which were almost completely destroyed at Dickinson and suffered losses of 50 percent at Beach and 33 percent at Mandan. Before the flights the population on the Beach area was approximately half as large as at Dickinson and Mandan, but when they were over residual populations were nearly the same on all areas.

TABLE 3.—Changes in grasshopper populations in southwestern North Dakota due to flights of *mexicanus*, 1938. Average number per square yard

Location	Before flights (June 28-30)	During flights (July 15-20)	After flights (August 1-3)
Mandan.....	4.2	10.0	5.6
Dickinson.....	4.4	18.0	5.4
Beach.....	2.3	12.0	5.0

Mills (6) published maps showing increases in grasshopper numbers in eastern Montana counties due to flights of *mexicanus* during the first 2 weeks of July 1938. His data are summarized in table 4. Population figures are based on counts made in habitats where grasshoppers were most likely to be found.

TABLE 4.—Changes in grasshopper populations in eastern Montana counties due to flights of *mexicanus* during the period July 1-14, 1938. Average number per square yard

County	Before migration (June 25-30)	After migration (July 12-14)	Increase
Carter.....	10	12	2
Powder River.....	3	6	3
Fallon.....	4	9	5
Wibaux.....	2	16	14
Custer.....	2	30	28
Dawson.....	10	47	37
McCone.....	3	54	51
Prairie.....	3	55	52
Richland.....	3	61	58
Rosebud.....	9	64	55
Garfield.....	1	138	137

Egg Deposition

Some migrant females laid eggs during the last 2 weeks of July and the first 2 weeks of August, but peak egg laying did not begin until about August 15, after nearly all flights had ceased. Temperatures were above normal during August, September, and October, and egg

laying continued until October 20 in some localities. According to E. G. Davis (unpublished data), the main egg-laying period of *mexicanus* on the Mandan, N. Dak., study area extended from August 15 to October 20 in 1938 as compared with an average period of August 18 to September 30 from 1937 to 1943.

Since egg deposits on study areas at Mandan, Dickinson, and Beach, N. Dak., were more in line with adult numbers during flights than with smaller populations after flights were over, it seems certain that some migrant females laid eggs and then joined swarms that moved to other localities. The more usual thing was for gravid females to drop out of swarms and lay all their eggs in one locality. Consequently egg deposition in a locality was proportional to the number of females in the swarm that were ready for egg laying, being heaviest where the flight terminated.

In the fall of 1938 surveys were conducted to determine the habitats most commonly selected by migrant *mexicanus* females for egg laying. The results of such surveys in Montana, North Dakota, Nebraska, South Dakota, and Wyoming are summarized in table 5.

TABLE 5.—*Distribution of mexicanus eggs by habitat, fall of 1938 (from Shotwell 10)*

Habitat	Survey stops	Egg pods per square foot
	Number	Number
Cropped fields.....	323	1.1
Idle land.....	541	1.1
Open range.....	280	.3
Range within 1 mile of crops.....	414	.4

There were fewer pods per square foot in open range than in other habitats, but large numbers were sometimes found. Greatest numbers occurred where native grasses had been partially replaced by annual weeds, such as Russian-thistle and peppergrass. Heavy egg concentrations were sometimes found in compacted drift soil around sagebrush and cactus. Since the spots where large numbers were found comprised only a small portion of the total range acreage surveyed, the number found there did not materially increase the average for the open range. The large numbers found in weeds showed that very severe infestations might develop if the range became seriously depleted by drought, soil erosion, or overgrazing by livestock or grasshoppers.

An unusual habitat selected for egg laying by migrant females was discovered in the spring of 1939, when great numbers of nymphs were found in the river bottoms and breaks of the Missouri and Little Missouri Rivers in the badlands of western North Dakota. Few *mexicanus* nymphs were found in open grasslands where gramagrass was dominant, but many were found in mixed stands of bluestem, bluegrass, and needlegrass in and adjacent to patches of snowberries and rose bushes along dry creek beds, coulee bottoms, draws, and river bottoms. From 50 to 500 per square yard were common in the edges of brush and sur-

rounding grasses. Most of the infestation extended only a rod or two into the grasses, but often the nymphs were found all through the brush if it was not shaded by trees.

The close association of the nymphal infestations with patches of snowberry and rose bushes left no doubt that migrant females of the previous year had gathered there for egg laying. Previous to 1938 no such concentration of eggs in brush of any kind had ever been seen by persons with many years of experience in studying *melicampus* in the northern Great Plains.

Handford (3) reported a similar unusual concentration of eggs in the bottom lands of the Pembina River in southern Manitoba after swarms of *melicampus* from the United States had invaded that area in 1938.

Several reasons for the unusual concentrations of eggs in and near brush in coulees, draws, and river bottoms are suggested: (1) Females dropping out of swarms were heavy with eggs and were forced to deposit them at once in an area devoid of the cropped and idle land where eggs are usually laid in greatest numbers. (2) snowberry and rose bushes supplied green food and escape from high ground temperatures. (3) soil shaded by the brush was softer and more favorable for egg laying than surrounding ground, and (4) swarms remained settled for longer periods of egg laying because light winds needed to initiate flights were less frequent than on higher unprotected ground.

Egg laying by migratory swarms of *melicampus* in the United States was heaviest in the following areas: (1) Eastern Montana and western North Dakota; (2) northwestern Minnesota and northeastern North Dakota; and (3) southwestern South Dakota, northwestern Nebraska, and eastern Wyoming. In Canada egg laying was heaviest in southern Manitoba and southern Saskatchewan. The boundaries of the United States areas were determined by egg surveys in the fall of 1938 and nymphal surveys in the spring of 1939. In Manitoba and Saskatchewan these areas were based mainly on fall egg surveys. The areas shown in figure 1 represent only the known severe and very severe infestations, and their boundaries are only approximately correct. Severe infestations often gradually declined from one locality to another, so that it was difficult to establish a boundary between them and threatening infestations.

FLIGHTS IN 1939

The mass flights in 1939 are discussed by geographical areas in the United States where swarms of *melicampus* laid eggs in greatest numbers in 1938, as shown in figure 1.

The most data were obtained in eastern Montana and western North Dakota, because one member of the project was assigned to this area to study migratory populations throughout the season. Other members spent considerable time within and around the area in connection with other duties. Conditions in Montana were particularly favorable for studying flights. The boundaries of heavy egg deposition by 1938 swarms were better defined than in other areas, and the remainder of the State was so lightly infested that 1939 swarms could be easily spotted and followed from one locality to another.

One person was detailed to study flights in southwestern South Dakota, northwestern Nebraska, and eastern Wyoming, but he had less assistance than was available in the Montana-North Dakota area.

No special plans were made for studying flights in northwestern Minnesota and northeastern North Dakota. All data for this area were obtained from State grasshopper-control leaders.

Information on flights from the United States into Alberta, Saskatchewan, and Manitoba was obtained from Canadian entomologists.

Seasonal Development

Eastern Montana and Western North Dakota

The main hatch started on May 5, 2 weeks earlier than normal, and was 90 percent complete by June 1. Nymphal development was retarded by cool, wet weather during the third week in May, but no reduction in numbers was noted. The first adults were seen the first week in June, and by July 7 over 90 percent of the population was adult.

Northwestern Minnesota and Northeastern North Dakota

Hatching started the first week in May and was 90 percent complete by June 1. The first adults were seen on June 3, and by July 15 over 90 percent of the population was in the adult stage.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Hatching began the last week in April, was general during the first week in May, and was practically complete by June 1 except in the Black Hills, where hatching and nymphal development were 7 to 10 days later. The first adults were seen on May 30. By July 1 from 75 to 95 percent of the population were adults except in the Black Hills, where 1 to 15 percent were adults.

Where Greatest Numbers of Nymphs Hatched

Eastern Montana and Western North Dakota

As predicted by the egg survey in the fall of 1938, grasshoppers hatched in large numbers in idle land, small grains, and field margins. The maximum numbers per square yard were 140 in field margins, 115 in idle land, and 65 in small grains.

In the river bottoms, draws, and coulees of the Yellowstone, Missouri, and Little Missouri Rivers from 50 to 500 nymphs per square yard were common in and around clumps of rose and snowberry bushes.

In rangeland more grasshoppers hatched than was indicated by the fall egg survey. Few were found in good stands of gramagrass and sedge, which are dominant over much of the range, but very severe infestations occurred where some of these plants had been killed and replaced by weeds because of overgrazing and drought. Weed patches of less than 1 square yard frequently harbored several hundred nymphs, and in larger patches there were sometimes as many as 1,000 per square yard.

Nymphs were much more abundant in western wheatgrass and needlegrass than in gramagrass and sedge. Infestations were particularly severe, 50 to 500 per square yard, in creek bottoms and draws

where these grasses had remained green and attractive for egg laying during the 1938 flight period.

Large numbers also hatched in drift soil around sagebrush and pricklypear cactus. These habitats comprised only 10 to 25 percent of the vegetative cover, but they produced enough young grasshoppers to cause heavy infestations of entire sections of rangeland.

Field men making frequent observations in eastern Montana estimated that the average nymphal population in approximately 8 million acres of rangeland in that area was at least 50 per square yard.

Northwestern Minnesota and Northeastern North Dakota

Large numbers of grasshoppers hatched in small grains, alfalfa, cutover land, pastures, and in bottom land along the Red River. Average nymphal populations in various habitats were not reported, but extensive control operations were employed to protect crops.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Small grains were the most important crops and comprised the largest acreage of nymphal infestations. At their peak nymphs averaged 60 per square yard in fields and 500 in their margins. Small grains seeded in unworked stubble were more heavily infested than when planted in deeply plowed land. In weedy idle land and alfalfa populations were higher than in small grains, but infested acreages were smaller. Average numbers per square yard were 75 in idle land and 115 in alfalfa.

Heaviest concentrations of nymphs were found in the mountain hay meadows and pastures of the Black Hills, where they averaged 600 per square yard and frequently exceeded 1,000 per square yard. Rangeland was not heavily infested except in small areas adjacent to infested crops or idle land.

Damage by Nymphs and Their Food Preferences

Eastern Montana and Western North Dakota

Nymphal infestations in small grains were not so common as in other habitats, but when present they were usually very severe and destroyed most of the crop unless control measures were employed. Many grainfields not originally infested were repeatedly invaded by nymphal migration from heavily infested range and idle land, and some crops were destroyed in spite of several applications of bait.

