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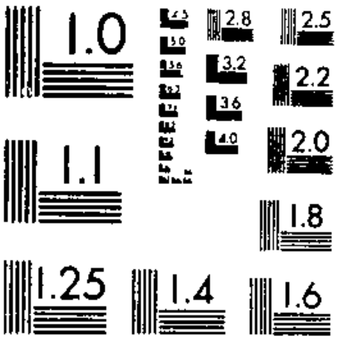

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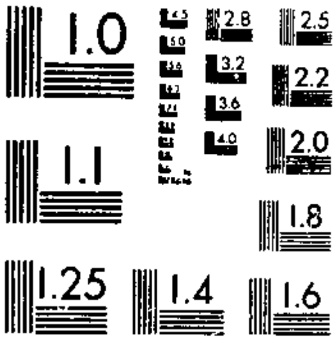

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Field Studies of the Alfalfa Weevil and Its Environment[1]

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CONTENTS

INTRODUCTION

The object of this ecological study, which has been carried on since 1929, was to gain an understanding of the adjustment of the alfalfa weevil (*Hypera postica* (Gyll.)) to its environment in the western

[1] Received for publication Feb. 27, 1947.

[2] The authors are indebted to G. I. Reeves, whose sympathetic interest contributed to making this investigation possible. The senior author planned and directed the studies, devised the mathematical conception employed in analyzing the results, and prepared the manuscript. M. M. Darley, G. W. Haug, F. H. Harries, C. W. McBeth, L. J. Farmer, and W. E. Peay assisted in this research. J. C. Hamlin died on June 8, 1943.

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part of the United States. For, although this Old World species has been known in Utah since 1904, no investigation had been made of its response to the environment as a whole. The earlier work by State and Federal investigators produced general biological data which served as a foundation for the research. Since the general information has been summarized in excellent form by Essig and Michelbacher (*3*)[3] the references herein are limited to those having a particular bearing upon the present study.

Past studies had shown marked diminution of weevil damage since about 1917, apparent parasitization of upwards of 90 percent of weevil larvae by the introduced parasite *Bathyplectes curculionis* (Thoms.), wholesale destruction of the larval population after the first cutting in favorable haying weather, and the important influence of temperature upon some activities of the weevil. Moreover, spraying and dusting with calcium arsenate (*12*, *13*) had been advanced as artificial control measures but had never been generally adopted.

Notwithstanding, there was lacking a broad understanding of the mechanism governing fluctuations of weevil abundance and the consequent crop damage. Climatic variations from year to year did not suffice to explain the fluctuations in damage, because the widest possible differences in injury were found to exist even in adjacent fields. On the other hand, there was little doubt of the important influence of weather conditions. The abundance of *Bathyplectes* indicated that it might have been responsible for reduction of weevil damage, although much of this parasitization was wasted upon larvae that were killed following harvest of the first alfalfa crop.[4]

This, then, was the general status of the alfalfa weevil problem in 1929, when it was attacked from the ecological approach; that is, by simultaneous studies of the biological, meteorological, and cultural influences upon the weevil. But first it is desirable to indicate the present distribution of the weevil in the United States, the location of these studies, and the broad sequence of events during the cropping season.

WEEVIL DISTRIBUTION AND AREAS STUDIED

Since the alfalfa weevil was discovered near Salt Lake City, Utah, it has spread into 11 States. Its known distribution in the United States in January 1940 is shown in figure 1. The studies here reported are based primarily on periodic censuses taken during the period 1930–32 in Salt Lake Valley, one of the areas in which damage is now frequent. Less extensive data taken in Rogue River Valley, Oreg., have been employed for comparative purposes, and data obtained in western Nevada, eastern Idaho, and western Colorado, together with more general studies throughout the weevil-infested territory, have been drawn upon to widen the scope of this bulletin. These supplementary studies were made during the period 1932–38.

[3] Italic numbers in parentheses refer to Literature Cited, p. 84.

[4] Unpublished results of laboratory experiments conducted by L. D. Christenson in 1927 indicate that parasitized larvae consume approximately one-fourth less food than unparasitized larvae. Thus, parasitization of larvae later killed by cultural methods is beneficial to this extent.

WEATHER AND THE CROPPING SYSTEM

Springlike weather begins in Salt Lake Valley early in March, and the temperature rises, with many interruptions, to a peak late in July and then declines until November, when winter conditions prevail. Precipitation decreases from a maximum of approximately 2 inches monthly during March, April, and May to a minimum of ½ inch in July and then rises gradually to about 1½ inches during October. Rainfall is supplemented by irrigation with water from the melting of the winter's snow held on the mountains, the quantity of which fluctuates from year to year. The usual practice in Salt

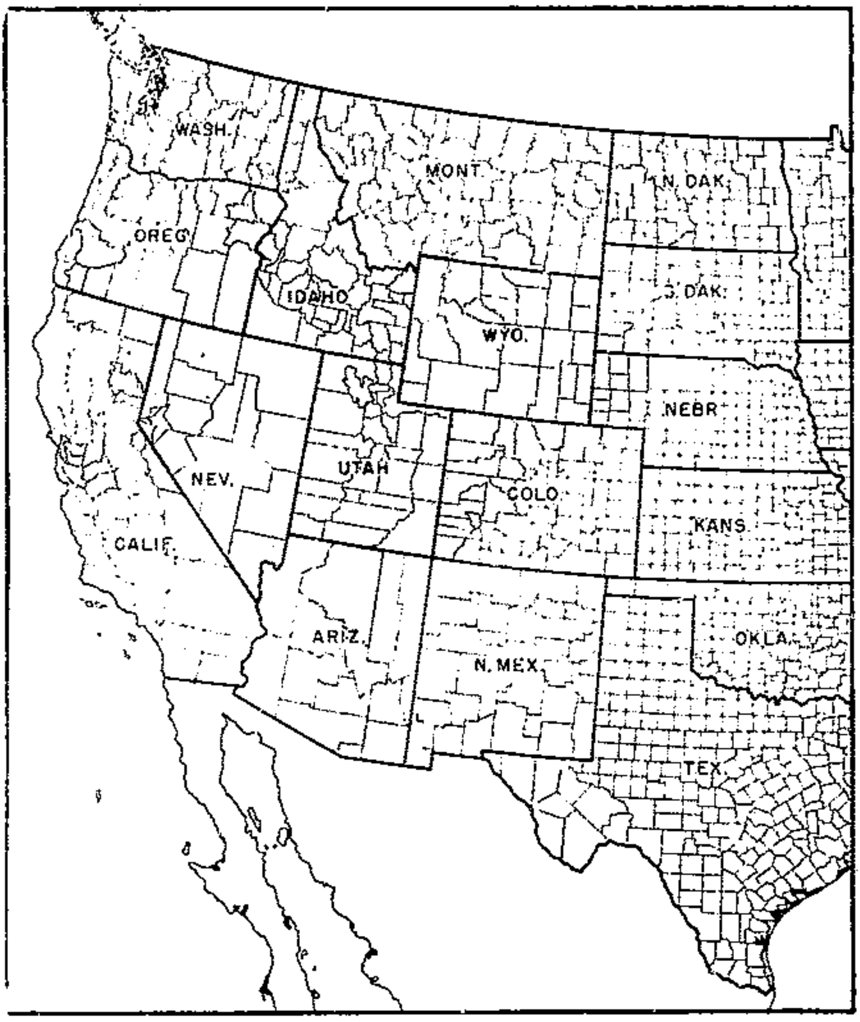

FIGURE 1.—Known distribution of the alfalfa weevil in the United States, January 1940.

Lake Valley is to give two irrigations to each alfalfa crop, but this varies with the supply of snow water, with the amount of spring precipitation, and with the water needs of other crops. Even wider variation prevails throughout the Great Basin.

Growers of alfalfa hay in the Great Basin usually harvest three crops annually. In the lower valleys a few farmers make four cuttings, while in higher valleys only two crops are cut. The three-crop system is the one under which this investigation was conducted, and to which reference is made throughout this bulletin unless otherwise specified. In Salt Lake Valley ordinarily the first cutting is made in the first half of June, the second near the end of July, and the third about the middle of September. After the third cutting the alfalfa makes some further growth, which is used as fall pasture.

SEASONAL HISTORY OF THE ALFALFA WEEVIL

The alfalfa weevil [5] winters in the adult stage and begins laying eggs soon after the snow covering of the field has melted in the spring. At this time there is no growth of the alfalfa plants, and all early eggs are laid in dead and broken alfalfa or grass stems. When the alfalfa has reached a height of 6 to 8 inches, the weevils begin laying eggs in the growing stems, and as the season advances they lay more in the stems and less in litter.

Hatching begins in April, and the number of larvae increases rapidly. In April also the parasites, which have spent the winter as larvae in cocoons and pupated in March, begin to emerge as adults and to deposit their eggs in the increasing population of weevil larvae. Before the larvae or the parasites in them have completed their development, however, the first alfalfa crop is ready for harvesting, and this cutting destroys most of the larval population.

After the first cutting only a few eggs are deposited, and they give rise to a numerically insignificant larval population living on the second growth of alfalfa. Those few individuals that escape both the biological and the cultural kill of the first- and second-cutting periods spin cocoons, pupate, and become the overwintering adult weevils. These new-generation adult weevils produce only a few eggs in the fall.

NATURE OF DAMAGE

The principal damage occasioned by the alfalfa weevil results from the feeding of larvae upon the first growth of alfalfa. The first instars feed within the growing tips of the stems, but the later instars feed increasingly upon the opened leaves, devouring all except the veins and the lower epidermis, which soon dry and take on a grayish to whitish cast. This whitish appearance over the field is characteristic of severe weevil damage, and when it involves the buds the plants stop growing. Little nutritive material is left in the hay when injury has progressed to this extent, although the stems still produce a fair tonnage.

[5] The various stages of the weevil and the damage caused by it have been pictured by other writers, such as Titus (*16*), Webster (*18*), Reeves (*12*), and Essig and Michelbacher (*3*).

Backward spring weather, which especially favors the accumulation of eggs in the field, is in some years followed by a sudden change to seasonal temperatures, with the result that great numbers of larvae hatch in a very short time. Since the alfalfa continues to grow during the cool weather, these larvae may fall upon the crop when it is ready to cut. The tiny larvae, living exclusively inside the growing buds, produce a characteristic effect upon the plants. The grayish cast, instead of appearing generally over the upper several inches of the plants, is confined largely to the buds, giving them a frazzled appearance and stopping growth, although there is no large amount of feeding on the leaves as in the more typical damage. If cutting is delayed, injury tends toward the usual type.

The literature mentions another type of severe injury, directed against the young second growth and caused by larvae that were living on the first alfalfa crop when it was cut. All the early writers mention this phenomenon of the larvae holding back the second crop, sometimes so long that only two crops could be harvested during the season. As early as 1924 Chamberlin (*1*) noted the general absence of this type of damage, and during the present study it has only occasionally been suggested by slight retardation of the second crop. The weevil problem has thus shifted considerably since the early years of devasting injury to the young second growth. The circumstances that appear to have wrought the change will be discussed in the section on Ecological Interpretation, following a study of the weevil's response to conditions now obtaining in Salt Lake Valley.

METHODS OF STUDY

Extreme conditions of every kind were avoided in selection of the study field; it was located in the midst of a homogeneous alfalfa-growing district, was managed according to cultural and harvesting practices common to the district, and had a stand of average age and density. The plan of study was to measure throughout the season the rise and fall of each component of a weevil population freely exposed to all forces of nature, while simultaneously measuring or recording the incidence of the principal biological, meteorological, and cultural factors. The chief biological factors were the primary parasite *Bathyplectes curculionis* (Thoms.) and the secondary parasite *Eupteromalus viridescens* Walsh; their abundance was measured along with that of the weevil.

The incidence of cultivation and irrigation, density of stand, size and stage of development of alfalfa plants, dates of crop cutting, and harvesting practices were recorded and their effect sought through study of fluctuations in abundance of the weevil and parasites. The weather conditions measured were temperature and precipitation. Additional studies were made in the same field or in others as supplementary data were needed.

Sampling Weevil and Parasite Populations

Sampling of the study field was facilitated by considering it to be composed of as many longitudinal strips as the number of samples for each census, each strip being divided into approximately square blocks (10×11 paces). Disproportionate representation of the different quarters of the field was prevented by sampling opposite halves of adjacent strips. Chance determined from which half of the first strip the first sample should be taken, and the particular block in this half-strip was decided by random selection from numbered cards. Eight 1-square-foot samples were taken weekly from positions in the study field determined in this fashion.

While the blocks may be considered as chosen at random, the samples themselves were carefully selected by an experienced sampler. Standing in the middle of the chosen block, the sampler selected, within a radius of approximately 5 yards of himself, a square-foot area representative of the average condition within the block. Since many alfalfa weevil eggs occur in litter that collects in the bottom of the field corrugations, and this debris at times also affords shelter for more advanced weevil stages, each sample chosen included both part of the furrow and part of the ridge. If many bare spots, much grass and weeds, or a large amount of litter were present, the sample reflected such conditions.

Complete fortuity, though perhaps preferable in sampling to determine a single component of a population, in this study would have increased the variation in the results and necessitated a much larger number of samples, the examination of which would have involved a prohibitive amount of labor. Hence, the procedure outlined was adopted as the best possible compromise between the desideratum of random sampling and the necessity of keeping the work within the limits of practicability.

The selected area was enclosed by a steel die with sides 4 inches high, which was driven into the soil about 2 inches. All material inside the frame constituted the sample. The procedure varied somewhat with the condition of the alfalfa growth, but the material was always taken in the order of its availability. For example, early in the season when there was no appreciable growth or just after a crop had been cut, the stubble was cut level with the ground, and this, together with the litter, was collected first and placed in a paper bag; the soil was then bagged separately. Later in the season growing alfalfa shoots, carefully severed where they emerge from the crown, comprised the first portion of the sample, the litter the second, and the soil the third. The steps in sampling are detailed as follows:

The sampling frame was lowered over the selected area in such a way that twisted and bent stems fell, according to their attachment to the crown, either in or out of the selected area. The frame was then driven firmly into the soil, and a piece of canvas was spread along one side, with its edge slightly overlapping the frame to prevent loss of larvae or adults. The stems were then taken singly or by twos or threes, bent outward over the canvas, and cut off at the crown.

All stems, including grass if present, constituted the green-stem sample. The stubble was next cut even with the earth, and all material was collected cleanly by repeated raking with the fingers and sweeping with a small paint brush. This material, together with loose soil, constituted the litter sample. When the field was extremely wet, the litter contained much mud, which was later removed by washing the sample in a sieve partially submerged in a tub of water.

Finally, the soil was removed with a small trowel to a depth of about 1½ inches, or as deep as cracks extended into the soil. The alfalfa crowns were scraped clean, and all loose material was included in the soil sample.

Counting and Classifying

The samples were examined in the laboratory, the order of examination depending upon the diversity of the insect stages present and whether refrigeration facilities were at hand.

The green-stem portion of the sample was especially important because it supplied most of the larvae and many of the eggs. The leaf stalks were torn from the main stem, and the leaves as well as the separated leaflets of the growing tip were carefully examined for larvae. Occasional weevil cocoons and adults were found in the green-stem sample. The stems were split to expose the egg clusters, which were recorded by size and location in the stem. The eggs were then incubated on moist blotting paper to determine their parasitization. The litter sample also yielded many eggs and, during midsummer, the majority of the weevil cocoons. Examination of this sample therefore consisted in removing and counting weevil larvae, cocoons, and adults as well as any parasite cocoons. The dead stems were segregated and split, and the eggs were recorded by number per cluster.

The soil sample contained adult weevils and practically all parasite cocoons. Examination of these samples, approximating 1 gallon each, was facilitated by washing, which reduced their volume to a few cubic inches. The water washed most of the soil through two screens; large objects remained on the top (4-mesh) screen, where they were cleaned with a strong stream of water, while the insects and some finer material collected on the bottom (16-mesh) screen and were washed gently with a spray. The washed samples were wrapped in paper toweling to dry and examined on a white tray under a bright light.