Bluegrass was preferred to all other grasses and was the most severely injured. Little of it ever reached the flowering stage, and by the middle of June most of it was eaten to the roots. Western wheatgrass suffered about 50-percent foliage damage and almost complete loss of seed. Damage to needlegrass foliage and seed was slightly less than to western wheatgrass. Sedge foliage and seed heads were only slightly damaged. Gramagrass was injured the least of all the grasses. Its leaves often remained uneaten when grasshoppers had destroyed all other vegetation. Some of its early flower heads were eaten, but it blooms later than most grasses and by the time it was in full bloom nymphs had transformed to adults and had left the area.

Of the annual weeds, peppergrass and Russian-thistle were preferred to all others, but the latter was eaten readily only when newly

sprouted and a few inches in height. Dry Russian-thistle plants were eaten when no other food was available.

Sagebrush was frequently defoliated and the bark eaten, leaving only bare, dry twigs. The foliage of wild roses, rabbitbrush, and snowberries was eaten, and they were often stripped of their bark. Blooms of the pricklypear cactus were eaten almost as soon as they formed, and fleshy leaves were frequently so gorged out that they shriveled and turned black.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Small grains were favorite foods, and many fields of barley, oats, and spring-seeded wheat were completely destroyed. It was estimated that the harvest of small grains for the area as a whole was reduced 25 to 35 percent and that losses due to grasshopper damage would have been twice as large if control measures had not been employed.

Alfalfa was eaten more readily than sweetclover, and yields were reduced 10 to 15 percent. Timothy, crested wheatgrass, brome, and other mountain meadow grasses in the Black Hills were all so severely attacked that practically no hay was harvested.

Of the common range grasses, bluegrass, western wheatgrass, and needlegrass were preferred; gramagrass was seldom eaten. Damage to range was severe in spots, but averaged only 10 to 20 percent.

Weeds most commonly fed upon were Russian-thistle, peppergrass, lambsquarters, sunflowers, and dock. Gunweed and skeletonweed remained uneaten even when other food was scarce.

Sagebrush, rose bushes, and snowberry often were fed upon and were sometimes stripped of foliage and bark.

Nymphal Migrations

Eastern Montana and Western North Dakota

Nymphs hatching from eggs laid by females in the 1938 flights showed a greater tendency to migrate than did nymphs in localities where flights had not occurred for several years. First-instar nymphs dispersed into surrounding vegetation without forming bands. Later instars frequently marched in bands in characteristic migratory fashion. Some bands moved from idle land and depleted range into small grains, and others left grainfields after they had destroyed the crops. Nearly all migrations were toward greener or more abundant vegetation, but sometimes they left fields where there was plenty of green food and moved to less favorable environments. The direction of migrations on level ground was generally upwind. In rolling terrain bands left ridges and slopes and moved to lower, more nearly level land without regard to wind direction. Slowly flowing small streams did not retard their progress or change their course. The young grasshoppers merely hopped into the water, swam rapidly across, and continued on their way.

Migrations started when air temperatures first ranged from 68° to 75° F. and the sky was clear, and stopped when the temperature dropped below 68° or the sky became overcast. Bands traveled at the rate of about 1/10 mile per hour.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Migrations of young grasshoppers were common on clear days when the temperature was 68° F. or higher. Movements were mostly from idle land and field margins to small grains and alfalfa. Most of the migrations observed were upwind toward more succulent or more abundant food. Marching bands of *mexicanus* were not joined by other kinds of immature grasshoppers, even when they passed through places where other species were numerous. A few *mexicanus* bands were interspersed with newly transformed adults of the same species.

Dates, Locations, Directions, and Intensities of High Flights

Eastern Montana and Western North Dakota

Flights became frequent as soon as 25 to 50 percent of the *mexicanus* populations became adult. Less time was spent in preliminary low milling flights than in 1938. Newly transformed adults seemed to have inherited a migratory urge and took to the air whenever temperature and winds were favorable, even when favorite foods and shade were available.

The first flights observed in Montana were in Rosebud County on June 20. First flights in North Dakota were seen in McKenzie, Stark, and Mercer Counties on June 26-28. All of them were within the area of heavy egg deposition by 1938 swarms. Swarms continued to fly out of the area until July 20, when it became almost completely devoid of *mexicanus* infestations of economic importance. Swarms were sighted in adjacent previously uninfested localities during the last days of June and continued to move in various directions on favorable days throughout July. Flights decreased rapidly after August 1, and the last one of any importance was seen on August 22.

During the flight period 451 detailed observations were recorded on flights in progress within the zone where they originated or the localities that they invaded. This does not mean that 451 separate swarms were seen. Different personnel sometimes observed the same swarm on one day in one locality and on other days as it moved to another locality. The location, direction, and intensity of the flights observed are shown in figure 3.

Of the total number of observations in this area, 24 percent were classified as heavy, 16 percent as moderate, and 60 percent as light. Twelve percent occurred during the last 10 days in June, 83 percent during July, and 5 percent during August. Seventy percent of all heavy and moderate flights took place between June 26 and July 15. No heavy flights and only four moderate flights were observed after August 1.

Winds were variable during the flight period and swarms were carried in all directions. With one exception, which might be explained by possible difference in direction of upper and lower air currents, all flights, except those classified as milling, were in the same direction as the low-level prevailing wind. Of the observed flights to various points of the compass, the directions were as follows:

	Percent		Percent
North.....	6	Southwest.....	8
Northeast.....	10	West.....	20
East.....	7	Northwest.....	21
Southeast.....	12	Without direction (milling).....	11
South.....	4		

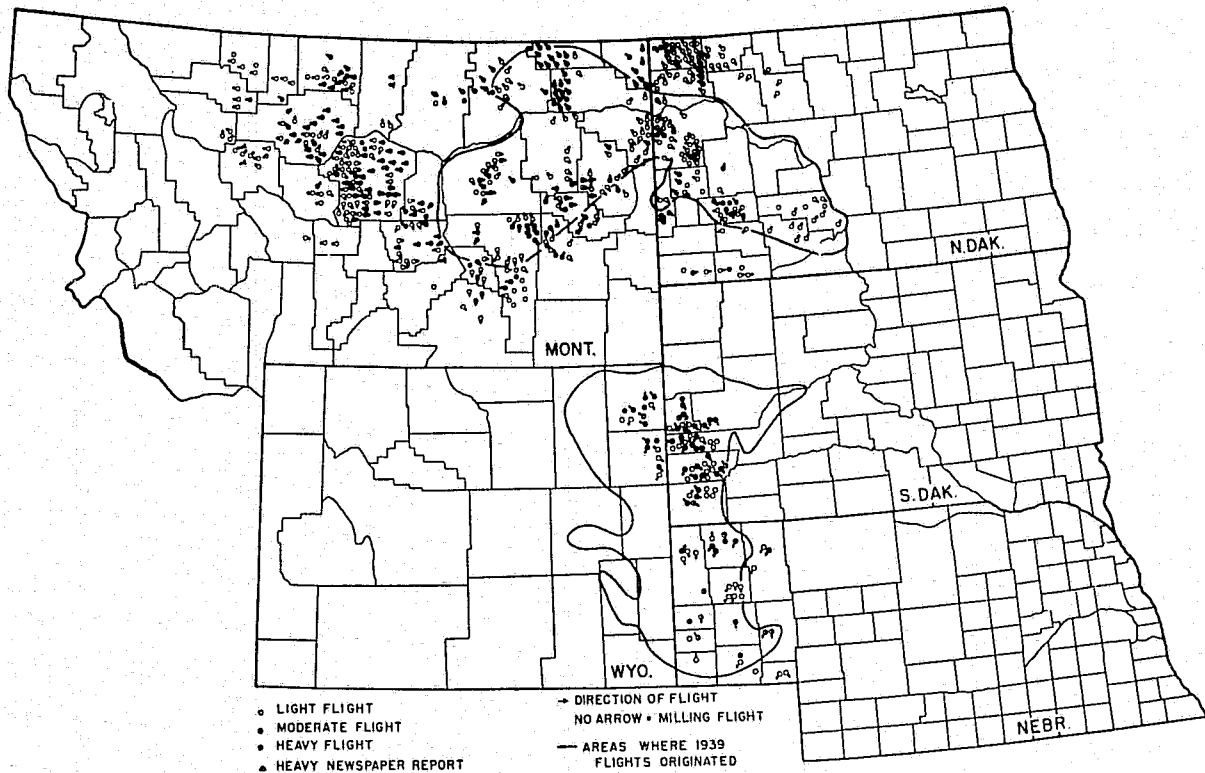


FIGURE 3.—Flights of *mexicanus* observed and recorded in 1939.

Seventy percent of all heavy flights, those most important in populating previously uninfested areas, were toward the west or northwest. In Montana the progress of heavy flights across the north-central part of the State was easily followed for approximately 235 miles from the starting point in eastern Montana. The invading swarms failed to reach the foothills of the Rocky Mountains, the western limits being the eastern parts of Teton, Pondera, and Toole Counties. The Highwood, Little Belt, and Big Snowy Mountains in Cascade, Judith Basin, and Fergus Counties roughly delimit the southern boundary of the heavily invaded area. The progress of swarms as they moved across north-central Montana is shown in figure 4.

According to Canadian entomologists, *mexicanus* swarms started crossing the Montana-Canadian border in the southeast corner of Alberta on July 9, and by July 17 had reached the South Saskatchewan River Valley, where flights terminated. This part of Alberta, like north-central Montana, had had no economic infestation of *mexicanus* before the flights, and the progress of swarms could be easily followed by the sudden increases in populations left in their path. From where flights originated in Montana to where they terminated in Alberta is approximately 300 miles, the longest known distance traveled by 1939 swarms. This is approximately half as far as some swarms traveled in 1938.

Heavy flights from Montana also entered southwestern Saskatchewan on July 9, the same day that southeastern Alberta was first invaded. Previously there had been no economic infestation of *mexicanus* in this part of Saskatchewan, but by July 27 approximately 3,500 square miles had become threateningly to severely infested. Most of the flights into this area terminated before or on reaching the South Saskatchewan River about 110 miles north of the international boundary, but several were observed 50 miles farther north.

Southeastern Saskatchewan was also invaded on July 9 by swarms from northeastern Montana and northwestern North Dakota. These flights continued on favorable days during the rest of July and extended to the Qu'Appelle River approximately 100 miles north of the international boundary. Increases in local populations due to flights were not so well distributed or so large as in southwestern Saskatchewan, but threatening to severe infestations of adult migrants were common throughout the southeastern corner of the Province. This part of Saskatchewan was invaded by flights of *mexicanus* from the United States in 1938, and economic infestations of this species were present before the 1939 flights began. Some of the 1939 flights may have originated within the Province, but it is certain that many of them came from Montana and North Dakota.

In Montana and western North Dakota the heaviest and most frequent flights to the west, northwest, and north were followed most closely by field personnel. Some flights toward other points of the compass were observed within the zone of origin, and several were seen in adjacent territory, but they were not followed in enough detail to chart their progress and little is known about their final destination. It seems probable that flights heavy enough to cause a sudden increase

in local infestations and injure crops would have been reported by landowners or county agricultural agents. Since this was not the case, it is assumed that flights other than those to the west, northwest, and north were of minor importance.

Northwestern Minnesota and Northeastern North Dakota

It appears that light flights began in both States about June 25, when approximately 10 percent of the *mexicanus* population was adult. The first heavy flights reported occurred in the Red River Valley on July 9, when 80 percent of the population was adult. Heavy flights were reported in Marshall, Kittson, and Polk Counties in Minnesota and in Pembina, Walsh, and Grand Forks Counties in North Dakota from July 16 to 23. Some were from North Dakota into Minnesota and others in the opposite direction. There were heavy flights from Grand Forks County into Marshall and Polk Counties from August 8 to 16. Moderate swarms flying east and northeast on August 19, 20, 21, and 24 settled in previously uninfested sections of Marshall, Polk, Pennington, Red Lake, Mahanomen, and Becker Counties in Minnesota.

Flights into south-central Manitoba from Rolette, Towner, Cavalier, and Pembina Counties in northeastern North Dakota were frequent during July and August. They began on July 10, when swarms from Cavalier County were seen crossing the international boundary along the Pembina River. Moderate to severe infestations resulting from eggs laid by 1938 migrants from North Dakota were present in the Canadian section of the Pembina River system before flights started. Heavy flights from North Dakota to the north and northwest on July 14, 18, 19, and 20 caused previous moderate and severe infestations to become very severe and greatly increased the size of the area infested. By July 25 flights had extended slightly beyond the Pembina River drainage to the north and northwest and were entering districts that were previously only lightly infested. Increases of 15 grasshoppers per square yard were reported in some of the newly invaded localities. Few flights were seen after August 20. By that date swarms had progressed northward to the Assiniboine River and northwestward across the Souris River to the Saskatchewan border.

A heavy flight from Manitoba into North Dakota was observed in Rolette County on August 13.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

The first flights observed in Nebraska were on June 21, in Wyoming on June 22, and in the Black Hills of South Dakota on June 26. Populations of *mexicanus* at this time were 15 to 50 percent adult. All heavy flights originated within the zone of heavy egg deposition by swarms that came from north-central South Dakota in 1938. Their sources were in the northern half of the Black Hills in Lawrence and Pennington Counties, South Dakota; Box Butte, Sioux, Morrill, and Scotts Bluff Counties, Nebraska; and eastern Wyoming.

From the first observed flight on June 21 to August 22 when flights were over, observations were made at 102 places within the zone where they originated, as shown in figure 3. Of the total number of high flights observed in this zone, 23 percent were heavy, 32 percent were moderate, and 45 percent were light. No heavy flights were seen before June 27 or after July 17. Eighty percent of all flights observed

occurred during this period. Only 7 moderate and 10 light flights were seen between July 18 and August 22.

Thirty-four flights were classed as milling. They took place on hot days when winds were very light, intermittent, and variable in direction. During milling flights local populations shifted constantly, and in some of them grasshoppers could be seen taking off and landing in about equal numbers. At such times they tended to concentrate in spring wheat, oats, and barley, which offered an abundance of green food.

When light winds blew steadily in one direction, swarms took to the air, even when green food was plentiful, and traveled with the prevailing wind. The numbers of flights observed traveling in various directions were as follows: North 3, northeast 2, east 0, southeast 18, south 10, southwest 11, west 9, and northwest 15. The flights to the west and northwest attracted no attention outside the zone of origin, and no heavy egg deposits could be definitely attributed to them. The 5 flights going north and northeast likewise attracted no attention. Flights to the southeast, south, and southwest represented 51 percent of all the directional flights observed. These flights were seen as they progressed through the southern sections of the zones of origin, where some of the swarms settled for egg laying; others kept on moving and invaded new territory to the south.

Swarms carried to the south and southwest invaded the irrigated sections of Colorado along the eastern slope of the Rocky Mountains. Flights into this area were noticed from June 27 to July 21. Large increases in *mexicanus* numbers were reported in irrigated crops from Fort Collins in Larimer County to Boulder in Boulder County and smaller increases as far south as La Junta in Otero County.

Swarms traveling south entered northeastern Colorado, where they increased infestations in irrigated crops in the South Platte River Valley. Other swarms settled in dry rangeland south of the river and later moved westward to the already invaded irrigated section from Fort Collins to Boulder.

Swarms flying to the southeast were seen in southwestern Nebraska, and some of them may have continued into western Kansas, where heavy flights were reported during the first 10 days of July. Since large numbers of *mexicanus* were present in Kansas before flights occurred, it could not be definitely determined whether they were of local origin or from distant sources.

Changes in *mexicanus* Populations Due to Flights

Montana

Data on changes in *mexicanus* populations due to flights were obtained more easily in Montana than in other States. Previous to flights *mexicanus* numbers were extremely low in central and north-central Montana, and any sudden increases due to flights from the very heavily infested area in eastern Montana were easily recognized.

Estimates of the numbers of *mexicanus* adults before, during, and after flights were obtained by establishing stations in infested places in eastern Montana where flights originated, between zones where they originated and where they terminated, and in north-central Montana where they terminated. The changes in populations at some of these stations are shown in table 6.

TABLE 6.—Numbers of mexicanus adults per square yard before, during, and after flights at stations within the three Montana zones, 1939

Zone of flight and county	Habitat	Observation station	Before flights	During flights			After flights
				June 30	July 1-7	July 8-10	July 24
Origin:							
Garfield-----	Range-----	1	June 25, 60-----	25	20	5	2
		2	June 25, 45-----	30	-----	3	0
		3	June 28, 30-----	20	-----	20	2
		4	July 1, 50-----	-----	40	35	2
Petroleum-----	do-----	6	June 3, 25-----	-----	25	25	1
Rosebud-----	do-----	8	June 24, 30-----	25	20	15	2
		10	June 28, 30-----	30	15	10	0
				July 10-13	July 22-26	-----	Aug. 21-22
Between origin and end:							
Petroleum-----	Range-----	11	June 26, 1-----	10	4	-----	3
Musselshell-----	Oats-----	13	June 25, 1-----	9	12	-----	3
Fergus-----	Alfalfa-----	14	July 1, 5-----	100	10	-----	3
	Flax-----	15	July 6, 0-----	4	25	-----	6
	Wheat-----	20	July 7, 4-----	100	45	-----	6
				July 13-15	July 21-22	Aug. 2-4	Aug. 17-19
End:							
Chouteau-----	Wheat-----	21	July 9, 2-----	12	15	15	5
Fergus-----	Flax-----	23	July 6, 0-----	4	25	35	3
Hill-----	Wheat-----	25	July 8, 1-----	20	25	10	5
	do-----	28	July 8, 0-----	15	30	8	4

In eastern Montana the numbers ranged from 25 to 60 per square yard before flights, dropped sharply as a result of flights during the first 10 days in July, and by July 24, when flights within the area were over, did not exceed 2 per square yard at any station.

At stations between the zone where flights originated and the one where they terminated the numbers before flights were noneconomic and did not exceed 5 per square yard at any station. During the flight period numbers increased and decreased erratically through a range of 4 to 100 per square yard. Larger numbers were often seen in fields not used as observation stations. Alternate arrivals and departures of swarms sometimes increased or decreased local populations by several hundred per square yard within a few days. Most of the migrants eventually moved on, and by the third week of August, when all flights were over, the average population, computed from observation at all stations, was 4.2 per square yard as compared with 2.2 before flights.

In north-central Montana where flights terminated, numbers before flights ranged from 0 to 2 per square yard with an average of only 0.8. Populations increased at all stations during July as a result of flights from the east and southeast and reached their highest numbers in late July and early August. On August 2-4 infestations ranged from 8 to 35 per square yard with an average of 17. There were no flights from the east and southeast after August 4, but light to moderate flights originated within the already invaded zone at irregular periods until August 22. These flights redistributed populations within the zone and extended its western boundary 25 to 40 miles. As a result of these changes and the dying of spent grasshoppers, populations on August 17-19 had declined to 4.2, which was still 3.4 more than before the zone was invaded.

The changes in populations shown in table 6 confirm the following conclusions drawn from observations of flights while they were in progress and of swarms after they settled for egg laying: (1) Flights from the zone of origin reduced populations within it from very severe to noneconomic infestations; (2) intermittent flights between the zone of origin and the area where they terminated resulted in sharp temporary increases in local populations, but when flights were over, numbers were only slightly higher than before flights; and (3) in the zone where flights terminated previously noneconomic infestations increased to severe infestations and remained in this category for several weeks after the last flight.

During the second week in July, 15 observation stations were selected in Glacier, Pondera, Teton, and Cascade Counties at points 40 to 50 miles west of the terminal zone, at that time heavily populated by *meiicenus* migrants. The invaded zone expanded slightly to the west after the middle of the month, but no flights were seen at or west of any of the new stations and no significant increases were recorded. Average numbers of *meiicenus* adults per square yard were as follows: 0.5 on July 14, 0.4 on July 20, 1.4 on August 3, and 1.3 on August 17. The slight increase may have been due to stray migrants from the heavily infested zone.

These estimates are nearly the same as those recorded before flights in the intermediate zone in Petroleum, Musselshell, and eastern Fergus Counties and in the terminal zone in Chouteau, Hill, and western

Fergus Counties. All of them show the extremely low level in central and north-central Montana counties before they were invaded by swarms from eastern Montana. Low numbers also prevailed in eastern Montana just before it became heavily populated by migrants from South Dakota in July 1938 (see table 4, p. 11).