Segregation of the Insect Material

After being counted and recorded, the insect material was combined in various ways for further studies. Weekly collections of eggs from dead and green stems were combined separately, and incubated to detect parasitization.

All larvae originating in a single sample were assembled and then segregated by instars according to the head capsule. Larvae of *Hypera punctata* (F.), which frequently occur with those of *H. postica*, are distinguished mainly by the width of the head, measurements of which are given in table 1. In the third and fourth instars the range of head widths of *H. postica* overlaps that of the first and second instars, respectively, of *H. punctata*, but here color differences permit separation. After being classified, the larvae were saved for dissection to determine the percentage parasitized by *Bathyplectes curculionis*.

The weevil cocoons were similarly combined according to sample, and opened to determine the mortality of cocooned weevil stages and the percentage parasitized by *Bathyplectes*.

TABLE 1.—*Width of head capsule of larvae of Hypera postica and H. punctata*[1]

Instar	Width of head capsule of—					
	Hypera postica larvae			*Hypera punctata* larvae		
	Range	Mean	Probable error[2]	Range	Mean	Probable error[2]
	Millimeters	*Millimeters*	*Millimeters*	*Millimeters*	*Millimeters*	*Millimeters*
First	0.1840 to 0.2210	0.2018	0.0054	0.3170 to 0.3670	0.3445	0.0107
Second	.2338 to .2980	.2708	.0072	.4760 to .5845	.5264	.0148
Third	.3507 to .4342	.3904	.0112	.6600 to .8800	.7938	.0081
Fourth	.4593 to .6179	.5489	.0221	1.1000 to 1.3000	1.2010	.0099

[1] Each instar based upon measurement of 100 heads from fresh specimens.
[2] Probable error of a single observation (0.6745 times standard deviation).

The female weevils, combined from all eight samples, were killed and fixed, imbedded in paraffin, and dissected to learn the extent of ovarian development, along the general lines laid down by Snow (*14*).

All free-existing cocoons of *Bathyplectes* from a given sample were combined and dissected to determine development, mortality, and parasitization by *Eupteromalus*.

DETERMINATION OF PARASITIZATION AFFECTING WEEVIL LARVAE

In the preliminary work of 1929 the percentage of weevil larvae parasitized by *Bathyplectes* was determined by rearing. However, the mortality of third and fourth instars from causes other than parasitization was high, and introduced a question as to the accuracy of estimates of parasitization so obtained. For example, 231 larvae collected on June 10 yielded 74 adult weevils, 84 parasite cocoons, and 73 dead weevil larvae. If the dead larvae are excluded, the parasitization was 53.16 percent. The mortality of parasitized larvae was probably higher than that of unparasitized individuals, in which case the above percentage underestimates the true parasitization.

However, we cannot assume that all the larvae that died before cocooning were parasitized and thus calculate 67.97 percent parasitization. The true percentage was most likely between 53.16 and 67.97, but this range emphasizes the uncertainty of estimates obtained by the rearing method. Rearing of first and second instars was not attempted, but their mortality would undoubtedly have been much greater.

Experience thus indicated that future work could be lightened and the results much improved if the living larvae were dissected promptly after being classified. The dissections were made under a binocular, each larva being placed with water in a watch glass, the head severed, and the body turned wrong side out over the point of a dissecting needle.[6] A black cloth beneath the watch glass aided detection of the translucent eggs and larvae of the parasite.

Reasonably accurate results were generally obtained from dissection of 25 of each instar from each of the 8 samples, but since a constant degree of accuracy was sought the number of larvae dissected was not fixed. Instead, a given batch of larvae, representing the collection of a certain instar from a single sample, was thoroughly mixed and 5 were taken at random, the process being repeated until 5 lots had been obtained. The number of parasitized individuals in each lot was recorded separately, and the variability of sampling was measured by the probable error of the mean. When this value exceeded an arbitrarily established standard, 25 more larvae of like origin were similarly chosen and dissected, and the results were combined with those from the first group. If the mean of the 10 lots did not meet the required standard of homogeneity, the process was continued until it was realized. As a matter of fact only occasionally were the results of the first 5 lots so variable as to necessitate dissection of a second set, and very rarely was a third set needed.

The method may be illustrated by the dissection record of second instars from samples taken May 25, 1931, as shown in table 2. Parasitization in one sample was very variable, as reflected by the first five lots dissected, and the probable error of the mean exceeded the arbitrary standard of 7 percent. Consequently, five more lots from the same sample were dissected and the results combined with those from the first set. The probable error of the mean was now found to come within the established limit of variability for a single sample. This result was combined with data from the other seven samples taken on May 25, none of which required dissection of more than five

TABLE 2.—*Parasitization of second-instar alfalfa weevil larvae in a single sample and in 8 samples representing one entire weekly collection taken May 25, 1931, Salt Lake Valley, Utah*

Percentage of parasitization	Frequency of occurrence: In a single sample—Based upon 5 lots	Frequency of occurrence: In a single sample—Based upon 10 lots	Frequency of occurrence: In 45 lots from 8 samples
0	0	0	0
20	1	1	5
40	0	0	7
60	2	4	16
80	1	4	15
100	1	1	2
	Percent	*Percent*	*Percent*
Mean ± 0.6745	64 ± 9	68 ± 4.6	60.89 ± 2.14

[6] This method, devised by F. H. Harries, of the Bureau of Entomology and Plant Quarantine, was adopted in 1930 and employed thereafter.

lots, and provided the mean parasitization of second instars for that census.

In general, then, each weekly percentage for each instar was based upon at least 40 lots, or 200 individuals. Early in the season before the larvae became sufficiently abundant for each sample to supply 25 of each instar, the foregoing procedure could only be approximated. This condition also obtained after cutting of the first alfalfa crop.

Measurement of Temperature and Precipitation

Because of the important influence of heat upon insect activities, in this study the temperature was measured in the place inhabited by the weevil; that is, in an alfalfa field. At any one time, however, an alfalfa field provides a wide range of temperatures resulting from exposure of different sides of the alfalfa crowns and the field corrugations to the sun and the irregular pattern of shade afforded by the plants. Moreover, these differences change with the angle of incidence of the sun's rays during the day, as well as from day to day with the seasonal advance and the growth of the alfalfa. In addition there are differences in temperature at different levels among the alfalfa plants, due chiefly to the greater or lesser influence of the soil or air temperature. It is manifestly impossible therefore to represent by a single measurement the temperature affecting the entire weevil population; but since the weevil itself is mobile in its larval and adult stages, much of the effect of the variation tends to be averaged out.

Since not all stages of the weevil live at the same level, the most useful temperature is that prevailing near the point where most of the eggs occur, because the effects of temperature upon them also influence the succeeding immature stages. Accordingly, the temperature was measured 3 to 4 inches above the surface of the soil. This level also approximates that near which most of the weevil cocoons are spun and the adults spend much of their time. For this purpose a thermograph [7] was placed in one corner of an alfalfa field adjacent to the field in which the weevil population was studied. Accurate temperature readings were obtained by shading the thermometric element and a minimum of the surrounding area with small strips of canvas, which were adjusted to compensate for seasonal changes in sunlight.

The temperature was expressed in effective day-degrees, computed from the thermograph charts by measuring with a planimeter the area lying below the line traced by the recording pen and above 50° F.,[8] 1 day-degree being equivalent to 1° above the threshold of development for 24 hours. In this manner the number of day-degrees was computed for each day of the 6-year period 1928-33.

Precipitation was measured by means of a standard Weather Bureau rain gage suitably located on the same farm. However, Weather Bureau records taken at Midvale, Utah, 2 miles distant, have been used, since they showed no marked differences and provided a longer record.

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[7] This thermograph was installed in 1928 by G. I. Reeves, of the Bureau of Entomology and Plant Quarantine.

[8] Selected as the most useful average of the differing zeros of effective temperature for the activities of oviposition, incubation, and larval development as indicated by unpublished results of F. H. Harries, S. J. Snow, and I. M. Hawley.

TRENDS OF THE WEEVIL POPULATION

The trend of each phase of the weevil population, based upon 3 years' data, may now be described separately to show its general characteristics. Later (p. 73) the successive phases in a season will be treated as a whole to bring out the net effect of the environment upon a weevil population.

Population of Overwintered Adult Weevils

The population of overwintered adults begins to decline in April and decreases rapidly in May and June. The few that survive into July gradually die out and disappear by the end of the summer. This

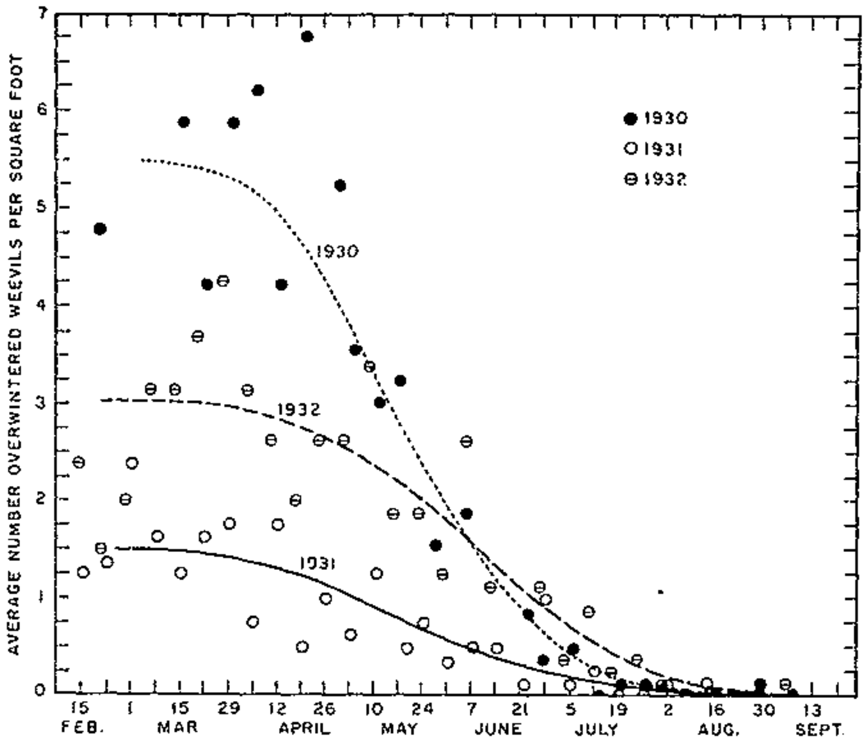

Figure 2.—Population of overwintered adult alfalfa weevils, by month and year, 1930–32, Salt Lake Valley, Utah.

trend is shown in figure 2. Beginning with averages of 5.59 adults[9] in the spring of 1930, 1.54 in 1931, and 2.86 in 1932, these populations had vanished by September of each year.

The parent weevils present in the spring were produced the preceding summer, and only a small percentage of the females developed

[9] Unless otherwise specified, all estimates of abundance refer to square-foot areas.

mature eggs before winter.[10] With the coming of early-spring warmth the percentage with eggs increases over a period of several weeks. In 1932, for example, samplings made in the study field at weekly intervals from March 14 to April 4 showed 15, 31, 88, and 100 percent of the females gravid.

Egg Population

EFFECT OF TEMPERATURE AND PRECIPITATION ON EGG LAYING

The first egg laying in the spring is restricted to females that reached sexual maturity the preceding fall. With rising temperature and more females developing eggs there comes an enormous increase in the egg population, followed after a time by a decrease due to hatching. Since the larvae increase at the expense of the egg population, the fairest index of egg production is the increase in the immature population, including both eggs and larvae. Just what conditions promote the egg laying upon which this increase depends may be determined by resolving the day-degree value of each week into its components of time and temperature. These values for the 3 years of the study are plotted in figure 3.

Each season the two curves follow roughly the same path, rising from zero near the end of winter, when only a small fraction of the day has temperatures over 50° F., to maximum values in midsummer, when the temperature exceeds 50° nearly all day. The immature population begins to increase shortly after the first temperatures above 50° are recorded, and reaches its peak soon after the middle of the upward trend of the curves. The period of most rapid increase slightly precedes the middle third of the upward slope of the curves. Thus the most abundant egg laying occurs when the temperature oscillates daily about 50°.

Unpublished data obtained by F. H. Harries show that the rates of egg deposition at 80° and 90° F. exceeded those at all lower temperatures, but that egg laying was not long continued and ceased abruptly. The temperatures most suitable for oviposition were not the most favorable for ovogenesis; that is, the development of the eggs in the ovaries. On the other hand, the abundance of full-sized eggs in mature females collected from the field during late winter or early spring indicates that ovogenesis may proceed at temperatures considerably below 50°, which are little suited to oviposition. That this is actually the case may be shown by unpublished data recorded by S. J. Snow. Female weevils collected September 27 to October 3 showed slight ovarian development, only 16 percent with ovaries segmented or with mature eggs. Dissection of lots of 40 to 100 females after they had been kept in constant-temperature cabinets for 13 weeks at 60°, 50°, and 40° showed 23, 42, and 90 percent, respectively, with ovaries developed as far as the segmentation stage. It thus appears that the daily oscillation at a temperature of about 50° promotes the most abundant ovulation, the negative phase favoring ovogenesis and the positive phase favoring oviposition.

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[10] Recent studies at Grand Junction, Colo., show that under different climatic conditions a greater percentage of females may mature and deposit eggs before halted by winter cold.

The most rapid increase in the immature population takes place in the spring when, during periods of 5 to 15 hours per day, the temperature averages 5° to 15° above 50° F. Multiplying the extremes of these two values gives 25 to 225 as the range of hour-degrees per day, which is equivalent to 7.29 to 65.63 day-degrees per week. These may be considered as the limits of optimum conditions for egg laying;

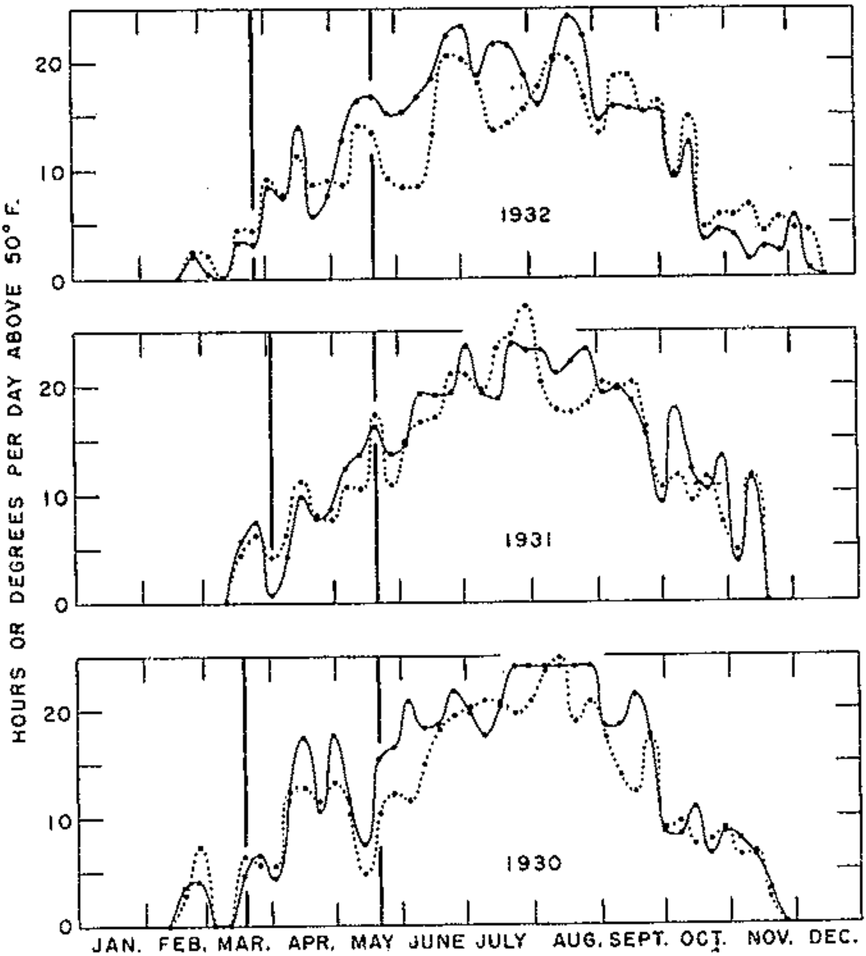

FIGURE 3.—Egg laying of the alfalfa weevil with reference to time and number of degrees above 50° F., 1930–32, Salt Lake Valley, Utah. The solid line represents the average hours per day, the dotted line the average degrees above 50°. The space between the vertical lines represents the period of most rapid egg laying.

but they are not rigid limits, since egg laying in any 1 week is affected by antecedent conditions, particularly the temperature of the preceding week. For instance, a week totaling more than 65 day-degrees will favor egg laying when it follows a week having low temperatures, while the same amount of heat per week sustained for 3 to 4 weeks greatly reduces egg laying. The effect of a given number of day-degrees is also modified by the decreasing egg-laying potentiality of females as the season advances.