It is evident that natural factors were holding local populations to noneconomic numbers in Montana during both years and that no severe outbreak would have occurred except for the mass migrations from other States.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Flights out of this area did not drain it so completely of *mexicanus* adults as they did eastern Montana, but nearly all very severe and severe infestations were reduced to threatening or light (table 7).

Flights from one locality to another within the zone of origin sometimes caused increases of 10 to 50 grasshoppers per square yard (table 8). Most of these swarms moved on again within a few days. Increases due to flights were most common in northwestern Nebraska.

Reliable data on increases in numbers caused by swarms after they left the zone of origin are available for only one locality. In the vicinity of Fort Collins, Colo., populations in irrigated crops were very low before flights and only about 40 percent of the grasshoppers were *mexicanus*. A survey of this locality on July 21 after flights were over showed that *mexicanus* comprised 95 percent of the populations, and the following numbers per square yard were recorded: Alfalfa 47, barley 30, and oats 20.

Crops Damaged by Adult Migrants

North-Central Montana

The areas in eastern Montana invaded by 1938 flights were predominantly rangelands, and there were few chances for swarms to choose between range plants and crops. The new districts invaded in 1939 included large acreages of wheat, barley, oats, flax, alfalfa, and sweetclover. Swarms tended to settle in these crops in preference to surrounding rangeland.

Crop injury was comparatively light in the intermediate zone, where swarms settled for a few days and then moved on. In Blaine, Chouteau, Fergus, Hill, and Liberty Counties, where flights terminated, crop injury was frequently severe in spite of repeated baitings. Immature small grains were stripped of their foliage, and heads of ripening grain were eaten or cut off. Flax bolls were cut off, and new growth in recently cut alfalfa fields was seriously injured. Harvesting in late July and early August saved many of the crops. Successive observations at stations within the 5 counties showed crop damage by adult migrants to be as follows: Wheat 15, oats 7.5, flax 10, and alfalfa 10 percent. There was practically no damage to range vegetation.

Northwestern Minnesota and Northeastern North Dakota

As in Montana, migrants settled in small grains, flax, alfalfa, and sweetclover in preference to range vegetation. Severe damage was prevented by extensive baiting operations and early harvesting.

TABLE 7.—Numbers of mexicanus adults per square yard before, during, and after flights at stations within the zone where flights originated, 1939

State and county	Habitat	Observation station	Before flights	During flights	After flights
Nebraska:					
Box Butte	Wheat	1	June 16, 100	July 5, 35	July 20, 25.
		2	June 16, 50	July 5, 5	July 20, 1.
	Barley	3	June 16, 75	July 5, 40	July 20, 3.
Kimball	Wheat	4	June 30, 50		July 19, 3.
Sioux	Idle land	5	June 17, 50	June 30, 10	July 20, 10.
South Dakota:					
Custer	Range	6	June 17, 30		July 21, 2.
		7	June 16, 35		July 13, 5.
Lawrence	Hay meadow	8	June 21, 150		July 14, 15.
			June 21, 400		July 14, 20.
Pennington	do	9	June 21, 150		July 14, 20.
Wyoming:					
Crook	Wheat	10	June 26, 25		July 14, 5.
Converse	Wheatgrass	11	June 27, 60		July 18, 8.
Goshen	Idle land	12	June 27, 40		July 18, 3.
Platte	Wheat	13	June 28, 75	July 7, 10	July 19, 1.
	Barley	14	June 28, 75	July 7, 35	July 19, 10.
Weston	Wheat	15	June 26, 100		July 15, 5.
Niobrara	Rye	16	June 27, 20	July 7, 25	July 18, 3.

TABLE 8.—Numbers of mexicanus adults per square yard before and after flights at stations in northwestern Nebraska, 1939

County	Habitat	Observation station	Before flights	After flights
Sioux.....	Wheat....	1	June 28, 5....	July 3, 15.
Dawes.....	do.....	2	June 28, 2....	July 3, 25.
Scotts Bluff.....	Alfalfa....	3	June 28, 8....	July 4, 36.
Morrill.....	do.....	4	June 29, 2....	July 12, 12.
Kimball.....	Wheat....	5	June 29, 3....	July 5, 50.
Cheyenne.....	Oats.....	6	June 29, 2....	July 5, 25.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Green crops were eaten in preference to range plants. Early harvesting of small grains plus a well-organized control program prevented serious crop damage. Increased damage due to flights within the zone of origin was estimated as 10 percent for small grains and 5 percent for alfalfa. Damage by migrants was less than expected because of the tendency of swarms to keep moving and eventually leave the zone. This was in marked contrast to the behavior of the swarms that entered the zone in 1938, which caused severe damage to crops wherever they settled for egg laying.

Only a few estimates are available on crop damage by migrants after they left the zone of origin, but it is known that they injured crops in the southwestern corner of the Nebraska Panhandle and in northeastern Colorado. The increased damage due to flights into Kimball, Cheyenne, and Deuel Counties in the Nebraska Panhandle was 25 percent in small grains, 15 in alfalfa, and 12 in corn. Similar estimates for damage caused by flights into northeastern Colorado were 15 percent in alfalfa, 5 in small grains, and 5 in corn. Damage in both areas would have been much greater if control measures had not been employed.

Ovarian Development and Time of Egg Laying

Eastern and North-Central Montana

In Montana ovarian development was followed throughout the flight period. Observations were made at 134 stations within the zone in eastern Montana where flights originated, 33 in the intermediate zone which grasshoppers passed through before laying many eggs, and 97 in the zone where they deposited the most eggs. At each station the contents of the abdomens of 5 to 10 females were removed and examined. The degree of ovarian development was roughly classified as follows: None, if the eggs were not visible in the oviducts; slight, if they were visible but less than one-fourth of full size; moderate, if they were one-fourth to three-fourths of full size; and mature, if three-fourths to full size.

The progress of ovarian development in the three zones is shown in table 9.

TABLE 9.—Percentage of eggs of *mexicanus* flight females in different degrees of development in three Montana zones, 1939

Period	Zone of origin			Intermediate zone		Zone of heavy egg deposition	
	None	Slight	Moderate	Slight	Moderate	Moderate	Mature
June 20-26	80	20		100			
June 27-July 3	54	46		87	13		
July 4-10	38	48	14	50	50	100	
July 11-17				50	50	72	28
July 18-24				80	20	70	30
July 25-31					100	78	22
Aug. 1-7						64	36
Aug. 8-14							
Aug. 15-21						51	49
Aug. 22-28						15	85

No females with mature eggs were found within the zone where flights originated, an indication of almost complete exodus of *mexicanus* shortly after reaching the adult stage. Females with moderate ovarian development were found in the intermediate zone in increasing numbers from June 27 to July 31, but none were found with mature eggs. This seems to explain the extremely low egg populations found in the intermediate zone in the fall of 1939. Females with mature eggs were found in the zone of heavy egg deposition on July 11-17. This was only a few days after swarms first arrived and about 3 weeks after flights started in eastern Montana. The percentage of females with mature eggs increased to 36 by August 1-7, 49 by August 15-21, and 85 by August 22-28.

Eggs of flight females in both the intermediate zone and the zone where they settled for egg laying were more fully developed than those of nonflight females in noninvaded counties nearby.

Mating became general by the last week in June and continued throughout the summer. Mating occurred from early morning until late evening over a temperature range from 68° to 105° F., but most commonly from 10 a. m. to 3:30 p. m. between 75° and 95°.

In the heavily invaded counties of north-central Montana egg laying was observed on July 15, within a few days after the arrival of the first swarms. Heavy egg laying was in progress by August 1, continued until September 15, and then fell off rapidly as the adults died in late September and early October. Egg surveys made in 30 fields showed 0.6 egg pod per square foot from August 15 to 22 and 1.15 from September 20 to 30. This indicates that approximately half of the eggs were laid by August 15-22. A third survey in November showed no increase over the September counts.

Egg deposition was observed throughout the temperature range of 72° to 100° F. and occurred most frequently between 10 a. m. and 4 p. m.

Northwestern Minnesota and Northeastern North Dakota

No observations on ovarian development were made. Oviposition was first observed on July 11, became general by July 20, continued heavy until September 1, and was practically complete by September 15.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

In numerous comparisons throughout the area from June 21 to July 15, egg development in flight females was invariably more advanced than in nonflight females. From 50 to 75 percent of the flight females carried moderately to fully matured eggs as compared with only 10 percent in nonflight females.

Egg deposition began the last week in June, increased slightly early in July, but did not become general until July 15, when it was estimated that 25 percent of the *musicans* females were ready to lay eggs. Heavy egg laying continued through the remainder of July and all of August.

Areas Where the Most Eggs Were Laid

North-Central Montana

Eggs were laid in greatest numbers in and around the cropped fields where migrants congregated when flights terminated. Habitats favored for egg laying were winter and spring wheat, flax, alfalfa, field margins, roadsides, and weedy idle land. Spring and winter wheat comprised the largest acreage in crops and was the greatest source of eggs. Weedy grain stubble contained more eggs than clean stubble. The number of egg pods per square foot in roadsides and field margins was about the same as in fields, an unusual finding. Few eggs were laid in rangeland and there were no concentrations of eggs in river bottom land and brushy draws, such as were found in western North Dakota and eastern Montana in 1939.

Eggs were deposited most heavily throughout the cropped sections of Blaine, Chouteau, Fergus, Hill, and Liberty Counties and in parts of Teton, Pondera, Toole, and Phillips Counties. The most heavily infested areas are shown in figure 1.

In the regular fall egg survey 1,938 samples were taken from 215 fields in the 5 most heavily infested counties. The average numbers of egg pods per square foot were as follows: Blaine 2.4, Chouteau 1.6, Fergus 1.7, Hill 7.1, and Liberty 1.4. The average for the 5 counties was 2.3 in fields and 2.8 in the margins. An average of 2.3 pods per square foot in large fields constitutes a severe infestation. The average of 7.1 found in Hill County was the highest for any county in the United States in 1939.

A special survey was conducted in November to determine the number of egg pods per square foot in the zone where flights originated, in newly invaded territory, and in localities slightly beyond the limits of the 1939 flights. The results of this survey are shown in figure 5.

Egg-pod infestations were about as would be expected from the adult populations shown in table 6. No eggs were found in Garfield County, out of which nearly all the adults flew before the females were ready for egg laying. Eggs were obtained at only one of the

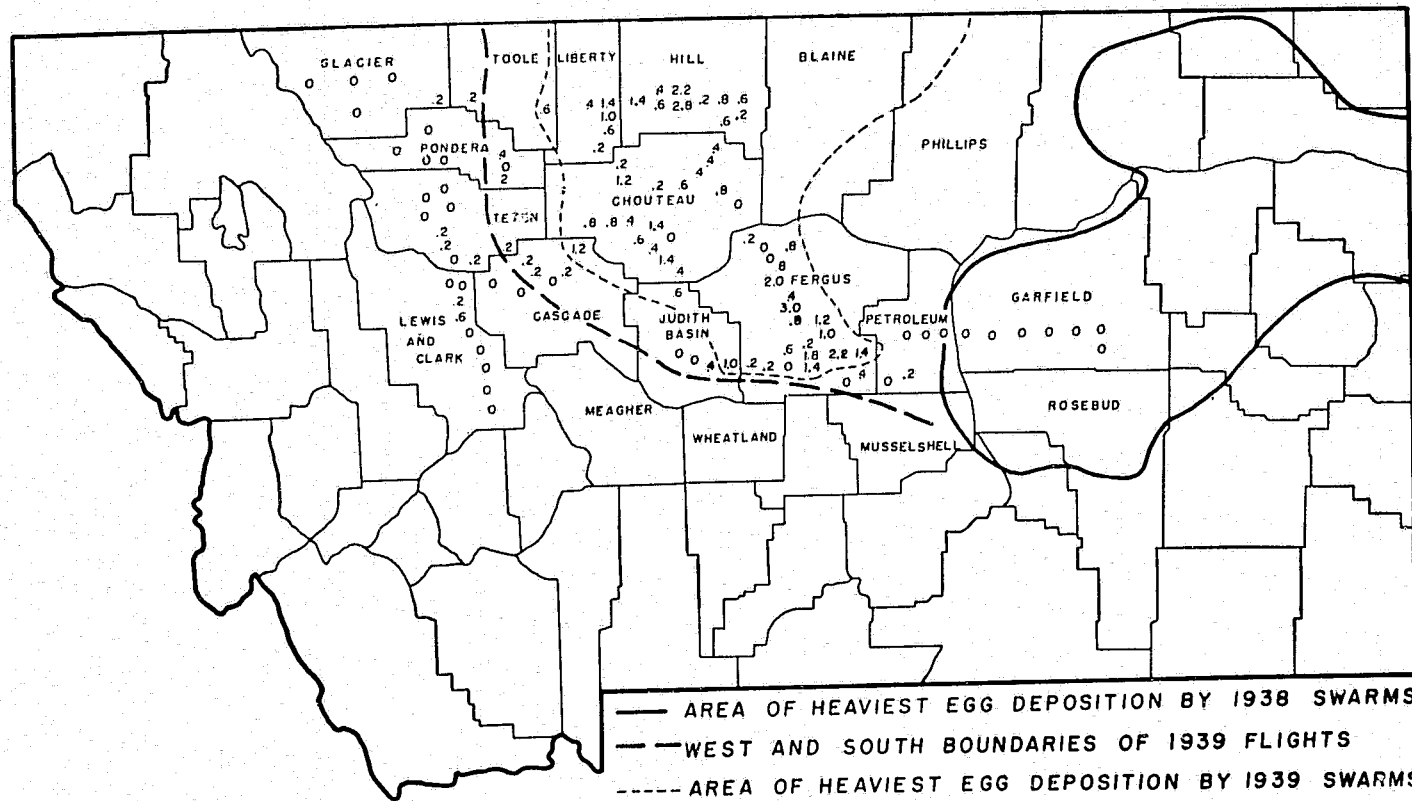


FIGURE 5.—Number of egg pods per square foot laid by *mexicanus* swarms in Montana in 1939 (special survey).

stations in Petroleum County, which was passed over but not heavily populated by flights. Egg counts were high in Fergus, Hill, Chouteau, and Liberty Counties, where migrants settled in greatest numbers. Similar counts probably would have been obtained in the northern third of Blaine County if it had been included in the survey. The average number of egg pods per square foot dropped sharply in the zone between the most heavily invaded area and the western limits of flights and was of noneconomic importance at all stations adjacent to but beyond the western limits.

The unusually low egg-pod counts found outside the zone invaded by flights again emphasize the fact that natural factors were holding *mexicanus* to noneconomic numbers and that Montana would have had no major outbreak in 1939 had not overwhelming numbers entered the State by flight in 1938.

Northwestern Minnesota and Northeastern North Dakota

No detailed studies of flights were made: so there is no definite information as to where swarms laid eggs in greatest numbers. It is known that there were many flights within the area and some into surrounding territory on the east, west, and north, but they did not drain the area so completely of its *mexicanus* population as did flights in eastern Montana and western North Dakota. Population increases caused by flights into newly invaded areas were difficult to measure because of the existence of light to threatening infestations in many places before flights occurred. It is therefore impossible to state definitely whether *mexicanus* eggs found within the zone where flights originated or in newly invaded territory were laid by local or by flight grasshoppers.

The 1939 annual egg survey showed severe to very severe egg infestations in the same counties where eggs were laid most heavily in 1938 and equally severe infestations in nearby counties where few eggs were laid in 1938. The newly and heavily infested areas were in the following counties: Pennington, Red Lake, Polk, Mahanomen, and Becker in Minnesota and Ramsey, Nelson, Steele, Griggs, Eddy, Foster, and Wells in North Dakota.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Flights greatly reduced *mexicanus* adult populations, and fall egg infestations were much lighter than in 1938. In the counties listed in table 7 infestations ranged from severe to very severe in 1938 and from light to threatening in 1939. Average reductions in numbers of egg pods per square foot were as follows: Southwestern South Dakota 1.8 to 0.5, northwestern Nebraska 1.2 to 0.5, and eastern Wyoming 1.2 to 0.2. The greatest percent reduction in eastern Wyoming corresponds to the more complete evacuation of that area by flights.

North-Central Colorado

Severe egg infestations were found in Weld, Larimer, Boulder, Adams, and Gilpin Counties in north-central Colorado. It is believed that a large number of the eggs were laid by *mexicanus* migrants from Nebraska, South Dakota, and Wyoming, which invaded this area in July and August. The boundaries of severe infestation are shown in figure 1.

Canadian Provinces

Information on Canadian zones of heaviest egg deposition by *mexicanus* migrants from the United States is based on the annual fall surveys by entomologists in the invaded Provinces.

In Alberta very severe infestations were found in the extreme southeastern corner of the Province. This infestation was joined on the east by very severe egg deposits in nine municipalities in southwestern Saskatchewan. Infestations in grain stubble averaged 4.7 pods per square foot, the highest ever recorded in Saskatchewan. This compares with 2.4 for Blaine County and 7.1 for Hill County, the adjacent counties in Montana. Saskatchewan entomologists attribute the unusually heavy egg deposits in grain stubble to the fact that only about one-fifth of the land was under cultivation. Migrants settling in uncultivated land moved into grainfields to deposit most of their eggs.

Swarms of *mexicanus* that entered southeastern Saskatchewan did not lay as many eggs as expected. Small severe infestations were found in some localities, but it could not be definitely determined whether the eggs were laid by migrants or local grasshoppers.

In the Manitoba fall egg survey no severe or very severe infestations were found in any of the municipalities invaded by flights from the United States.

The boundaries of heaviest egg deposition in Alberta and Saskatchewan are shown in figure 1.

FLIGHTS IN 1940

The flights in 1940 were less important than the spectacular long-distance mass flights of 1938 and 1939. They were fewer, shorter, less intense, and did not result in egg infestations severe enough to cause major flights in 1941. The seasonal development and behavior of *mexicanus* in the areas where migrants laid eggs most heavily in 1939 were followed in 1940, and summaries of these observations are presented.

Montana

In the north-central counties where *mexicanus* migrants laid eggs most heavily in 1939, hatching began on May 11 and was 90 percent complete by June 1. Nymphal numbers were at their peak from June 10 to 25.

The average numbers of nymphs per square yard in principal sources of infestation were as follows: Field margins and roadsides 110, stubble fields 60, and weedy idle land 30. Some concentrations ran as high as 10,000 per square yard in field margins and 200 per square yard in stubble. Infestations in rangeland, river bottoms, and brushy draws were of slight importance. Few nymphs hatched in spring or winter wheat, but these crops became severely infested as a result of nymphal migrations from field margins and stubble fields and by June 25 carried populations averaging 40 per square yard.

Adults began to appear throughout the area on June 23, and 85 percent of the *mexicanus* population was adult by July 3. Adults showed the same migratory tendencies as in 1939 and took to the air shortly after getting their wings.

Plans were made in June for observing flights and determining changes in populations due to them. Stations were set up within the most heavily infested area in north-central Montana, in all the counties surrounding it, and in representative agricultural districts in eastern, southern, and western Montana—a total of 150 stations. Nymphal infestations were estimated in June, and surveys were made at 2-week intervals in July and August for the purpose of detecting any sudden changes due to flights. Egg surveys were made from October 20 to November 8.

Flights began on July 3 and continued when weather was favorable until August 30. During this period 132 records were made of flights in progress within the zone where they originated or in adjacent localities. This compares with 381 records made in the same general area in 1939. The location, intensity, and direction of these flights are shown in figure 6.

Nine and five-tenths percent of the flights were classified as heavy, 17.5 percent as moderate, and 73 percent as light. Heavy and moderate flights composed only 27 percent of all flights as compared with 40 percent in 1939. Heavy and moderate flights were most frequent from July 9 to 22 and were not seen after August 3.

All flights, except those classified as milling, were in the same direction as prevailing low-level winds. Directions of the 132 flights observed were as follows:

	Percent		Percent
North -----	6	Southwest -----	8
Northeast ----	11	West -----	6
East -----	13	Northwest -----	16
Southeast ----	15	Without direction (milling) -----	14
South -----	12		

There were fewer flights to the west and northwest than in 1938 and 1939. Only 22 percent of the 1940 flights were in these directions as compared with 41 percent in 1939. Forty percent of all flights were to the south, southeast, and east as compared with only 23 percent in 1939. The percentages of flights to the north, northeast, and southwest were practically the same as in 1939.