While egg laying has been discussed entirely in terms of temperature, it must be remembered that the temperature is much affected by precipitation in the spring, which normally is the wettest season in Salt Lake Valley. Indeed, the rainy periods at this time contribute largely to the unevenness of the transition from winter cold to summer heat. The spring precipitation thus has an important influence in prolonging or curtailing the conditions favorable to egg laying.

Precipitation may have independent effects upon egg laying, but this factor is so closely associated with temperature that in studies of this type under uncontrolled conditions little can be said definitely about it. The data indicate, however, that egg laying proceeds best when brief rainy periods occur frequently throughout the spring, but if the rainy period extends over 2 or more weeks the laying rate is temporarily reduced.

Egg laying by the dwindling number of overwintered females continues during midsummer, possibly being aided by the cooling effect of irrigation. Oviposition by the few mature females of the new generation produced in June and July begins in the rainy fall season when, in the course of the transition from summer heat to winter cold, the number of degrees and hours per day above 50° passes through the range above cited. In this case, however, the egg laying is terminated soon after it starts when the temperature remains below 50° throughout the day.

OCCURRENCE OF EGGS IN LITTER AND IN GROWING STEMS

Eggs occur both in litter on the ground, consisting mostly of broken dead alfalfa and grass stems, and in growing alfalfa stems. Table 3 shows that all the clusters found in dead stems were in those having diameters of over 0.5 to and including 3.5 mm. No doubt the weevils

TABLE 3.—*Distribution of egg clusters of the alfalfa weevil according to diameter of dead and growing alfalfa and grass stems, Salt Lake Valley, Utah, 1929*

Diameter of stems, in millimeters, up to and including—	Dead stems				Growing stems			
	Aggregate length		Egg clusters		Stems		Egg clusters	
	In.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
0.5	32.50	0.81	0	0	0	0	0	0
1.0	734.00	18.30	41	37.96	143	20.03	29	23.20
1.5	1,903.75	47.46	86	79.63	271	37.96	60	48.00
2.5	3,488.00	86.96	108	100.00	492	68.91	95	76.00
3.5	3,915.00	97.61	108	100.00	630	88.24	118	94.40
All sizes	4,011.00	100.00	108	100.00	714	100.00	125	100.00

prefer the thinner walls and softer texture of the smaller stems. This table further shows that eggs occur in growing stems of all sizes.

Figure 4 shows graphically the disproportionate selection of the smaller dead stems for oviposition, and the placing of eggs in growing stems with little regard to size.

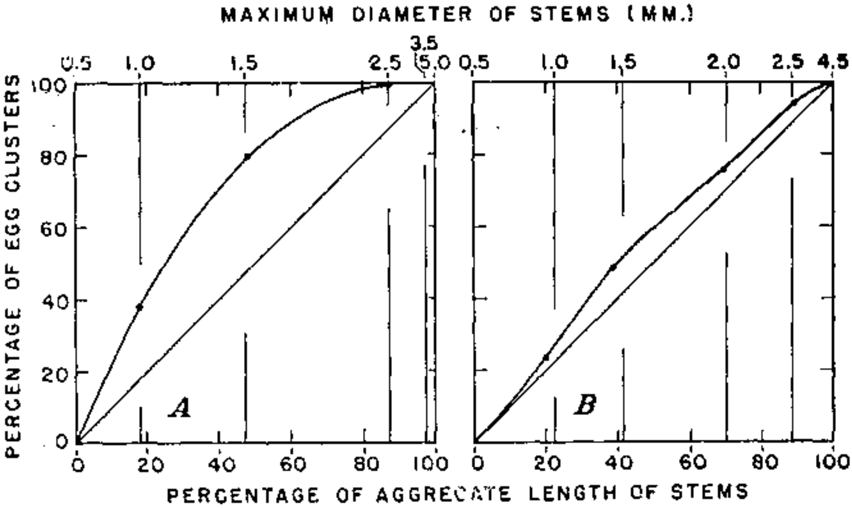

FIGURE 4.—Occurrence of egg clusters of the alfalfa weevil in dead (*A*) and growing (*B*) stems of different sizes, Salt Lake Valley, Utah, 1929. The curves show the percentage of clusters in stems up to a given diameter, and the diagonal lines show the distributions as they would be if eggs were deposited in stems at random.

The vertical distribution of egg clusters in growing alfalfa stems collected during the latter part of the first-crop periods of 1931 and 1932 is shown in figure 5. The study was limited to the period from May 20 to June 17, because egg laying was then plentiful and the

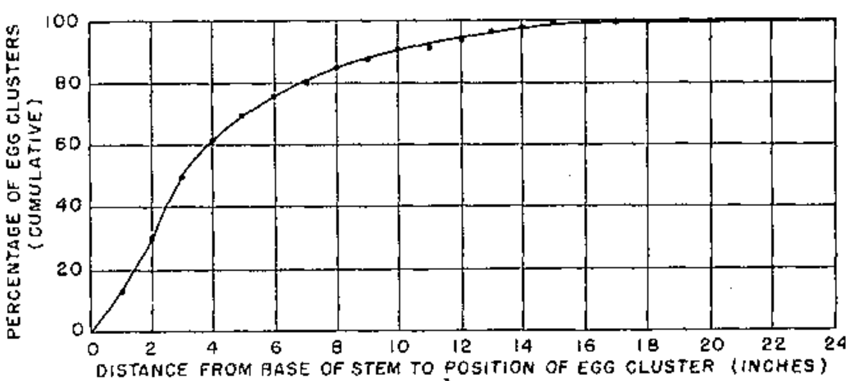

FIGURE 5.—Vertical distribution of 843 egg clusters of the alfalfa weevil in growing stems of all sizes. Salt Lake Valley, Utah, 1931 and 1932.

alfalfa close to its full height; earlier in the season eggs laid in the shorter plants were of necessity near the ground, and after the first harvest eggs were too scarce to permit valid studies of this point.

Although egg clusters were found as high as 2 feet above ground, the majority were near the base of the stem. Thus, 50 percent of the clusters were within 3 inches of the base, 60 percent in the lower 4 inches, and 90 percent in the lower 10 inches. A thermograph with its thermometric element 3 to 4 inches above the soil surface is thus very favorably located for temperature measurements, as discussed on p. 10.

In 1930 data were obtained relative to the structure of growing alfalfa stems at the points of egg deposition. As shown in table 4, the egg clusters were concentrated in the pithy part of growing alfalfa stems, those occurring in all other parts of the alfalfa plant barely exceeding the number found in grass stems. The few clusters found in terminal buds were deposited early in the season and represent an exceptional condition. The eggs found in grass stems occurred late in the period, May 18 to June 6, when the alfalfa was beginning to mature.

TABLE 4.—*Location of egg clusters of the alfalfa weevil in growing stems, first-crop period of 1930, Salt Lake Valley, Utah*

Location	Egg clusters	
	Number	*Percent*
Alfalfa stems:		
Terminal buds	5	0.50
Solid part	32	3.17
Pithy part	861	85.42
Hollow part	39	3.87
Grass stems	71	7.04

SIZE OF THE EGG CLUSTER

The egg clusters of the alfalfa weevil are placed inside the stems, through a circular hole made by the female. The size of these clusters has been stated by a number of workers. Titus (*16*) indicated the number of eggs as ranging from 1 to 28 with an average of 6.29 per puncture, and later (*17*) stated the range as 1 to 45. Webster (*18*) gave the range as 2 to over 30, with an average of about 10. Parks (*10*) indicated the usual number as 6 to 14 eggs, and later (*11*) gave the range as 2 to 30 and the usual number as 6 to 18. Hagan (*5*) stated the maximum number per puncture as 40. List and Wakeland (*9*) and Snow (*13*) indicated the range to be 1 to 30 or more. Reeves (*12*) gave the range as 4 to 16, with an average of about 10. Sweetman (*15*) gave a range of 3 to 12, with the usual number as 6 to 9, and the maximum as 45.

The eggs collected in the course of periodic field samplings during the present study (table 5) show considerable seasonal variation in the size of clusters, those in litter containing from 6.0 to 9.2 eggs, and those in growing stems from 6.5 to 10.0. The seasonal average for growing stems exceeded that in litter by 1.2 eggs per cluster.

"Cluster" as here used refers to a discrete group of eggs. Groups representing two separate depositions were frequently found which

TABLE 5.—*Seasonal variation in size of egg clusters of the alfalfa weevil, Salt Lake Valley, Utah, 1930–32*

Season of year	In litter			In growing stems		
	Clusters	Eggs	Mean eggs per cluster	Clusters	Eggs	Mean eggs per cluster
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
October through February	164	1, 210	7. 4	------	------	------
March	332	2, 553	7. 7	------	------	------
April	1, 934	17, 713	9. 2	165	1, 083	6. 6
May	3, 278	26, 737	8. 2	1, 525	15, 226	10. 0
June, before first cutting	470	3, 297	7. 0	541	5, 431	10. 0
June, after first cutting, through September	188	1, 129	6. 0	178	1, 150	6. 5
Total or mean	6, 366	52, 639	8. 3	2, 409	22, 890	9. 5

were but slightly separated, and occasionally large clusters showed a difference in coloration which clearly indicated them to represent two separate depositions. A few groups, however, were recorded as single clusters because no evidence of multiple origin was discernible in the necessarily rapid inspection, although it is the authors' belief that they represent multiple clusters which were laid at so nearly the same time that differences could not be detected.

Statistically there is only 1 chance out of 200 that a true single cluster would deviate more than 3 times the standard error from the average size, and Chauvenet's criterion, although of questionable applicability to these data, indicates 3.7 times the standard error as the limit of fortuitous occurrence. The evidence of multiple origin supplied by differences in coloration and gelatinous envelope in the case of many of the exceptionally large groups lends weight to the statistical indication that green-stem clusters in excess of 28 eggs and litter clusters in excess of 26 eggs are probably of multiple origin.

The clusters taken from litter ranged from 1 to 45 eggs, exactly the range given by Titus (*17*), and clusters from growing stems ranged from 1 to 33 eggs. These great ranges vitiate somewhat the usefulness of the averages given above and indicate that a better idea of cluster size may be gained from the relative frequency of different-sized clusters and the relative proportion of the total egg population contributed by clusters of each size. The graph of the data relating to eggs in both litter and growing stems, presented in figure 6, reveals a considerable positive skew. The most frequently encountered cluster in litter contains 6 eggs, while clusters of 8 eggs are most frequent in growing stems. Likewise, clusters of 9 and 11 eggs in litter and growing stems, respectively, contribute the greatest proportion of total eggs.

The approximate limits of cluster size within which various proportions of the egg populations occur may be determined by grouping the cluster sizes contributing the largest percentages of eggs, as in table 6.

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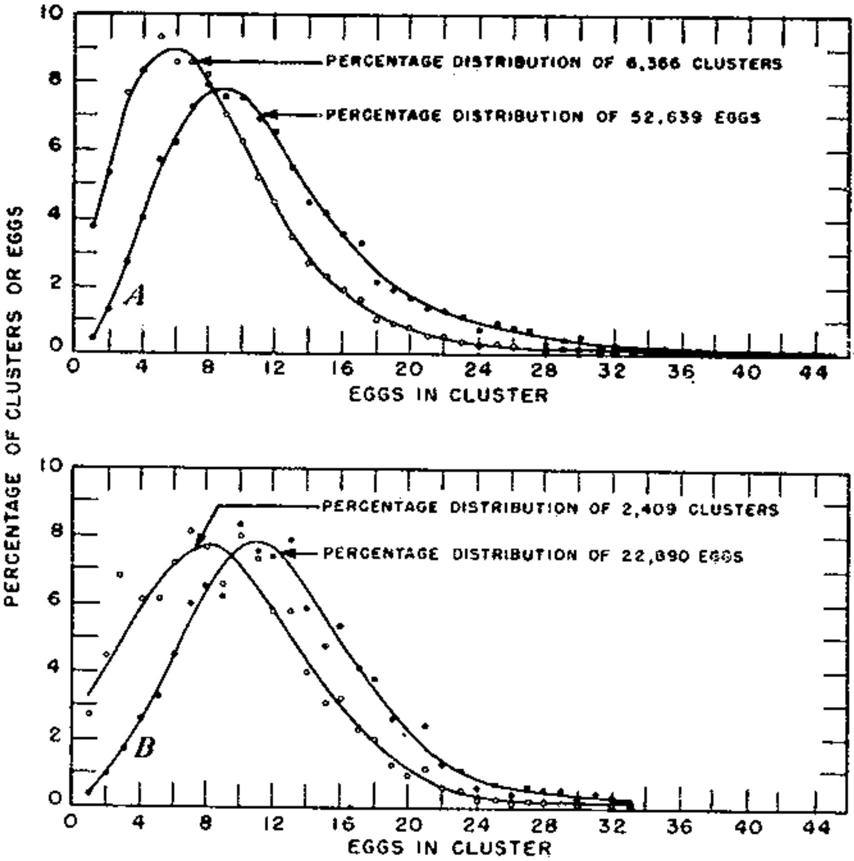

FIGURE 6.—Percentage of clusters and eggs of the alfalfa weevil (*A*) different-sized egg clusters from litter and (*B*) from growing stems, Salt Lake Valley, Utah.

TABLE 6.—*Size of clusters containing half or more of the alfalfa weevil eggs laid in litter and growing stems, Salt Lake Valley, Utah*

Class grouping of population, in percent	Eggs per cluster—In litter	Eggs per cluster—In growing stems	Class grouping of population in percent	Eggs per cluster—In litter	Eggs per cluster—In growing stems
	Number	*Number*		*Number*	*Number*
50	6 to 12	7 to 13	90	3 to 20	4 to 21
67	5 to 14	7 to 16	100	1 to 45	1 to 33
75	4 to 15	6 to 17			

SEQUENCE OF EGG ABUNDANCE IN LITTER AND IN GROWING STEMS

Although the early egg laying is restricted to litter, a few eggs are found in the growing alfalfa stems when the crop becomes about 6 inches tall. As the season advances, the egg population shifts more and more from the litter, until late in the first-crop period the eggs preponderate in the growing stems. The relation between these two parts of the egg population for each of the 3 years under study is shown in figure 7. The peak abundance in litter is reached about the end of April, and that in growing stems about the third week in May.