The first invasion of new territory began on July 13, when light flights crossed the southern boundary of the area into previously uninfested counties in south-central Montana. By August 30, when all flights were over, the newly invaded zone extended 10 to 30 miles beyond the western and southwestern borders of the zone of origin and 10 to 60 miles beyond its southern border. Nearly all the flights within the newly invaded zone were light, and repeated surveys at observation stations disclosed no moderate or severe infestations of adults due to flights. Parts of Big Horn, Stillwater, Treasure, and Yellowstone Counties were included in the invaded zone in southern Montana, even though no detailed flight observations were recorded. Observers other than those making the detailed flight studies reported several flights in each of these counties, and surveys at observation stations showed slight increases in adults after flights started.

Light flights to the east and northeast reached the counties in eastern Montana that were so heavily infested in 1938 and 1939, but did not increase local populations above their light preflight ratings.

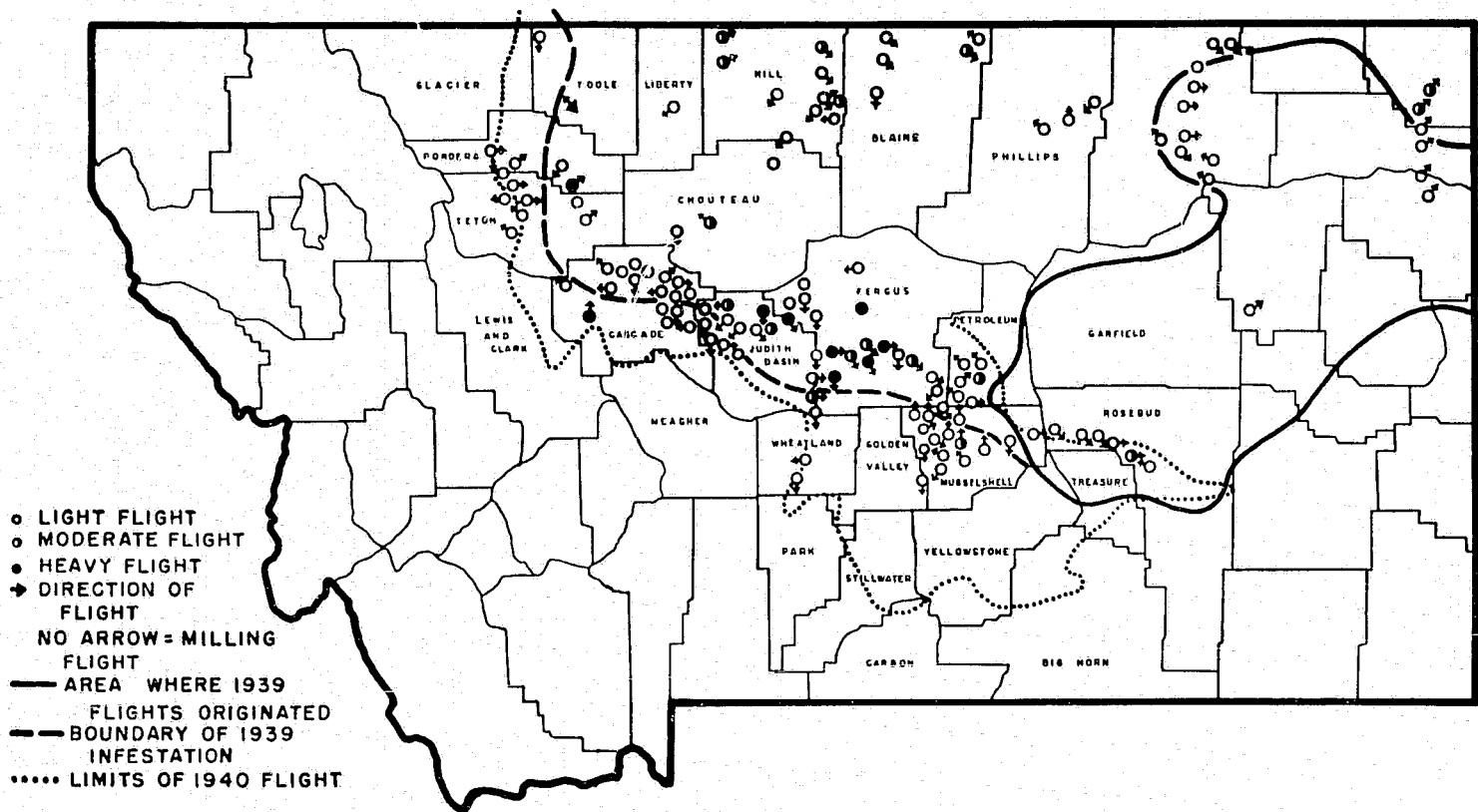


FIGURE 6.—Flights of *mexicanus* observed and recorded in Montana in 1940.

Flights from Montana into Canada and in the reverse direction occurred, but they did not materially change *mexicanus* populations on either side of the international boundary.

Flights into the invaded zone did not drain the zone of origin so completely of its *mexicanus* populations as did flights out of the heavily infested zone in eastern Montana in 1939. Instead of flying out of the zone so heavily infested in 1940, many of the swarms were carried by variable and intermittent winds to various points within it. Of the 132 flights observed in 1940, only 24 percent were in the newly invaded zone, and some of them were seen returning to the zone where they originated.

Populations within the zone where flights started shifted constantly from July 3, when flights began, until August 3, when all moderate and heavy flights were over. An adult survey conducted from August 5 to 10 disclosed no severe or very severe infestation at any of the observation stations within this zone or in the zone newly invaded by flights. Normal or light populations were found at most stations, but threatening infestations (8 to 15 per square yard) were found in two areas. One was in Pondera and Teton Counties along the western border of the zone where flights started and the other was in Cascade and Judith Basin Counties along its southern border.

Egg surveys were made during October and November at all observation stations within the zone where flights originated and in the invaded zone. Egg pods were found in fields at only 18 of the 86 stations surveyed. At only one station did the egg pods exceed 1 per square foot. The average for the 86 stations was 0.2 pod per square foot, which constituted a normal rating with no threat of economic infestation the following year.

In the fall egg survey very few severe and no very severe infestations were found in counties where flights started or in counties invaded by flights. Blaine, Chouteau, Fergus, Hill, and Liberty Counties in north-central Montana had a light infestation of 0.5 egg pod per square foot as compared with a severe infestation of 2.3 per square foot in 1939. Hill County had a normal infestation of 0.1 egg pod per square foot in contrast to a very severe infestation of 7.1 per square foot in 1939, when it was the most heavily egg-infested county in the United States.

Flights to uninfested areas had some effect in reducing populations within the zone so heavily infested in the spring of 1940, but major credit for the protection of crops, reduction of flights, and prevention of heavy egg deposition must be given to the State-Federal control campaign, which began May 29 and continued until July 25. Approximately 22,000 tons of bait were used on about 2 million acres of cropland. Enormous numbers of nymphs were killed, and the battle against adults was continued for 2 weeks after they began to fly. Had there been no control campaign, it seems certain that crop losses would have been much greater, that the invaded zone would have been much larger, and that eggs would have been deposited in sufficient numbers to cause severe and very severe infestations the next year. This campaign ended the grasshopper threat to Montana agriculture, which began when swarms entered eastern Montana in 1938.

Western North Dakota

Western North Dakota is not shown in figure 1 as an area where *mexicanus* migrants laid eggs most heavily in 1939. Severe egg infestations were found in parts of 13 counties in the fall egg survey, but there was no proof that most of the eggs were laid by migrants. It seems certain that some of them were laid by progeny of the swarms that invaded this area in 1938. A brief review of developments in 1940 will therefore be given.

Destruction of eggs by predators and tillage, as well as unfavorable weather during the hatching and nymphal periods, held populations to much lower numbers than expected.

Cool weather and rains prolonged the hatching period, which extended from May 20 to June 18 in southern counties and from June 11 to July 20 in northern counties. Nymphal mortality was high, and there were few migrations from field margins and idle land into crops.

Adults appeared the first week in July, and by the end of July 75 percent of the population was adult. Light to threatening infestations developed in some localities during August, but crop damage was slight.

Flights occurred from July 12 until September. Most flights were light and caused no major changes in population.

Egg deposition began about August 6 and was practically over by September 20. No definite areas of severe or very severe egg infestations were found.

Northwestern Minnesota and Northeastern North Dakota

Threatening to severe infestations of *mexicanus* nymphs hatched in many localities within the area where eggs were laid most heavily in 1939. Owing to cool, wet weather seasonal development was 2 weeks later than in 1939. Hatching began on May 15 and was 95 percent complete by July 1. Approximately 75 percent of the eggs hatched during June.

Newly hatched nymphs were most abundant in grain stubble, legumes, field margins, idle land, dry lake beds, and pastures. At the height of their abundance concentrations reached 150 per square yard in fields and 200 per square yard in their margins. Numbers at 103 observation stations in Minnesota and North Dakota averaged 18 per square yard in fields and 29 per square yard in margins.

First adults of *mexicanus* were seen on June 9, and by June 30 they were common throughout the area. On July 15 approximately 50 percent of the population was adult.

Light dispersal flights began on July 9 in Nelson County in North Dakota. Similar flights were seen in many of the counties within the area on favorable days during the remainder of July and the first half of August. On July 30 and 31 heavy flights of *mexicanus* and *Melanoplus bivittatus* (Say) were observed in Pembina, Ramsey, Nelson, and Grand Forks Counties in North Dakota and Kittson, Marshall, and Polk Counties in Minnesota. Flights were to the northwest, and grasshoppers from fields with only light infestations, as well as those from heavily infested fields, contributed to the flights. Moderate to heavy flights of *mexicanus* from North Dakota into Kittson, Marshall, and Polk Counties in Minnesota were also observed on August 15 and

16. The general effect of all flights was to disperse populations throughout the area rather than to concentrate them in restricted localities. No long-distance mass flights into counties outside the originally infested area were reported.

Egg deposition began the last week in July and continued until October.

According to the 1940 fall egg survey, the extent and severity of *mexicanus* egg infestations were almost the same as in 1939. None of the threatening or severe infestations found could be definitely attributed to flights into the area and as far as known none resulted from flights out of it.