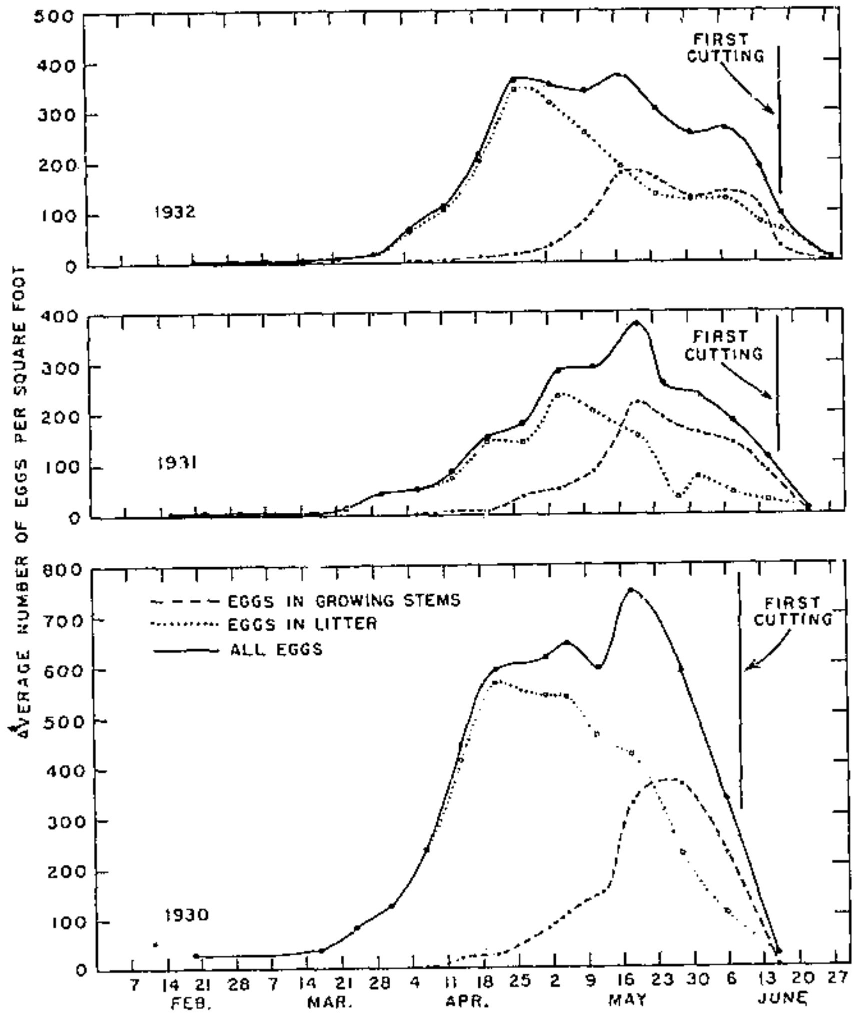

FIGURE 7.—Alfalfa weevil egg populations, showing the sequence of egg abundance in litter and in growing alfalfa stems, as well as that of all eggs laid, 1930-32, Salt Lake Valley, Utah.

This shift seems to be due partly to the drying and hardening of dead stems and partly to their location on the ground, which accelerates hatching.

DISTRIBUTION OF TOTAL EGG POPULATION

The curves for the entire egg population for each season (fig. 7) show that, beginning in March at the low level representing the few eggs that were laid the previous fall and survived the winter, the populations increase slightly at first, then rise rapidly to a peak in May, and finally decline to small values just after the cutting of the first alfalfa crop in June. The nature of these curves suggests that they may be approximations of the normal distribution, with equations of the type

$$y=\frac{N}{\sigma\sqrt{2\pi}}e^{-\frac{x^2}{2\sigma^2}}$$

where y is the magnitude of the egg population in any week, N is the total number of eggs present (sum of weekly abundance), σ is the standard deviation about the mean of the X axis, e is a constant, 2.718, the limit of $(1+\frac{1}{n})^n$ as $n \to \infty$; and x is the deviation in weeks from the mean (18.5) of the X axis.

The egg population for each week in 1930 calculated from this formula is shown in table 7.

TABLE 7.—*Calculated values of the alfalfa weevil egg population per square foot, during 1930, Salt Lake Valley, Utah*

Week of year	Plus or minus deviation from origin (18.5 week of year) (x)	Calculated egg population (y)	Week of year	Plus or minus deviation from origin (18.5 week of year) (x)	Calculated egg population (y)
18.5	0	731.06	12 and 25	6.5	77.36
18 and 19	.5	721.41	11 and 26	7.5	30.76
17 and 20	1.5	648.64	10 and 27	8.5	15.70
16 and 21	2.5	524.40	9 and 28	9.5	6.03
15 and 22	3.5	381.19	8 and 29	10.5	2.08
14 and 23	4.5	249.14	7 and 30	11.5	.65
13 and 24	5.5	146.41			

The agreement of these calculated values, representing the normal distribution, with those determined by actual counts are indicated in figure 8. By the same procedure normal-distribution curves have been fitted to the egg populations of 1931 and 1932, also shown in figure 8.

It will be noted that, although the magnitude of the egg populations varied considerably, particularly between 1930 and 1931, the general agreement of the mathematically computed curves with the observational curves is good, especially since the egg population was estimated

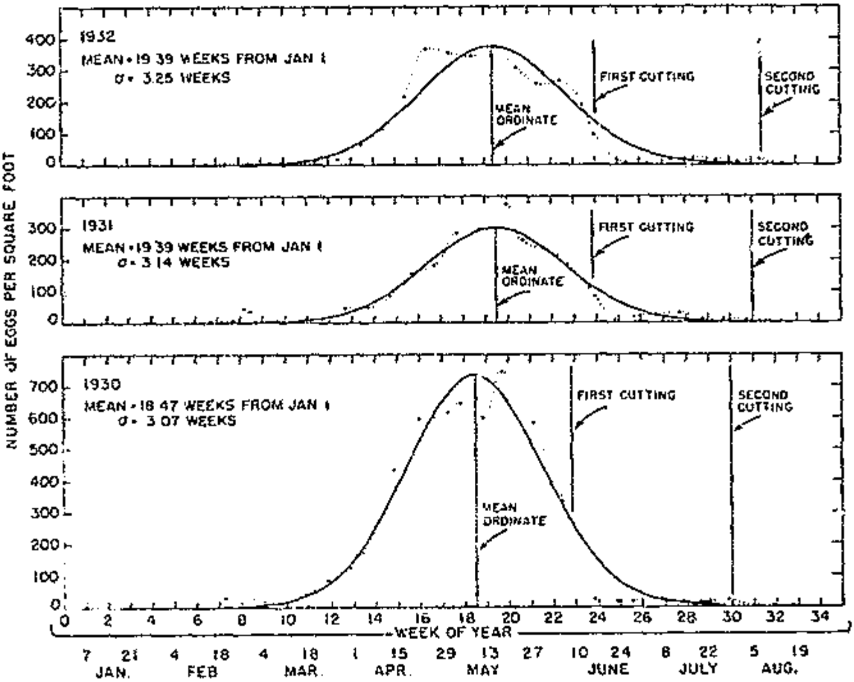

FIGURE 8.—Observed egg population of the alfalfa weevil as compared with the *normal distribution*, 1930–32, Salt Lake Valley, Utah. Continuous lines represent the calculated and dotted lines the observed populations.

from only eight samples per week. The experimental error thus doubtless accounts for the majority of the discrepancies between the two curves for each year. The discrepancies at the peak of the 1930 curve and those in 1932 are believed to be due to influences of the weather, as discussed on page 67.

A constant difference between the curves of each pair is shown just after the cutting of the first alfalfa crop, the observed values being much below those calculated. These differences are due to the perishing of the eggs, or of the resulting larvae, as a consequence of the drastic ecological changes produced by crop cutting. Nevertheless, the fit is sufficiently good to justify the conclusion that the normal distribution provides an adequate description of the egg population. Therefore, the egg population as it ordinarily exists in Salt Lake Valley may be characterized in terms of the mean of the oviposition season and its standard deviation (table 8).

The means of these distributions, as shown by their ordinates, indicate that the peak of the egg populations occurred about the nineteenth week of each year, and averaged May 14. In the case of the normal distribution 68.27 percent of the area under the curve lies within an interval of $\pm\sigma$, measured from the mean ordinate. Thus, with the average standard deviation of 3.15 weeks, approximately two-thirds of the egg population is concentrated in a period of 6.3 weeks centering on May 14.

TABLE 8.—*Mean and standard deviation (σ) of the oviposition season in Salt Lake Valley, Utah, 1930–32, and in Rogue River Valley, Oreg., 1932–33*

Year	Oviposition season			
	Salt Lake Valley		Rogue River Valley	
	Mean	σ	Mean	σ
	Week of year	*Weeks*	*Week of year*	*Weeks*
1930	18.5	3.07		
1931	19.5	3.14		
1932	19.4	3.25	15.4	4.14
1933			17.1	4.12
Average	19.1	3.15	16.3	4.13

The building up of a large egg population, proportioned of course to the number of overwintered adult weevils, results from the trend of the spring temperatures, shown in figure 3. At first the range is suitable for oviposition but does not promote rapid hatching, and there is built up a large reservoir of eggs in varying degrees of incubation. With continued rise in temperature, conditions favorable to hatching are reached, and the reservoir pours huge numbers of larvae on the alfalfa crop in a short period of time, the effect being comparable to the breaking of a dam.

This phenomenon is characteristic of Salt Lake Valley conditions and accounts for the fact that weevil larvae frequently do considerable damage in that area. As shown above σ measures the extent to which the egg population is concentrated. Therefore, when σ has been determined for different areas, it may be employed as an index to the weevil's injuriousness. More exactly, σ provides an index of the modifying influence of weather upon the potential injuriousness of the weevil.

EGG POPULATIONS IN ROGUE RIVER VALLEY

Similar data from Rogue River Valley (fig. 9) permit comparison of the egg populations under climatic conditions somewhat different from those in Salt Lake Valley. In both 1932 and 1933 the egg population showed the same sequence in litter and growing stems as in Salt Lake Valley; the total egg population also showed a general resemblance to that in Salt Lake Valley, although the curves are more flattened.

When normal-distribution curves have been fitted to the data (fig. 10), it is clear that the agreement is satisfactory. In both years the observed values lie below the computed ones just after the first cutting, although this discrepancy is not so marked as in the graphs for Salt Lake Valley. The other differences appear to be due mostly to experimental error together with weather influences.

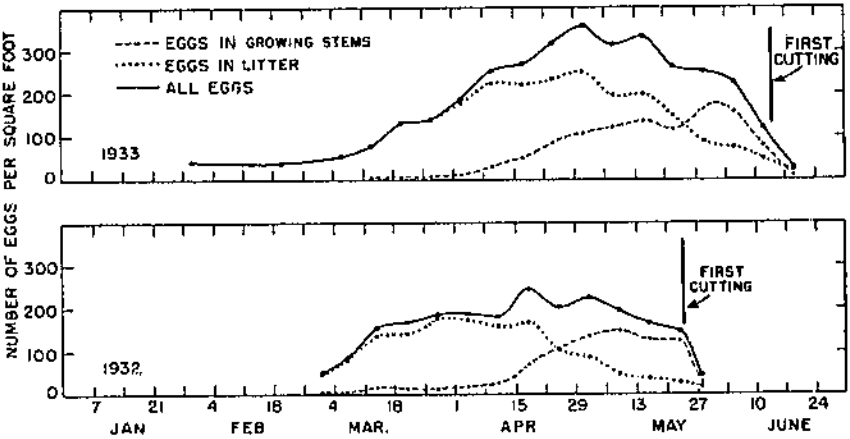

FIGURE 9.—Alfalfa weevil egg populations, showing the sequence of egg abundance in litter and in growing alfalfa stems, as well as that of all eggs laid, 1932–33, Rogue River Valley, Oreg.

The statistical descriptions of these populations are included in table 8. The central peak of the population occurred about the sixteenth week of the year, or April 24, which is practically 3 weeks earlier than at Salt Lake. Moreover, the standard deviation of the oviposition season, 4.13 weeks, exceeds that for Salt Lake by 1 week and shows a greater dispersion of the egg population. This means that approximately 8.3 weeks is required to include roughly two-thirds of the egg population as compared with 6.3 weeks for the same proportion at Salt Lake.

The composition of the egg population is constantly changing owing to continued oviposition and hatching. Early in the season there is virtually no loss through hatching, and all eggs laid result in increasing the egg population. As the season advances the increase due to egg laying is partly offset by losses due to hatching, and this

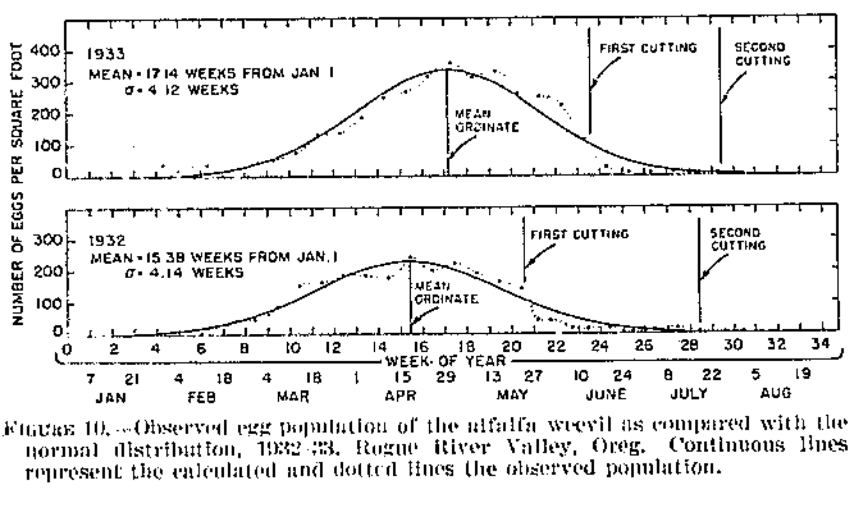

FIGURE 10.—Observed egg population of the alfalfa weevil as compared with the normal distribution, 1932–33, Rogue River Valley, Oreg. Continuous lines represent the calculated and dotted lines the observed population.

trend continues until the two processes balance each other, when the procedure is reversed. The temperatures suitable for hatching are not so long delayed in Rogue River Valley as in Salt Lake Valley, and, once begun, hatching tends more nearly to keep pace with oviposition. Consequently the egg population is prevented from rising to a well-defined peak, and the curve is more flattened. This is the physical meaning of the greater value of σ in the Rogue River Valley.

If, then, σ is a valid measure of the potential injuriousness of the alfalfa weevil, a given population of overwintered adults should cause less damage in Rogue River Valley than in Salt Lake Valley. As a matter of fact, in the spring of 1932, the study fields in these areas had almost identical adult populations, and the damage to the first crop was less severe in Rogue River Valley.

The injuriousness of the alfalfa weevil thus appears to vary inversely with the standard deviation of the oviposition season, which is determined by the character of the spring climate. This does not mean that crop damage will necessarily be light in areas where the oviposition season has a large value of σ, but rather that a larger population of adults will be required to produce damage. In such areas other factors may contribute to the production and survival of large adult populations.

There may be sections of weevil-infested territory where the spring weather is such as to produce a small value of σ and thus allow damage to the first crop by fewer parent weevils. On the other hand, it seems likely that the climate of the infested lowland districts in California would give a still larger value of σ than that found for Rogue River Valley, and thus diminish the injuriousness of the pest. The present studies, however, have been conducted entirely in districts following the three-crop harvesting system; in districts, such as parts of California, having more cuttings annually, or in others cutting but twice in the year, these indications of the meaning of σ have not been tested.

EGG POPULATIONS DURING THE SECOND-CROP PERIOD

The discussion of the egg population up to this point has been concerned almost exclusively with the main part of that population which obtains during the first-crop growing period. Figure 8, however, shows a tailing out of the egg population, mainly during the second-crop period, which reflects oviposition by the few overwintered adults that survive the first cutting.

The second-crop part of the population is trivial numerically, the peak abundance amounting to only 3.5, 7.6, and 5.3 percent of the first-crop peak in Salt Lake Valley during 1930, 1931, and 1932, respectively. Nevertheless, because of their production of new-generation weevils these second-crop eggs are important out of all proportion to their number, and may contribute the principal part of the adult population that will form the basis of the succeeding year's attack on the alfalfa crop. The conditions that bring this about are discussed on page 45.

Larval Population

Hatching of the accumulated eggs begins in volume about the first of May in Salt Lake Valley, and in general the larval population grows most rapidly during this month, as shown in figure 11. Early in June, however, the trend of these curves is halted by the cutting of the first alfalfa crop, and the larval population decreases virtually to zero within 1 to 2 weeks. Then, with renewed growth of the alfalfa, and originating from the tailing-out egg population just men-

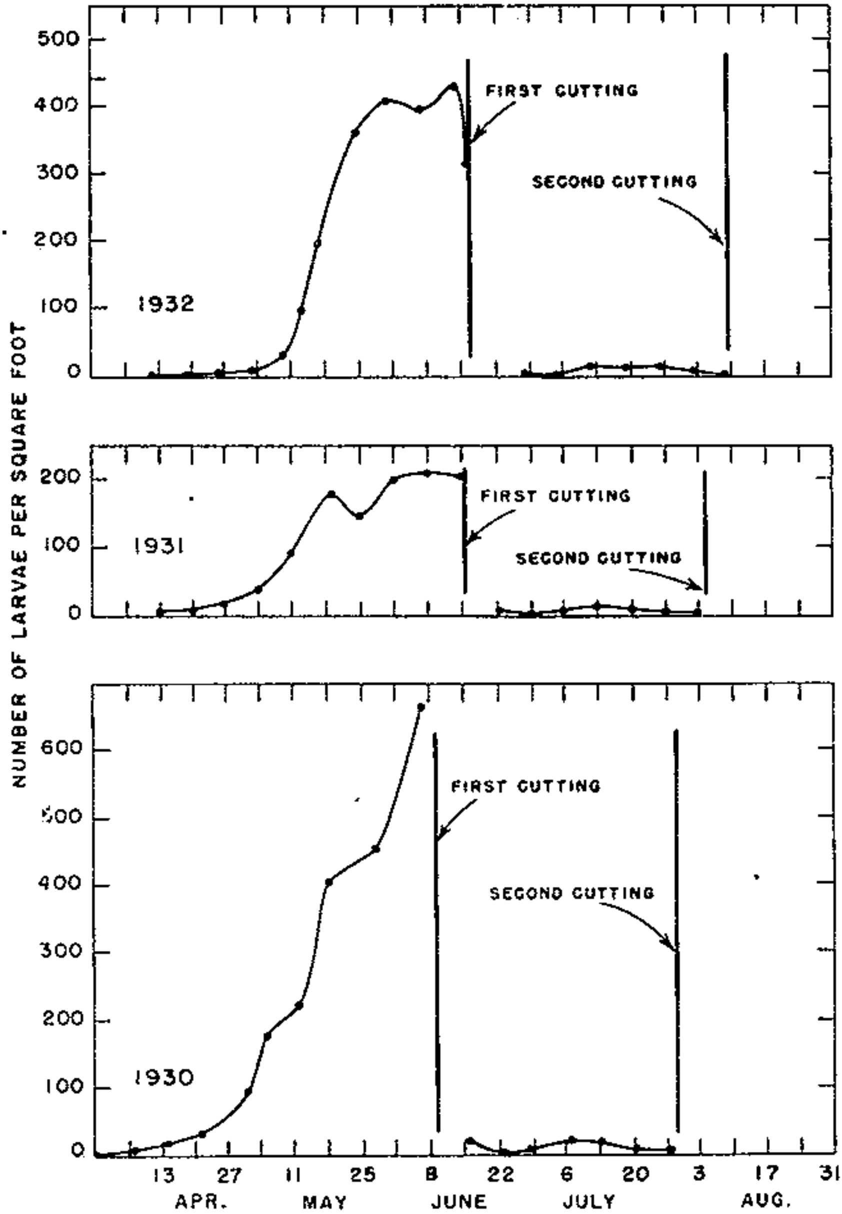

FIGURE 11.—Larval population of the alfalfa weevil, 1930–32, Salt Lake Valley, Utah.

tioned, the larval population again increases during the second-crop period, although the peak is only a mere fraction of that attained during the first-crop period. Occasional larvae are found in the third-crop period, but they are of little consequence.

The curves for 1931 and 1932 indicate that the larval populations had already reached their maxima before the first cutting and that, but for the interruption of the trends thus occasioned, they would have graded off to small values much as the egg populations do. In fact, in instances where great delay in cutting the first crop has allowed the larval population to run its course, it has risen to a peak and then gradually subsided. There is thus small doubt that the trend of the larval population, like that of the egg population, would approximate the normal-distribution curve in the absence of cultural interruption.

LARVAL LAG

Comparison of figures 8 and 11 shows a general resemblance in the up slope of the egg and larval populations, although one comes earlier in the year than the other. Consequently the time lag between a given abundance of eggs and the same abundance of larvae may readily be measured. The interval, which may be called the larval lag, is determined by plotting the parts of the egg and larval curves having a pronounced positive slope as in figure 12, drawing smooth freehand curves for both, and measuring the horizontal distance between them. Begining on the 50 level, measurements of the interval were made for each increase of 25 in both populations during the first-crop period. Thus in 1930 in Salt Lake Valley the lag, on the level of 50 eggs and 50 larvae, was 35 days; on the 200 level, 33 days; on the 400 level, 38 days; and so on.

The larval lag differs from the incubation period both in concept and in manner of determination. That is, the lag is lengthened by any natural mortality of the species; and, since it is derived from an entire field population freely exposed to natural forces, it is free from the errors of the incubation period exactly determined but affected by abnormalities the extent of which are unknown.

In 1930 the larval lag was 35 days early in the season (late March to the end of April), dropped to a minimum of 33 days, and then with the arrival of cool, rainy weather rose to 42 days late in the first-crop period (mid-April to late May). In 1931, a dry year, the lag decreased steadily from 32 to 20 days, and during 1932 it declined from 37 to 28 days.

Early in the season, before the alfalfa has made much growth, the eggs get nearly the full effect of the sun's heat, but as the plants shade the ground more and more this shade largely offsets the increasing seasonal heat. Thus, the larval lag is but little shortened with the advance of the season, and it was actually lengthened in 1930 during a rainy period.

In Rogue River Valley in 1932, when the weather was exceptionally dry and warm early in the season and later was wet and cool, the larval lag increased from 47 to 52 days; but in 1933 the lag decreased from 47 to 22 days, when the season showed a steadily increasing deficiency of precipitation, tending to make the spring weather more like that in Salt Lake Valley. Table 9 shows that there was considerable seasonal

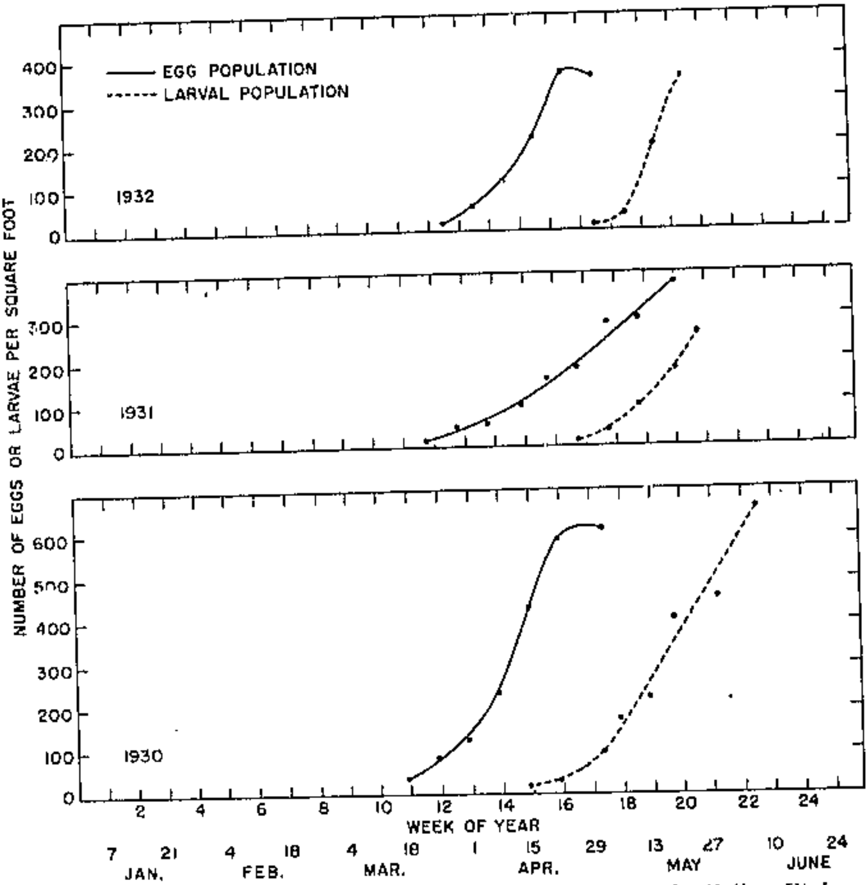

FIGURE 12.—Larval lag of the alfalfa weevil, 1930–32, Salt Lake Valley, Utah.

TABLE 9.—*Larval lag of the alfalfa weevil during the first-crop period in Salt Lake Valley, Utah, 1930–32, and Rogue River Valley, Oreg., 1932–33*

Year	Average larval lag	
	Salt Lake Valley	Rogue River Valley
	Days	*Days*
1930	36. 71	----------
1931	26. 17	----------
1932	30. 62	49. 54
1933	----------	30. 23
Average	31. 17	39. 89

variation in the larval lag in both localities, and that in Rogue River Valley the lag averages approximately 1 week longer than in Salt Lake Valley.

COMPOSITION OF LARVAL POPULATION

Although the harvesting interruption to the trend of the larval population occurred at nearly the same date in all 3 years, its incidence as regards the trends themselves was very different (fig. 11). The 1930 trend was broken while it was still tending upward, but in 1931 and 1932 the peak was reached before the cutting. The meaning of these differences is most easily visualized by breaking down each larval population into the instars composing it, and viewing their trends separately, as in figure 13. In 1931 and 1932 each instar had its own peak of abundance. The first instar, being initially affected by the egg population, established its peak earliest, followed in order by the second, third, and fourth instars. There can be little doubt that this succession of peaks represents the normal course of events when the first cutting is belated. In 1930, however, not even the first instar had reached a peak by the time of the first cutting. Similar timing of the harvest in 1931 and 1932 would have required cutting the first crop roughly 2½ weeks earlier than it was cut.

The composition of the larval population at the time of the first cutting has much to do with the perpetuation of the species, owing to the differential mortality of the several instars. The reductions in total larval population shown in table 10 as occurring 7 or 10 days after the first cutting represent decreases of 96.5, 97.4, and 98.3 percent in 1930, 1931, and 1932, respectively. However, practically all the

TABLE 10.—*Differential reduction of larval instars of the alfalfa weevil following harvest of the first alfalfa crop, 1930–32, Salt Lake Valley, Utah*

Year and interval from first cutting	Larvae per square foot in different instars: First	Second	Third	Fourth	Total larvae per square foot
1930	*Number*	*Number*	*Number*	*Number*	*Number*
3 days before	272.25	173.13	110.00	111.75	667.13
7 days after	0	.25	1.88	21.50	23.63
14 days after	0	.25	.50	1.63	2.38
1931					
1 day before	19.38	42.25	55.13	87.88	204.64
7 days after	0	0	0	5.25	5.25
13 days after	0	.50	.25	.25	1.00
1932					
Few hours before	33.25	57.25	74.38	147.50	312.38
10 days after	0	.13	0	5.25	5.38
17 days after	.50	1.13	.25	.88	2.76

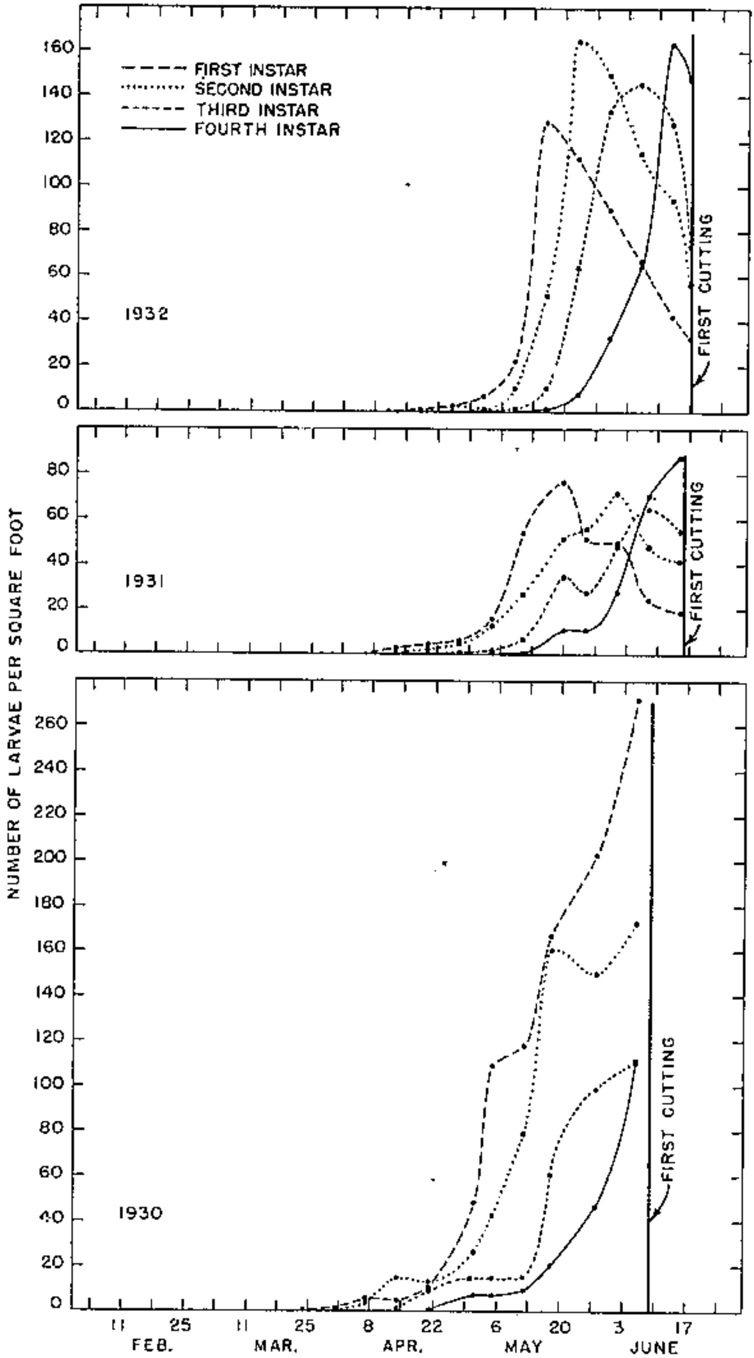

FIGURE 13.—Composition of the larval population of the alfalfa weevil during the first-crop period of 1930–32, Salt Lake Valley, Utah.

survivors are fourth instars. The virtual extinction of the earlier instars results from their starvation and exposure to the sun's rays following removal of the alfalfa. Fourth instars are better able to withstand these adverse conditions; moreover, many of them are mature and therefore subject only to the lethal action of the sun, which some escape by crawling into crevices and beneath the alfalfa crowns to spin their cocoons.

BEHAVIOR OF LARVAE IN STUBBLEFIELD

The behavior of larvae when deprived of the first alfalfa crop was observed in 1930 in the experimental field, which averaged 667.13 larvae per square foot, or over 29 million per acre, 3 days before cutting (table 10). The clear, hot weather was favorable to high mortality. In the midafternoon of the first day after cutting, multitudes of larvae were observed crawling, mostly upward, on the stubble in the open areas between the haycocks. Many larvae were at the top of the stubs, extending their bodies upward into the air apparently in an effort to find some other object upon which to crawl. Further inspection revealed several larvae entering tips of stubs as well as one or more larvae within many of the stubs. The great difference between the temperature of the soil surface and that of the air leaves little doubt that this larval behavior was a reaction from the heated field surface. Moisture of the green stubs and protection afforded from the sun's rays doubtless were the stimuli to which the larvae reacted in entering open ends of the stubs.

Information on the prevalence of this habit was obtained by taking 8 random samples of 100 stubs each at intervals of 2, 5, and 6 days after cutting. The abundance of larvae 2 days after cutting averaged 44.5 per 100 stubs, equivalent to approximately 2 million per acre, and declined to 9.9 per 100 stubs 6 days after cutting. The smaller larvae accounted for the greater part of this decrease. Thus first, second, and third instars present 6 days after cutting represented only 20, 13, and 15 percent, respectively, of the number found on the second day following harvest, as compared with 57 percent for the fourth instars.