Southwestern South Dakota, Northwestern Nebraska, and Eastern Wyoming

Hatching of *mexicanus* began the first week in May and was nearly completed by the first week in June.

The 1939 fall egg survey showed a much lighter infestation than the previous year, but still it indicated threatening conditions for most of the area in 1940. Nymphs hatched in smaller numbers than expected, and there were further decreases in population from natural causes as the season advanced. Nymphs hatched in greatest numbers in alfalfa but, except for a few fields, infestations were light. Small grains, which were the main source of nymphal infestations in 1939, were practically free from grasshoppers in 1940.

Adults appeared the first week in June, and by the 20th of July 90 percent of the population was in the adult stage. Adult infestations were normal to light. No flights were observed.

In the fall egg survey *mexicanus* infestations in all counties within the area were noneconomic.

North-Central Colorado

Infestations in this area did not develop to the extent indicated by the 1939 fall egg survey. Nymphs hatched in threatening numbers in alfalfa fields during May, but weather conditions during the nymphal period were unfavorable and adult populations were mostly noneconomic. No flights were observed, and no threatening or severe egg infestations were found in the 1940 fall survey.

Canadian Provinces

Alberta

In July there were light to moderate flights to the north and northwest from the southeastern corner of the Province where eggs were laid most heavily in 1939. Migrants reached the foothills of the Rocky Mountains to the west and slightly beyond the Red Deer River Valley to the north. They were scattered so thinly that no severe infestations traceable to flights of *mexicanus* were found in the adult survey. Weather conditions during the late summer and early fall were not favorable for egg laying, and it is doubtful whether the few eggs laid made any significant difference in 1941 grasshopper numbers.

Saskatchewan

Many nymphs hatched in the southwestern corner of the Province, where eggs were laid most heavily by 1939 migrants, but their numbers were greatly reduced by extensive baiting operations. Some adults survived, and there were light to moderate flights to the north and northeast. Few adults remained in the area so heavily infested originally, and no economic egg infestations were found there in the fall of 1940. Flights reached as far north as the South Saskatchewan River Valley, but little egg laying occurred in the invaded areas.

Manitoba

Light to moderate dispersal flights occurred locally within the general area invaded by swarms of *mexicanus* from the United States in 1939, but there were no reports of heavy egg deposition by migrants in any well-defined areas.

OTHER OBSERVATIONS ON FLIGHTS

Observations on takeoffs, low flights, and more detailed descriptions of high flights and their terminations are based on studies in all areas where flights occurred.

Takeoffs

The beginning of either a low or high flight is called a takeoff. Takeoffs occurred on clear days when the air temperature first approached 80° F. if winds were favorable and grasshoppers were inclined to fly. None were observed below 75°, and out of 38 recorded observations only 6 flights started at air temperatures below 80°. The time of takeoff varied from 9:30 a. m. to 3 p. m. but was most often between 11 a. m. and 1 p. m.

Wind was the final stimulus needed to get grasshoppers into the air. The most favorable wind was a gentle, intermittent breeze (2 to 4 m. p. h.), strong enough to flutter the leaves of trees and sway blades of grass and heads of grain. Takeoffs also occurred when there was a gust of wind up to 5-10 m. p. h. and that soon slowed to 2-4 m. p. h. If the wind was imperceptible or blowing more than 10 m. p. h., grasshoppers usually remained on the ground. Every observer remarked on the effect of wind in starting flights.

Takeoffs started with a few individuals rising here and there in short flights and then returning to the ground. These early risers seemed to incite others to flight, and larger numbers rose with each slight breeze or gust of wind, until all adults inclined and able to fly were in the air. The time taken to complete a takeoff varied greatly. When the temperature rose slowly and winds were intermittent with prolonged calm periods, a takeoff sometimes continued for several hours; when the temperature rose rapidly and calm periods were shorter, it was sometimes completed in half an hour. Swarms that had been flying for several days or weeks took off more quickly than those beginning their flight. Swarms that had settled during the day because of unfavorable conditions took off more quickly when conditions again became favorable than on their first flight of that day.

Adults that were roosting to escape a high ground temperature took off less readily than nonroosting adults. Roosting occurred on extremely hot days when winds were either too low or too strong to complete the takeoff that usually starts when the air temperature first approaches 80° F. Roosting was recorded 15 times between July 10 and August 4, 1939, at air temperatures ranging from 93° to 100°. It generally took place between 11 a. m. and 3 p. m., the time of day when the air temperature usually reached its maximum. In the absence of dense vegetation grasshoppers sought the shady side of fence and telephone posts or climbed as high as they could on sparse vegetation. After a short period of roosting, they became sluggish and paid little attention to moving objects. They could be picked by hand from posts, and flew only a few feet when flushed from vegetation by a person walking through it. Roosting was observed while high flights were in progress, but roosting adults rarely took off to join them. They remained motionless during light, intermittent winds that would have induced takeoffs earlier in the day, but sometimes they took off when dislodged by strong gusts of wind.

M. mexicanus fliers always take off into the wind. They can make some progress against winds up to 10 m. p. h., but they generally turn and fly downwind with their bodies at a slight angle to it. When they are flying with a light wind (2 to 5 m. p. h.), their speed is 10 to 12 miles per hour. This was determined by timing an automobile driven just fast enough to keep up with grasshoppers flying parallel to it.

When the sky was completely overcast, *mexicanus* did not take off even when the temperature and wind were favorable.

Low Flights

In 1939, of 610 flights recorded in Montana and western North Dakota, 21 percent were classed as low, or within approximately 25 feet of the ground.

Low flights were of four types—(1) flights of recently matured adults that remained low even when conditions for high flights were favorable, (2) preliminary flights that later changed to high flights, (3) preliminary flights that failed to become high flights because of unfavorable conditions, and (4) very low upwind flights toward green vegetation.

Adults with newly developed wings engaged in desultory low flights for several days, even when the temperature and wind were favorable for high flights. Low flights of this kind occurred for several weeks while the remaining nymphs were transforming to adults. Many of them took place during light winds of variable direction. The grasshoppers flew aimlessly in all directions, with many settling and others rising. The general effect of these flights was to redistribute adult populations without material expansion of the area originally infested. If the wind freshened slightly and blew in one direction while low milling flights were in progress, swarms streamed away with the wind without increasing their height above the ground. Grasshoppers in flights of this nature resembled large wind-driven snowflakes. Swarms carried by winds in low flights seldom flew more than a few miles before settling.

During the flight period of well-matured adults low flights always preceded high flights. When one of these low flights was first seen, it was impossible to predict whether it would develop into a high flight or stop before that stage was reached. When sky, temperature, and wind conditions remained favorable, these low flights generally developed into high flights, but if any one of these factors became unfavorable, flights stopped before they could be classed as high.

The change from low to high flights was usually gradual, sometimes requiring hours to complete. Because of limited personnel and time, it was considered inadvisable to follow each low flight until it changed to a high flight or until it terminated because of unfavorable flying conditions. Low flight ratings were therefore based on 10- to 30-minute observation periods. It is the authors' opinion that about half the observed low flights of well-matured adults developed into high flights.

A few very low flights were seen moving upwind toward green crops. The following description of one of these unusual flights is taken from the field notes of F. D. Butcher:

A high flight of *M. mexicanus* settled in the Brinkman, Montana Study Area between 3 and 4 p. m. on July 27, 1939. At 4:15 I noticed a heavy flight across clean summer fallow into the face of a southeastern wind to the margin of a wheatfield. These grasshoppers were close to the ground, my estimate being that none were higher than 40 inches and probably one-half of them were lower than 15 inches. Upon reaching the margin of the wheatfield, most of them landed and almost immediately started feeding. This is the first flight of this kind I have seen and I wonder if it may explain some of the tremendous populations we are encountering at field margins.

F. E. Skoog witnessed a similar flight in Sheridan County, Mont., on July 18, 1939:

Flight grasshoppers settled indiscriminately over 100 acres of clean plowed land late this afternoon. Shortly after settling an audible buzzing flight took place, the movement being from the plowed land, upwind, toward a green wheatfield. They flew at an altitude of 5 feet or less directly toward the crop, and landed in the margin where they numbered 400 to 500 per square yard.

Such low flights are hard to see and were probably more frequent than indicated in the reports.

High Flights

The changeover from low to high flights was a gradual process rather than a sudden upsurge of an entire low-flying swarm. It took place most quickly when the air temperature was above 85° F. and when winds were gusty but not over 10 m. p. h. Such gusts of wind appeared to stimulate grasshoppers to greater flight effort and rising currents of warm air assisted in carrying them upward. Under these conditions the changeover was sometimes completed within 30 minutes. When the air temperature remained at 80°-85° and winds were less favorable, 1 to 3 hours might elapse before most of the grasshoppers were flying higher than 25 feet.

At the beginning of high flights a few grasshoppers could be seen rising above their fellow fliers, and their upward progress could be followed for at least 150 feet. They were followed by others in increasing numbers until only a few remained within 25 feet of the

ground. Viewed from the ground, heavy high flights had no visible limitation. Myriads of grasshoppers were in view as high as unshaded eyes could see. By cupping the hands over the eyes and looking toward the edge of the sun one could see still higher myriads streaming by on steady winds or circling on variable light winds. Against the sun they looked like specks of glittering metal.

No one knows how high the human eye can follow grasshoppers in flight or the maximum height reached by swarms, but Mills (6) stated that airplanes encountered swarms in Montana at 7,000 and 11,000 feet during the *mexicanus* flight in July 1938.

Flight Terminations

Temperature and light were the most important ecological factors in stopping flights. The lowest air temperature at which flight termination was observed was 79° F. Since this is approximately the same temperature at which the first takeoff occurs on days when other conditions are favorable, it may be assumed to be close to the lowest temperature at which flights occur.

When the temperature declined gradually from 85° to 79° F. in the late afternoon and winds were light, *mexicanus* adults drifted slowly to the ground and landed without turning into the wind. Under such conditions the settling process sometimes continued for 30 to 45 minutes. No flights continued later than several hours before sunset, even when the temperature remained above 79° until after sunset.

Flights terminated abruptly at any time during the day when there was a sudden drop in temperature or when clouds obscured the sun. Under these conditions grasshoppers folded their wings and plummeted to within 25 to 30 feet of the ground, where they spread them again and landed into the wind. Occasionally stray individuals were seen descending in the same manner when flights were in full progress and flying conditions were excellent. This was observed most frequently when swarms were passing over green crops.