At the final examination 41.3 percent of the stubs, although containing neither living nor dead larvae, showed by the evidences of feeding on the interior walls that they had been inhabited; these, in addition to 8.8 percent containing living and 4.5 percent containing dead larvae, totaled 54.6 percent of the stubs. This greatly exceeds the highest percentage of stubs found inhabited at any one time and clearly indicates that the larvae did not remain in the stubs continuously but left them, probably at night, and later re-entered others in the heat of the day. Notwithstanding the prevalence of this habit, the rapidity with which the larval population declines (table 10) indicates that it is of little permanent benefit to the species.

The previous discussion shows that the contribution of the larval population to the adult weevil population depends largely upon those larvae that are mature at first cutting. Such dependence is especially detrimental to the species in view of the higher parasitization of fourth instars by *Bathyplectes curculionis*, as is shown in the section, Parasites Affecting the Alfalfa Weevil (p. 41).

The sparse larval population living on the second alfalfa crop develops rapidly, and a large proportion may thus escape the effect of cutting. At this time also, larvae enter the stubs, but an examination of 800 stubs 3 days after cutting showed that only 0.25 percent were inhabited by living larvae, 0.13 percent contained dead larvae, and 0.38 percent gave evidence of having been vacated.

Cocoon Population

Cocooning ordinarily begins the middle of May in Salt Lake Valley, but it does not occur in volume until near the first of June. The first cocoons thus appear 3 to 4 weeks before the first crop is cut. Therefore, cocooning has just begun to proceed rapidly when the almost complete destruction of the larval population consequent upon the first cutting interrupts it. The peak of the cocoon population is thereby established near the time of the first harvest. Cocooning of the few second-crop larvae produces either a small secondary peak just before the second cutting, as in 1930 and 1931, or merely breaks the downward trend, as in 1932. Within 3 to 4 weeks after the second cutting the number of weevil cocoons is negligible. These relations are shown in figure 14.

The difference in abundance between first- and second-crop cocoons is much less than between the corresponding divisions of larvae, because the huge first-crop larval population had only begun to cocoon when it was almost completely destroyed by cutting, while the numerically insignificant second-crop population had nearly reached its peak of cocooning before being interrupted by cutting.

The cocoons contain some individuals that retain the larval form and others that have either developed into pupae or have produced cocoons of the parasite *Bathyplectes curculionis*. The spun larvae may be either living or dead, and the living ones parasitized or not. The relation of the spun larvae to the entire cocoon population and their mortality for the three seasons under study are shown in table 11.

The spun larvae are most numerous just after the first cutting, and the mortality rises sharply at that time. During the following month their number steadily decreases and the percentage dead increases until only dead larvae remain, marking the end of cocooning of first-crop larvae. About the third week of July the number of spun larvae ceases declining and the percentage of dead larvae decreases, indicating the beginning of cocooning of second-crop larvae. A secondary peak of abundance is reached near the end of July, and following the second cutting most of the larvae are dead. The very high percentages of dead found in 1931 before removal of the second crop were no doubt due to the dry season and a 3-week period of extreme heat.

Of the individuals that develop beyond the larval stage, many produce parasite cocoons instead of weevil pupae, and those that do pupate are further reduced in number by cultural kill. The manner in which these factors operate to limit the production of living pupae is treated later in the section, Parasites Affecting the Alfalfa Weevil (pages 41-58).

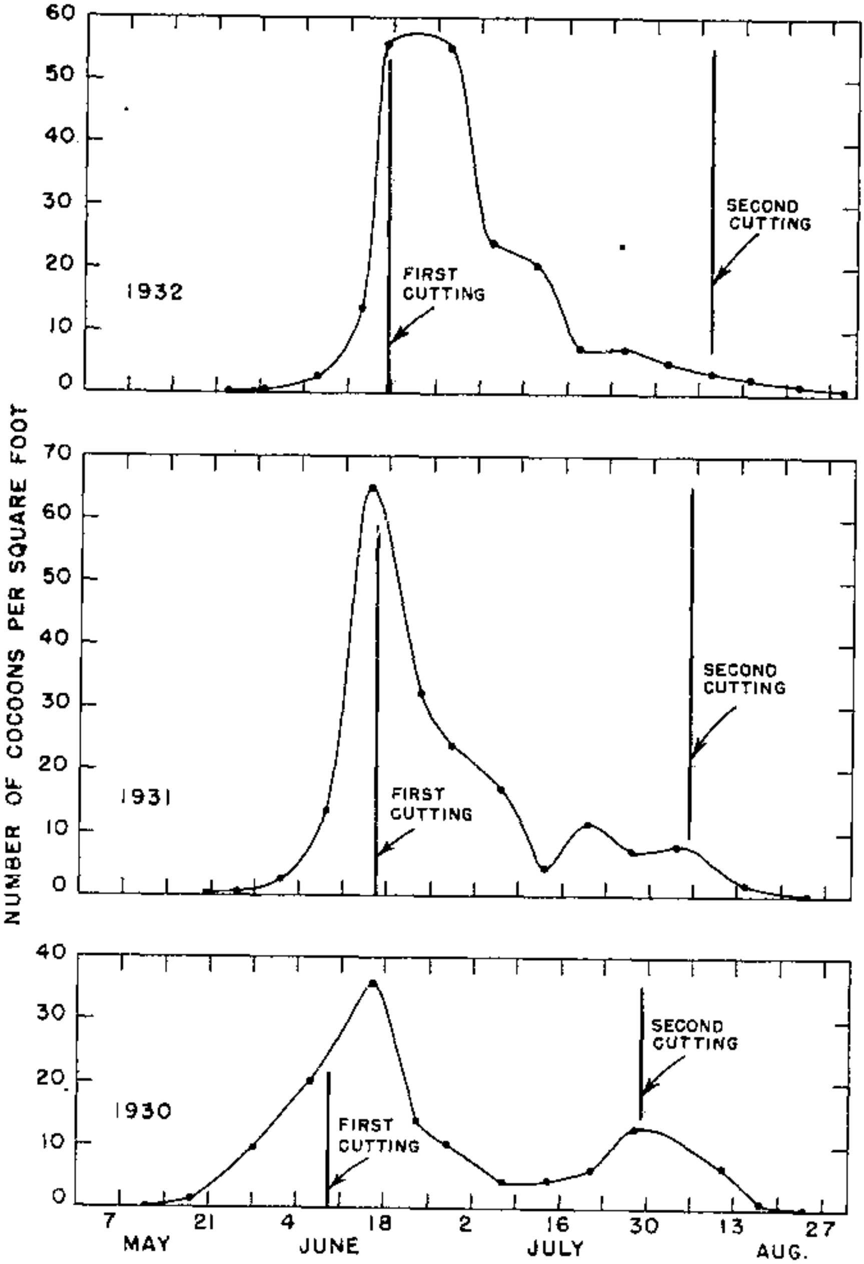

FIGURE 14.—Gross cocoon population of the alfalfa weevil, 1930–32, Salt Lake Valley, Utah.

TABLE 11.—*Alfalfa weevil cocoons containing spun larvae and mortality of these larvae, Salt Lake Valley, Utah, 1930–32*

Sampling and harvesting dates	Average cocoons per square foot		Mortality of spun larvae
	Total	Containing spun larvae	
1930	*Number*	*Number*	*Percent*
May 18	1.25	0.88	0
28	9.50	.50	0
June 6	20.25	3.13	0
[1] 9	--------	--------	--------
16	36.38	7.25	53
23	14.25	2.63	95
28	10.88	2.38	84
July 7	4.50	.75	100
14	4.88	1.13	11
21	6.38	2.88	22
28	13.25	4.00	22
[2] 29	--------	--------	--------
Aug. 4	--------	--------	--------
11	7.13	1.50	92
17	1.13	.13	0
25	0	0	
1931			
May 20	.38	.25	0
25	.25	0	--------
June 1	2.25	.13	0
8	13.50	.63	0
15	65.25	5.75	54
[1] 16	--------	--------	--------
23	32.50	8.38	90
29	23.13	7.25	98
1931	*Number*	*Number*	*Percent*
July 6	17.50	4.13	94
13	4.63	.38	100
20	11.88	.63	60
27	7.38	1.13	100
Aug. 3	8.13	.75	100
[2] 5	--------	--------	--------
14	2.00	.38	67
24	.25	0	--------
Sept. 8	.25	0	--------
1932			
May 23	.25	0	--------
30	.63	.25	0
June 6	2.63	1.13	0
13	13.63	4.13	15
[1] 17	55.88	13.63	13
27	55.00	14.13	94
July 4	24.00	4.13	97
11	20.50	4.00	100
18	7.13	1.00	63
25	7.13	1.38	18
Aug. 1	5.00	.75	17
[2] 8	3.50	.75	0
15	2.25	.88	86
22	1.50	.50	100
29	.75	.13	100

[1] First crop cut.
[2] Second crop cut.

POPULATIONS OF NEW-GENERATION ADULT WEEVILS

ABUNDANCE IN ALFALFA FIELDS AND BORDERS

The populations of living pupae produced during 1930, 1931, and 1932 are shown in figure 15, together with the populations of new-generation weevils. These graphs show that in general the production of adults was in proportion to the number of living pupae. In 1930 the major part of the adult abundance came from second-crop pupae, whereas in 1932 the greater number came from first-crop pupae, and in 1931 the two nodes of pupal abundance contributed almost equally. Since the pupal abundance is greatly influenced by the time of cutting and the weather immediately afterward, it is clear that

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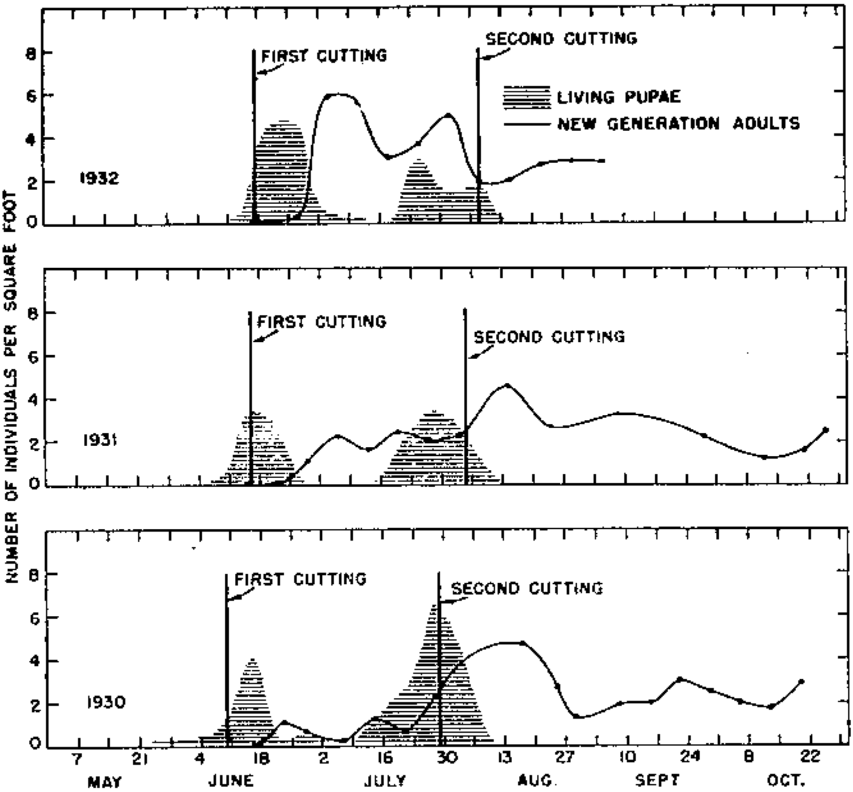

FIGURE 15.—Populations of living pupae and new-generation adults of the alfalfa weevil, 1930–32, Salt Lake Valley, Utah.

the new generation of adult weevils may derive mostly from the larval population living on the first growth of alfalfa or from the very small second-crop larval population or equally from both.

In 1930 the living pupae represented by the node occurring on June 16 did not produce a commensurate number of adults, and the discrepancy was not accounted for by dead pupae, as would be expected if they had died naturally. Instead, by the following week the total number of pupae as well as the number living had declined greatly. As a matter of fact the field was harrowed on June 17, 1 day after the early peak of living pupae. The tearing, raking action of the harrow, pulling at the crowns and passing through the stubble, breaks many of the delicate cocoons tucked away under the crowns and mashes the pupae or exposes them to the heat. This treatment thus supplemented the biological and harvesting kill and accounts alike for the reduction in number of cocoons and pupae and the abnormally small production of weevils from the early node of living pupae.

The curves of adult abundance are, of course, affected by the experimental error of the periodic averages, and this error is considerable when the averages are derived from only eight 1-square-foot samples of a population as sparse as that of the adult weevils. This sampling error is doubtless responsible for most of the fluctuations in the curves, but the magnitude and constancy of the decrease in abundance during August of each year definitely indicate that some of the weevils had either died or left the field. A decrease due to mortality would be indicated by the presence of dead weevils, and in one season this was the case.

Shortly after the middle of August 1930 the samples first contained dead weevils of the new generation, most of which, as has just been shown, had issued only 2 to 3 weeks earlier. These adults were intact and had masses of white fungus growth protruding from beneath the wing covers and along the ventral thoracic and abdominal sutures. The abundance of dead weevils was first accurately determined early in September by examinations of the dry soil before it was washed. These examinations were continued for 6 weeks and showed that the average abundance of dead weevils was two-thirds that of living weevils during the same period (table 12). This finding was unique in the course of the present study, as was also the weather of August and September of that year. The precipitation was among the heaviest on record for those months, and August was very humid and warm. The fact that weather conditions were favorable for fungus development and that there was an almost universal occurrence of fungus growth on the dead weevils suggests that there is a causal relationship between the fungus and the weevil mortality. However, this was not established.

TABLE 12.—*Relative abundance of dead and living weevils in the ecological study field, autumn of 1930, Salt Lake Valley, Utah*

Date	Weevils per square foot		Date	Weevils per square foot	
	Dead	Living		Dead	Living
	Number	*Number*		*Number*	*Number*
Sept. 8	1.13	1.88	Oct. 6	1.38	2.00
Sept. 15	1.25	2.00	Oct. 13	1.38	1.75
Sept. 22	1.75	3.00			
Sept. 29	1.63	2.50	Average	1.42	2.10

In 1931 and 1932 there was no such mortality; yet the adult populations declined in August of these years as well, indicating that many of the adults left the field at this time. Moreover, although the curves show no definite decrease in July, there could be a movement from the field in the latter half of the month that would not be reflected by the curves, since any losses at that time would be obscured by replacements from individuals issuing from the July node of living pupae. Supplementary evidence from other fields studied in 1931 shows that adults from the June node of pupae sometimes leave the field in July (table 13).

In two fields there was a great decrease of adults about the middle of July during a period of extreme heat but no significant change occurred in the other two fields. It appears, therefore, that the emigration of weevils in July varies greatly in different fields, presumably on account of differences in temperature, which in turn depend upon the shade afforded, the frequency and incidence of irrigation, and the character of the soil.

TABLE 13.—*Changes in average abundance of alfalfa weevil populations in 4 fields in Salt Lake Valley, Utah, during July 1931*

Field	Day of month	Average weevils per square foot	Field	Day of month	Average weevils per square foot
		Number			*Number*
1	2	14.44	3	6	3.33
	10	18.89		13	1.89
	16	5.78	4	7	3.44
2	2	30.22		14	4.33
	10	26.00		22	1.89
	16	9.78			

By the time the border waste areas of these fields were sampled in the first week of September, the late contingent of weevils had already issued, and possibly some of them had moved out of the field. Certainly there were many new-generation adults in the borders, the maximum density being 154 per square foot. The averages are shown in table 14. The large probable errors doubtless reflect the heterogeneous vegetative covering of the field borders, since the weevils are more abundant in places affording a dense covering, such as grassy areas. But such areas are mostly along the banks of irrigation ditches which border the alfalfa fields, and the concentration of weevils there may be a response to moisture.

How extensive is this movement of weevils into the field borders? The foregoing results do not reflect the average conditions, because they were obtained adjacent to fields having above-average popula-

TABLE 14.—*New-generation alfalfa weevils in borders of 4 fields, September 1–3, 1931, Salt Lake Valley, Utah*

Field	Average weevils per square foot in border of field[1]			
	East	South	West	North
	Number	*Number*	*Number*	*Number*
1	18.0 ± 0.84	15.5 ±2.38	18.5 ±4.44	4.7 ±0.54
2	80.0 ±11.25	13.0 ±2.83	3.0 ± .55	
3	10.0 ± 1.30	23.5 ±1.96	24.2 ± 5.46	23.3 ±3.09
4	70.5 ±15.27	1.8 ±1.50	0.8 ± .24	

[1] Numbers following ± signs are probable errors.

tions. For this reason from the early part of September to the middle of October 1931 the weevil populations of 27 alfalfa fields and their borders were determined. To obtain these estimates 27 samples were taken from each field and 4 samples from each border waste area. The average populations are presented in table 15. It is clear from these figures that the ratio of border to field populations varied much, one extreme showing 0.93 weevil per square foot in the field and 0.37 in the borders and the other extreme showing 1.22 in the field and 35.13 in the borders. The average density was 4.79 times as great in the border areas as in the fields. Since the border areas averaged only 8.71 percent of the field area, however, the average field had in its adjoining fence rows and ditchbanks 41.72 percent as many weevils as did the field itself.

TABLE 15.—*Average populations of new-generation alfalfa weevils in 27 alfalfa fields and their borders, fall of 1931, Salt Lake Valley, Utah*

Date sampled	Average weevils per square foot—		Date sampled	Average weevils per square foot—	
	In fields	In borders of fields		In fields	In borders of fields
	Number	*Number*		*Number*	*Number*
Sept. 9	4.15	18.58	Sept. 29	1.56	7.75
Sept. 10	.89	3.83		3.37	9.92
Sept. 14	1.26	9.08	Oct. 5	1.11	2.80
	1.07	1.50		1.22	2.42
Sept. 15	1.19	6.75		.67	10.50
Sept. 16	1.52	5.00		.70	4.50
	2.70	11.80	Oct. 6	2.19	2.33
Sept. 21	.44	10.83		.30	.50
	1.37	10.50	Oct. 7	.63	.75
	6.89	11.31		2.78	13.75
Sept. 22	1.19	11.13	Oct. 13	1.15	7.25
	1.22	35.13		.96	5.33
Sept. 23	.26	.86	Average	1.59	7.62
	.93	.37			
Sept. 28	1.30	1.33			

Whether the weevils reached the field borders by crawling or by flying is not known. Certainly they left the field at the time Titus (*16*) indicated summer flight. Suffice it to say that a part of the weevils may leave alfalfa fields during July and August, and that an important fraction of the new generation is found in the field borders during the fall of the year.

The data in table 13 show—and other data support it—that, despite a large emigration of weevils, the fields producing large populations tend to retain large populations.

What happens to the weevils in the field borders? To obtain information on this point the most heavily populated border of 7 of the same 27 fields was resampled about the first of November, when lower temperatures rendered further migration unlikely. Improved estimates were obtained by taking 9 samples in each case, and the average populations ranged from 2.67 to 27.78 adults to the square foot. These borders were sampled again the first half of the following March, when it was found that the population had decreased slightly in 4 and greatly in 3 cases. A third sampling in mid-April, just after a week of warm weather, showed that practically all the weevils had left. These changes are shown in figure 16.

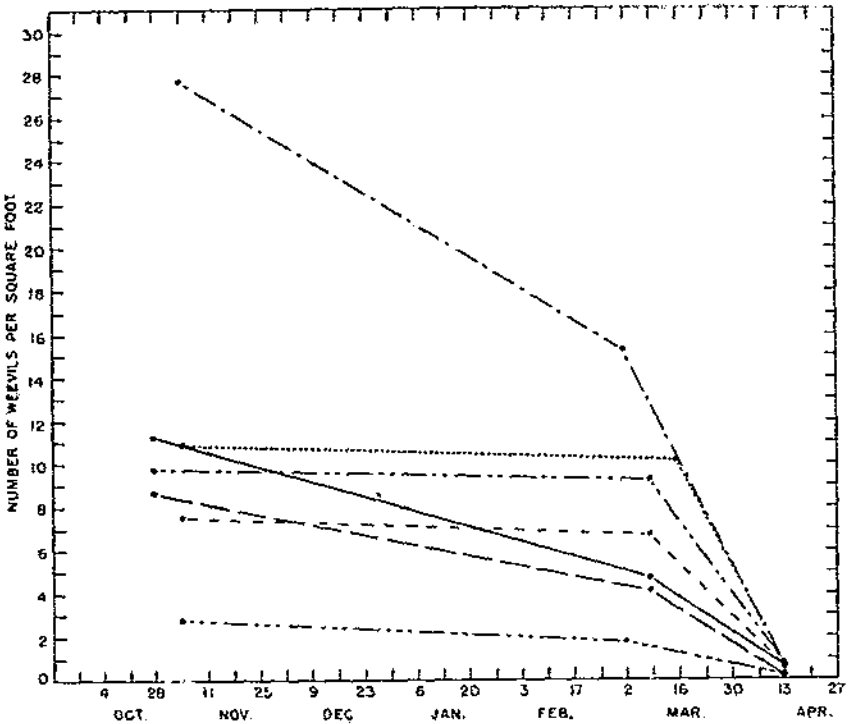

FIGURE 16.—Alfalfa weevil populations in the most heavily populated border of seven fields, fall to spring, 1931–32, Salt Lake Valley, Utah.

This movement of the weevils would be expected to result in an increase of the population in the field itself. Reference to figure 2, which shows the general decline of overwintered adults, provides indications of this expected early-spring increase, especially noticeable in 1932. However, poor sampling conditions and the inherent variability of averages based on so few samples of a small population prevent definite establishment of this point.

SEXUAL MATURITY OF NEW-GENERATION FEMALES IN ALFALFA FIELDS AND BORDERS

The population of new-generation adults, originally separated by the cropping system into 2 divisions of different age, is redivided by partial migration into 1 part that passes the winter in the alfalfa field and another that winters in field borders. In these different habitats the development of eggs within the females was increasingly different during the fall and winter, as shown by dissection of females collected from the 27 fields and their borders in the fall and from 7 of these fields during the following spring. The percentage of females in each habitat containing full-sized eggs is shown in table 16.

TABLE 16.—*Development of eggs within female alfalfa weevils in alfalfa fields and field borders, 1931–32, Salt Lake Valley, Utah*

Month collected	Weevils in fields		Weevils in borders	
	Females dissected	Females with full-sized eggs	Females dissected	Females with full-sized eggs
1931	*Number*	*Percent*	*Number*	*Percent*
September	319	1	795	0
October	131	2	230	0
1932				
March	153	28	195	0
April			12	25

These percentages give general corroboration to the finding of Snow (*14*) that none of the new-generation females contain full-sized eggs until September, and then only a very small percentage of those remaining in alfalfa fields, whereas females of like generation in field borders do not produce eggs until the following spring. The present study, however, shows that only 2 percent of the field females were found with eggs in October and 28 percent the following March, as against Snow's figures of 24 percent in October and 73 percent in March. This difference may be due to the fact that Snow's collections were made during 1913, 1914, and 1915, when, because of ineffectiveness of the then recently introduced *Bathyplectes* parasite and later first cutting, it is believed that a much larger proportion of the new-generation weevil population was produced from first-crop larvae than at present. Certainly the description by Titus (*16*) of their abundance when the first hay crop was being put up leaves little doubt on this point.

Weevils produced early in the year have several weeks more of summer weather in which to feed and build up energy reserves, and thus with the coming of fall weather have more vitality for ovarian development than weevils originating from second-crop larvae.

That this is the explanation of the difference between Snow's figures and those obtained in the present investigation is suggested by the differing percentages of gravid females in the fall. By contrast with the very small percentages of females found to contain eggs in the September and October samplings of 1931, dissection of 207 females in September and 201 in October 1932 showed 2 and 15 percent, respectively, with eggs. In 1932 most of the new-generation weevils originated from first-crop larvae, whereas in 1931 they were produced more equally from first- and second-crop larvae. Sexual maturity of female weevils also varies in different areas during the same season. Extensive samplings of alfalfa fields in 5 Western States in the fall of 1932 show that in September small percentages of females contained eggs; thereafter, percentages increased unevenly, and in October they varied with the locality (table 17).

TABLE 17.—*New-generation female alfalfa weevils with full-sized eggs collected from alfalfa fields in 5 Western States, fall of 1932*

Location of fields	September samplings		October samplings		November samplings	
	Fields	Females with eggs	Fields	Females with eggs	Fields	Females with eggs
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Utah:						
Salt Lake Valley	9	2	15	15	------	------
Delta Tract (Millard County)	6	0	18	6	------	------
Uintah Basin	8	1	16	6	------	------
Idaho: Upper Snake River Valley	8	3	16	7	------	------
Colorado: Axial Basin	------	------	9	19	------	------
Nevada:						
Truckee Valley	2	5	10	16	------	------
Fallon (Newlands project)	------	------	------	------	22	42
Oregon: Rogue River Valley	------	------	6	2	3	25

The small numbers of eggs appearing in October represent the initial oviposition of the new-generation weevils. In ordinary fall seasons this egg laying is halted by declining temperatures before an important number of eggs have been laid. Thus during November the egg population averaged 8.38, 4.57, and 5.00 to the square foot in 1930, 1931, and 1932, respectively. Most of these few eggs survive and aid in carrying the species over the winter season.

In view of the delayed sexual maturity of the females wintering in field borders, and their movement from these situations in the spring, it is conceivable that they may be the chief source of the tailing-out oviposition which occurs during the growth of the second alfalfa crop, and which may contribute so heavily to the overwintering adult populations.

WEEVILS IN HAYSTACKS

In addition to weevils that migrate from fields to borders, many that congregate in haycocks are hauled out of the field with the hay. Large numbers of them are sifted out while the hay is being lifted onto the stack and remain in the chaff that accumulates at the base of haystacks. Weevils are most abundant in second-crop hay and occur in largest numbers on the side of the stack from which the hayracks are unloaded (table 18).

TABLE 18.—*Occurrence of new-generation adult weevils at base of haystacks in late summer, Salt Lake Valley, Utah, 1936*

Hay crop	Haystacks sampled	Average weevils per square foot on—	
		Stacking side	Other sides
	Number	*Number*	*Number*
1	4	41.25	13.33
1 and 2	3	57.33	22.66
2	3	130.66	34.55
Total or average	10	72.90	22.50

Many of the weevils carried into haystacks die, mortality in the upper part of stacks having been found to range from 91 to 98 percent (*8*). The survival of new-generation weevils in and around haystacks is believed to vary with their opportunity for feeding in the field before being hauled away with the crop of hay (*6*). Living weevils have been found in hay baled after 3 to 9 months in the haystack, and such weevils may mature and mate during favorable spring weather before feeding (*7*). Smaller numbers of weevils occur and survive in stacks of wild hay produced in weevil-infested areas (*7*). All these sources doubtless contribute to the winter carry-over of the species.

PARASITES AFFECTING THE ALFALFA WEEVIL

The principal biological agents affecting the alfalfa weevil are three species of parasitic insects, two introduced primaries and one native secondary.[11] Of these, *Bathyplectes curculionis*, parasitic on weevil larvae, is preeminent. It in turn is parasitized by the secondary *Eupteromalus viridescens*, which occasionally assumes importance through curtailing the abundance of *Bathyplectes*. The third species, *Anaphes pratensis* Foerst., is a parasite of weevil eggs.

BATHYPLECTES CURCULIONIS, PARASITE OF WEEVIL LARVAE

Bathyplectes curculionis has become well established wherever the alfalfa weevil occurs in the United States. Its spread has been accomplished by natural means or by domestic redistribution carried out by the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture in cooperation with various States. Data relating to one such redistribution show the rapidity and thoroughness of establishment. In the spring of 1934, 181 female and 140 male parasites were liberated in 4 fields near Medford in Rogue River Valley, Oreg., an area including about 20,000 acres of alfalfa. After 5 years the gross abundance of *Bathyplectes* in this district

[11] Excellent drawings of these parasites have been published by Chamberlin (*1*).

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(table 19) approximated that in areas where this parasite has been established for many years, and the viability of cocoons was higher than in older weevil-infested areas.

TABLE 19.—*Increase of Bathyplectes curculionis in Rogue River Valley, Oreg., from introduction made in the spring of 1934, as shown by annual fall surveys, 1934–38*

Year	Fields sampled	Fields from which cocoons recovered	Average cocoons per square foot	Cocoons viable
	Number	*Percent*	*Number*	*Percent*
1934	10	10	0.02	75.00
1935	8	37	.05	33.33
1936	25	72	1.03	47.57
1937	25	100	4.36	36.24
1938	25	100	7.78	29.69

Less detailed ecological studies conducted in 1936–38 show that the general trends and interrelationships of *Bathyplectes* are similar in all areas. These features may best be shown by the studies made in Salt Lake Valley, Utah.

ENDOPARASITIC PHASE

The percentage of weevil larvae parasitized was determined for each instar collected in each field sampling. The probable error of each mean percentage for that part of the first-crop period when larvae were numerous was calculated to show the degree of reliability of the percentages. Larvae collected early in the first-crop period and throughout the second-crop period were so scarce that percentages are variable and therefore of limited usefulness. They are included merely to round out the broad seasonal trend to be discussed later. The data obtained are presented in table 20.

Weevil larvae are parasitized in all instars. The more reliable estimates show at once that in each season the percentages of larvae parasitized increase with development of the larvae. Thus, on any given date in May and up to the first harvest in June, the percentage of each instar parasitized is usually higher than that of the next smaller instar. It is therefore concluded that the percentage parasitized increases with the length of time the larvae are exposed to *Bathyplectes* adults.

A seasonal trend in the percentages of larvae parasitized is also evident. Each year from late in April and early in May the percentages, although variable, gradually increased to the generally highest level between May 18 and 23, and then decreased abruptly to first-cutting time. This decline might reflect either a great increase in number of weevil larvae or lessened activity of the parasites, but, since there were no large influxes of larvae, exhaustion of the overwintered parasites seems the more likely cause. The decline was less rapid between June 8 and 15 in 1931 than in other years, a circum-

Table 20.—*Parasitization by Bathyplectes curculionis of the different instars of the alfalfa weevil, Salt Lake Valley, Utah, 1930–32*

Date	Larvae parasitized[1]			
	First instars	Second instars	Third instars	Fourth instars
1930	*Percent*	*Percent*	*Percent*	*Percent*
Apr. 21		10.00	38.30	52.46
May 1	42.06	85.42	91.67	73.33
May 5	44.60±2.20	79.20±2.60	90.00±2.20	80.00
May 12	55.00±2.80	79.40±1.60	93.00±1.80	82.60
May 18	47.00±2.20	80.60±2.00	91.00±1.40	97.40±0.80
May 28	57.00±2.00	55.00±2.20	83.60±1.60	93.60±1.20
June 6	8.40±1.20	27.00±2.00	65.00±2.20	81.00±1.20
June 9[2]				
June 16		50.00	53.33	69.63
June 23		50.00	75.00	53.85
June 28	33.33	55.56	20.00	54.55
July 7	6.52	8.33	12.50	35.48
July 14	0	0	0	1.92
July 21	0	0	0	3.57
July 28	0	0	18.75	17.02
July 29[3]				
1931				
Apr. 13	0	0		
Apr. 20	27.00	58.80	100.00	
Apr. 27	6.67±2.13	31.43±4.60	66.70	
May 4	23.00±2.74	37.50±3.95	81.80	100.00
May 11	30.00±2.40	58.52±2.82	77.80±6.60	100.00
May 20	16.80±1.60	69.00±2.00	94.20±1.60	96.20±1.40
May 25	30.80±2.00	60.89±2.14	87.20±1.80	93.80±2.00
June 1	21.60±1.80	59.20±2.40	84.60±1.80	92.50±1.20
June 8	9.60±2.60	41.00±2.80	73.60±2.20	88.00±1.40
June 15	8.00±1.60	45.80±2.40	68.60±2.20	83.60±1.60
June 16[2]				
June 23				55.00
June 29		0	0	100.00
July 6	0	33.00	20.00	100.00
July 13	0	4.00	0	4.00
July 20	0	0	3.00	4.00
July 27		0	0	0
Aug. 3		0	0	0
Aug. 5[3]				
1932				
Apr. 18	10.00	33.33		
Apr. 25	5.00	37.04	66.67	
May 2	14.55	80.00	66.67	
May 9	16.84±3.22	61.25±3.01	100.00	100.00
May 16	22.67±1.96	63.11±2.43	82.35±2.72	100.00
May 23	16.00±1.78	60.44±1.91	85.50±1.51	93.85±1.73
May 30	11.00±1.58	37.33±2.10	76.00±1.83	88.57±1.66
June 6	9.00±1.26	35.00±2.12	58.67±2.22	80.44±1.56
June 13	.69± .46	21.08±1.63	36.89±2.18	74.00±1.86
June 17[2]	2.42± .77	14.36±1.43	36.50±2.06	30.00±1.65
June 27		0		33.33
July 4	25.00	22.22	0	42.86
July 11	0	7.69	24.32	34.48
July 18	0	0	9.09	33.33
July 25	0	0	1.89	2.17
Aug. 1	0	0	0	5.00
Aug. 8[3]	0	0	0	11.76

[1] Numbers following ± are probable errors. [2] First crop cut.
[3] Second crop cut.

stance that other records (see p. 52) indicate as due to the issuance of adult *Bathyplectes* from the transforming type of cocoon. It is noteworthy that the percentages declined least among fourth instars, owing to the influence of the developmental trend discussed above. Thus, just before the first harvest in 1930 and 1931 the parasitization of fourth instars remained rather high (81 and 83.6 percent), while that of smaller larvae had dropped to moderate or low levels.