Flights usually terminated when ground winds exceeded 20-25 m. p. h., but since strong winds generally brought lower temperatures it was impossible to determine what stopped the flight.

STRUCTURE AND COLORATION OF ADULT MIGRANTS

Although the flights of *mexicanus* in 1938 and 1939 resembled the more extensive flights of the extreme migratory phase that occurred from 1874 to 1877, there was no similarity in size, wing length, or coloration between the 1938-39 adult migrants and the population formerly called *spretus*. According to Rehn, as quoted by Faure (2):

The only characters which seem to be of value in separating *spretus* from *mexicanus* are the greater size, relatively longer wings, and slightly more expanded posterior part of the pronotum of the former. Minute characters in the form of the cerci and the apex of the sub-genital plate were given by Scudder as additional features, but these appear to be individual fluctuations appearing as regularly in true *mexicanus*.

In earlier outbreaks of *mexicanus* in Montana specimens were occasionally taken that closely resembled *spretus* (Parker 8). They were larger, had longer wings in relation to body length, and were lighter

in body coloring than normal *mexicanus* adults. Some of them were then submitted to Morgan Hebard, one of the foremost systematic workers in Orthoptera in the United States, who expressed the following opinion: "We believe it wiser to consider these specimens representative of *mexicanus* showing divergence toward *spretus* in size and wing length."

It was expected that specimens resembling *spretus* would be found among the 1938 and 1939 migrants, but none were taken. They may have failed to appear because of prevailing low temperatures and abundant succulent food during most of the nymphal period. Parker (8) found that specimens of *mexicanus* reared exclusively on green succulent food such as *Tradescantia* were smaller and had shorter wings than those reared on a mixture of green food and dried alfalfa leaves. Parker, Shotwell (11), and Brett (1) reported that *mexicanus* and *Melanoplus differentialis* (Thos.) were much darker in color when reared at low rather than at high temperatures. Brett also found that *mexicanus* was smaller when reared at low temperatures.

The effects of low temperatures, frequent rains, and highly succulent vegetation on the structure and coloration of *mexicanus* adults were noted in eastern Montana in 1939. The main nymphal period for *mexicanus* extended from May 15 to June 21. Weather records for Miles City, Mont., show 22 days during this period when precipitation exceeded 0.01 inch and during the first 3 weeks in June only 7 days when the maximum temperature exceeded 68° F., the lower limit of grasshopper activity. Occasional breaks in the bad weather allowed nymphs to feed and develop without marked decreases in numbers, but adults were darker and smaller than the 1938 migrants from South Dakota and the 1940 migrants in north-central Montana. A few, 1 or 2 percent, were depauperate; their wings did not extend beyond the tips of the abdomens, and their bodies were one-fourth to one-half shorter than the body of the average *mexicanus* adult. The unfavorable conditions during the nymphal stage did not suppress the migratory urge, for all adults flew out of the area shortly after getting their wings.

INCREASES IN CROP LOSSES AND CONTROL COSTS DUE TO FLIGHTS

Flights of *mexicanus* greatly increased crop losses and the cost of grasshopper control in the invaded areas. Estimates of these increases obtained from entomologists in the States and Provinces where flights occurred are shown in table 10. Some increases resulted from flights of *mexicanus* from eastern Wyoming into northern Colorado and from north-central Montana into southeastern Alberta in 1940. Since they were difficult to estimate and of minor importance compared with those in other States and Provinces, they are not included in table 10.

Increases in crop losses totaled \$58,589,246 and increases in the cost of control amounted to \$3,939,970. No estimates of damage to range grass are available, but it is known to have been great, particularly in 1938 and 1939.

TABLE 10.—Increases in crop losses and control costs due to flights of mexicanus, 1938-40

State or Province	Increases in crop losses			Increases in control costs			Total of both items
	1938	1939	1940	1938	1939	1940	
Minnesota.....	\$378,444	\$1,221,024	\$486,168	\$85,009	\$388,714	\$133,782	\$2,694,041
Montana.....	6,694,468	2,810,564	2,112,518	50,166	990,267	942,399	13,600,382
Nebraska.....	1,174,019	913,403	135,266	45,172	70,775	6,397	2,351,032
North Dakota.....	6,138,938	2,733,545	245,029	336,194	524,860	36,653	10,015,219
South Dakota.....	2,734,827	883,092	300,056	118,452	73,579	13,208	4,183,214
Wyoming.....	450,000	417,000	11,700	3,955	37,038	2,450	922,143
Manitoba.....	45,000	532,980	10,305		0,000		597,285
Saskatchewan.....	16,500,000	7,800,000	3,800,000	5,000	10,000	50,000	28,165,000
Total.....	31,115,696	17,312,508	7,161,042	643,948	2,110,233	1,184,889	62,528,316

Crop losses in Canada and the United States would have been much greater had it not been for the Federally financed control program on idle land and roadsides conducted by the Bureau of Entomology and Plant Quarantine in 1939 and 1940. This program supplemented the cooperative efforts of private, State, and Federal agencies engaged in controlling grasshoppers in crops by baiting 5,090,376 acres of roadsides and idle land heavily infested with *mexicanus* nymphs. If this had not been done, countless millions would have moved into crops, taken their toll, matured, and greatly increased the size and number of swarms that moved into Canada.

It is regrettable that the extremely heavy infestation in the zone where flights originated in 1938 was not reduced sufficiently to prevent flights. It now seems probable that half a million dollars spent in controlling grasshoppers in range and idle cropland in 14 counties in North and South Dakota in the spring of 1938 would have prevented all major long-distance flights. Failure to do this was due largely to the low value of the land needing treatment, the lack of insecticides and equipment for quick treatment of large acreages of uncropped land, and the fact that no extensive flights had occurred in recent years to serve as a warning.

FUTURE FLIGHTS

What of the future? It seems certain that history will repeat itself and that future droughts will result in large acreages of depleted range and idle land, increased *mexicanus* populations, and threats of long-distance mass flights.

Future threats can be met with more potent insecticides and better methods of applying them than were available in 1938. Bulky baits distributed with ground equipment have been replaced by low-volume sprays applied by airplanes. The acres now treated in hours by aircraft required days to cover by ground machines. Experience gained since 1940 has proved that it is a sound practice to control nonmigratory grasshoppers in several million acres of rangeland even when there is no threat of long-distance mass flights. In view of the fact that *mexicanus* flights in 1938, 1939, and 1940 increased crop losses and control costs by \$62,528,316, failure to prevent their recurrence seems inconceivable.

SUMMARY

The most spectacular long-distance flights of grasshoppers in the United States and Canada for over half a century took place during the summers of 1938, 1939, and 1940. The species was the migratory grasshopper (*Melanoplus mexicanus mexicanus* (Saus.)).

Flights were preceded by a general increase in *mexicanus* numbers throughout the southeastern counties of North Dakota and the northeastern counties of South Dakota, which began in 1935 and resulted in unusually heavy egg deposition in 1937. Egg infestations for that year were heaviest and most widespread in a group of 9 counties in north-central South Dakota and in 5 adjacent counties in North Dakota.

In the spring of 1938 enormous numbers of nymphs hatched in the area where eggs were deposited most heavily in 1937. Great numbers

that attacked crops were killed by baiting, but still larger numbers in range and idle land became adults and were the main source of migrants.

Mass flights out of the zone of origin started in late June and continued on days favorable for flying until August 15. Swarms traveled in the same directions as the prevailing winds, which were mainly to the northwest and north, when temperatures were highest and flights were most likely to occur.

Swarms moving across southwestern North Dakota continued into eastern Montana. Some of them eventually reached the South Saskatchewan River in Canada, approximately 575 air miles from where they started. Other swarms flying northwest invaded northwestern North Dakota, southwestern Manitoba, and southeastern Saskatchewan. Swarms flying north and northeast settled in northeastern North Dakota, northwestern Minnesota, and south-central Manitoba. Large swarms, presumably from north-central South Dakota, ended their flights in southwestern South Dakota, northwestern Nebraska, and eastern Wyoming.

Egg deposition by migrants in 1938 was heaviest and most extensive in eastern Montana and western North Dakota; northwestern Minnesota and northeastern North Dakota; southwestern South Dakota, northwestern Nebraska, and eastern Wyoming; and southern Manitoba and southern Saskatchewan.

In 1939 mass flights started shortly after grasshoppers became adults in all areas where eggs were laid most heavily in 1938. Swarms from eastern Montana and western North Dakota invaded a large area in north-central Montana, southern Saskatchewan, and southeastern Alberta. Some of them traveled approximately 235 air miles. Swarms from northwestern Minnesota and northeastern North Dakota flew east and west into nearby areas and longer distances north and northwest into southern Manitoba. Swarms from southwestern South Dakota, northwestern Nebraska, and eastern Wyoming traveled southeast, south, and southwest into southwestern Nebraska and northern Colorado.

Migrants in 1939 deposited eggs most heavily in north-central Montana, northwestern Minnesota and northeastern North Dakota, north-central Colorado, and southeastern Alberta and southwestern Saskatchewan.

In 1940 mass flights were less important than in 1938 and 1939. They were fewer, shorter, less intense, and did not result in egg infestations severe enough to produce major flights in 1941.

Other observations were made on flights. Flights started on clear days when the air temperature first approached 80° F. if winds were favorable and adults had an urge to migrate. The time of takeoff was most often between 11 a. m. and 1 p. m. Wind was the final stimulus needed to get migrants into the air. The most favorable wind was a gentle, intermittent breeze. Migrants usually took off into the wind and then turned and flew with it. When they were flying with a light wind, their speed was 10 to 12 m. p. h. A few swarms were seen flying very low and upwind toward green crops.

Flights in progress terminated abruptly whenever there was a sudden drop in air temperature to below 80° F. or when clouds obscured the sun. On clear, warm days swarms drifted slowly to the ground

several hours before sunset, even when the air temperature remained above 79° until after sunset.

Crops were injured in all the areas invaded by migrants in spite of large-scale control campaigns waged against them. Entomologists in the States and Provinces most heavily invaded estimated that crop losses were increased \$58,589,246 and that control costs were \$3,939,070 more than they would have been had no flights occurred.

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