The decrease among the first three instars is not important, however, since these instars are virtually annihilated by starvation and heat after cutting. On the contrary, the high level of parasitization of fourth instars is important, because a substantial number of them survive cutting and might contribute to the succeeding generation. In 1932, however, the parasitization declined much faster than in 1930 and 1931, so that by the time of first cutting the fourth instars showed a parasitization about 20 percent lower than in the 2 preceding years. As will be shown later, this effect appears to have been due to the unusual abundance, during 1931, of the secondary parasite *Eupteromalus viridescens* Walsh.

The cultural and biological lethal factors are thus seen to be complementary; that is, instars having the lowest parasitization are hardest hit by the cultural kill, and fourth instars, least affected by cultural kill, suffer from the highest parasitization.

During all three seasons the parasitization affecting the small larval population living on the second crop was low at first and dropped practically to zero by the middle of that crop period, when the late larvae were most numerous.

While the percentages in table 20 are useful in revealing the general trends of parasitization by *Bathyplectes* in relation to seasonal and developmental changes, they do not tell the whole story because the larval population is constantly changing. For example, in 1931 the percentage of unparasitized fourth instars increased from 3.8 to 16.4 between May 20 and June 15. These figures indicate that the escapes increased 4.32 times in that interval, but this is true only if the number of larvae remained constant. As a matter of fact larvae increased in abundance 7.85 times, or from 11.20 to 87.88 per square foot. Thus, while the percentage of parasitization was decreasing the host population was expanding, with the result that the escapes really increased 33.91 times (4.32×7.85) from May 20 to June 15. For this reason the practical value of parasitization by *Bathyplectes* is more clearly shown by the number of unparasitized larvae than by the proportion parasitized.

Since nearly all the first three instars are killed after the first cutting, the parasitization of fourth instars is the primary consideration. Table 21 shows that in 1931 the earliest fourth instars appeared May 4 but no unparasitized instars were noted until May 20. The number of unparasitized individuals steadily increased until June 15, immediately before the first crop was cut. In the absence of *Bathyplectes* an unparasitized population of this magnitude would have obtained approximately 3 weeks earlier, as shown by the gross abundance on May 20 and 25.

Parasitization by *Bathyplectes* thus not only reduces the number of weevil larvae that may produce adults but also delays the appear-

TABLE 21.—*Average abundance of fourth instars of the alfalfa weevil and number unparasitized, first crop period, 1931, Salt Lake Valley, Utah*

Date	Average larvae per square foot		Date	Average larvae per square foot	
	Total	Unparasitized		Total	Unparasitized
	Number	*Number*		*Number*	*Number*
Apr. 27	0	0	May 25	11.00	.68
May 4	.80	0	June 1	28.13	2.11
May 11	1.20	0	June 8	70.63	8.48
May 20	11.20	.43	June 15	87.88	14.41

ance of the first pupae. Nearly all the earliest larvae are prevented from reaching the pupal stage, and the number of larvae that pupate is held to a low level until the crop is ready for harvest. This effect of itself would have slight practical value, because the unparasitized larvae would be sufficient to produce enough adult weevils to menace the crop the succeeding year. What does give point to this aspect of parasitization by *Bathyplectes* is the fact that the cultural kill caused by first cutting may be brought into play while the number of unparasitized larvae is still at a low level, and thus destroy many of those that have escaped parasitization. That this fact, revealed by the study for 1931, is characteristic of parasitization by *Bathyplectes* in general may be seen from figure 17, which shows that the same general condition obtained during the 3 years covered by this study.

Since, however, the parasite does not kill its host until the latter has spun its cocoon, the biological kill may best be viewed by studying the weevil-cocoon population. The curve for the abundance of cocoons containing individuals that had developed beyond the larval stage (see p. 31), as shown by the broken lines in figure 18, is similar to the curve of the gross abundance of cocoons, shown in figure 14, although the numbers are smaller. The effectiveness of parasitization by *Bathyplectes*, foreshadowed in the larval populations, may now be shown by reducing this cocoon population to those individuals that escaped parasitization and pupated, represented by the continuous lines in figure 18. The vertical distance between the two curves shows the tremendous reduction effected by *Bathyplectes* in the peak existing near first-cutting time, and the waning effect of this parasite thereafter.

As a result of this unequal incidence of parasitization, the overwhelming numerical advantage of the first-crop larval population, already largely lost in the cocoon population, has now been completely dissipated, and the pupal population has been reduced to two nodes of the same order of magnitude. The differences reflect the influence of variations in time of first cutting, in parasitization, and in weather conditions.

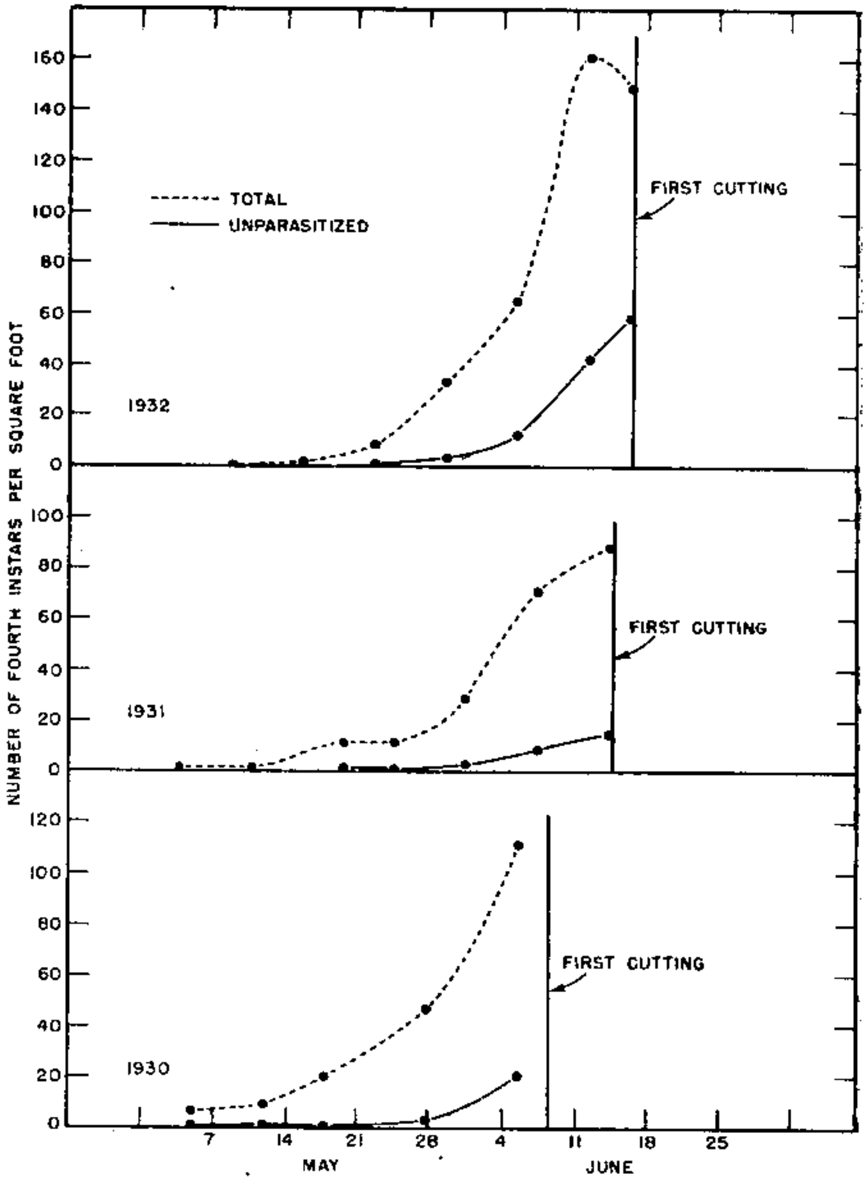

FIGURE 17.—Effect of parasitization by *Bathyplectes* in delaying and curtailing production of new-generation adult weevils, first-crop period, 1930–32, Salt Lake Valley, Utah.

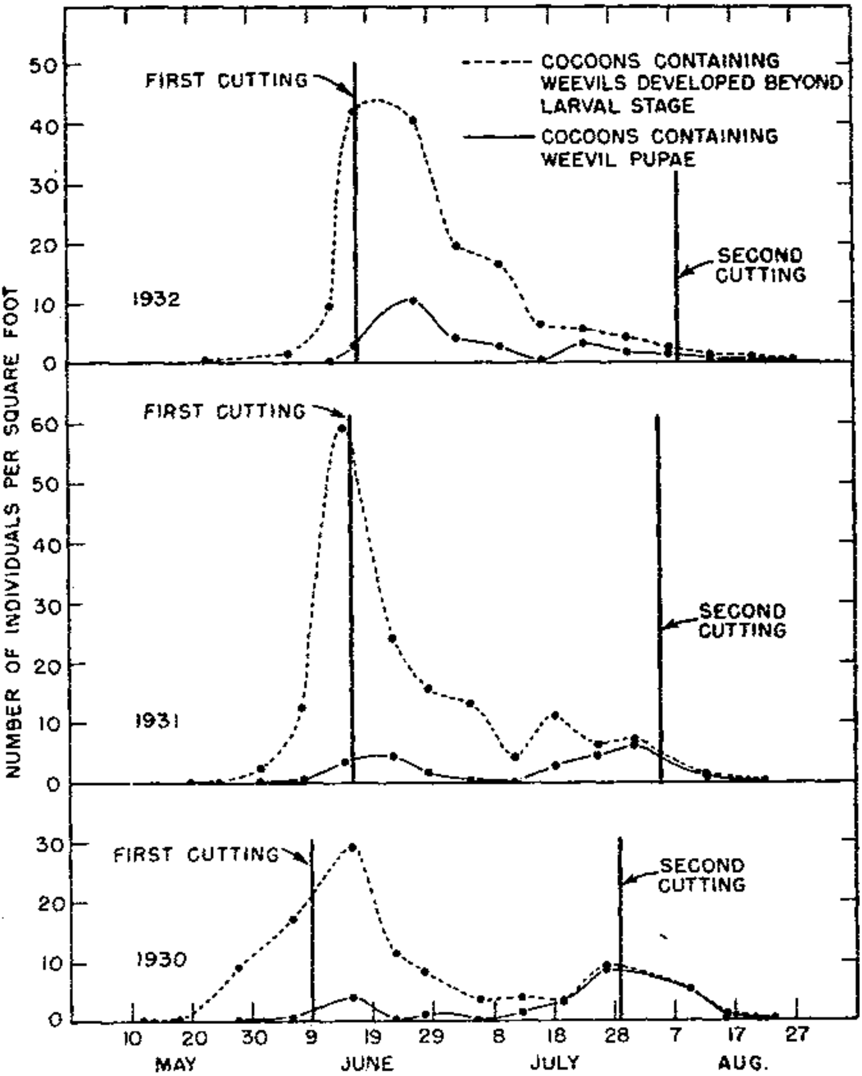

FIGURE 18.—Incidence of parasitization by *Bathyplectes* as shown by alfalfa weevil cocoons, 1930–32, Salt Lake Valley, Utah.

Thus in 1930, when the larval population reached approximately 29 million per acre, the farmer was forced to cut the first crop in order to save it. This was not a sacrifice, however, since the alfalfa was sufficiently mature to make the highest quality hay. As a consequence cutting occurred early in the development of the immature-weevil population, there being only 0.50 pupa and 21.23 unparasitized fourth instars to the square foot. With favorable haying weather the larval population of 667.13 produced a peak of but 4.13 pupae per square foot.

In 1931, owing to the small number of parent weevils, the larval population was inadequate to damage the first crop seriously regardless of the cutting date. In fact, the first cutting was delayed about 2 weeks after the plants had reached a stage of growth suited to production of the best hay, and, as has already been shown, the cutting came late in the development of the weevil population. Consequently, the number of unparasitized fourth instars increased to an average of 14.41 per square foot, approximately two-thirds as many as were present at cutting time in 1930 when the total larval population was three times as large. Moreover, the pupae numbered 3.5 before cutting and, despite favorable haying weather, rose to 4.5 after cutting. Thus the final result of the delay in first cutting was that a larval population too small to cause serious crop damage produced as many pupae as did the large number of larvae in 1930.

In 1932 the parent weevil population of nearly 3 per square foot indicated that the first crop would be damaged unless cut early; that is, in the flower-bud stage of growth. But when damage was manifested during the first week of June, rain threatened, and the owner delayed cutting. After he did cut and while the hay was yet on the field, there was a recurrence of cloudy, rainy weather, which diminished the cultural kill. Meanwhile the number of unparasitized fourth instars, aided by the rapid decline of parasitization as mentioned on page 44, increased to 59 per square foot. With this condition and lessened cultural kill the pupal population rose from 2.88 just before cutting to 10.38 ten days after cutting.

These events illustrate well the intimate relation between weather, parasitization, and the time of cutting the first crop in influencing the number of pupae produced at that time.

Not all the individuals that escape parasitization and transform to pupae complete their development. The principal mortality occurs during the stubble period after the first and second crops are cut, although some may die before the second cutting when the summer heat is most intense. The variable effect of cultural kill upon the pupal population is shown in figure 19. In 1930 it operated mostly upon the late node of the pupal population, and in 1931 about equally upon both early and late nodes, while in 1932 the greater effect fell upon the early node. The two nodes of living pupae in each season thus represent the individuals that escaped both biological and cultural kill and from which the new-generation adult weevils were produced.

The active phases of parasitization by *Bathyplectes* may now be summarized. The earliest cocooning larvae, which if unparasitized would mature before the crop could be cut, are almost completely destroyed by this parasite. In addition, the appearance of unparasitized individuals in numbers is delayed so that the majority, whether larvae or pupae, may be killed by exposure in the stubblefield when the first cutting is not delayed. Thus *Bathyplectes* is of the greatest practical value in minimizing the production of new-generation adults from the tremendous first-crop larval population. Nevertheless, because *Bathyplectes* parasitizes negligible proportions of the few weevil larvae living on the second alfalfa crop, these larvae may make an important contribution to the population of new-generation weevils unless the second crop is cut early enough to subject them to the stubblefield heat.

These benefits and deficiencies of *Bathyplectes* at once indicate the possibility of supplementing its work by introducing other, noncompetitive parasitic insects. The more important insects in this connection are (1) any species parasitizing the later weevil stages,

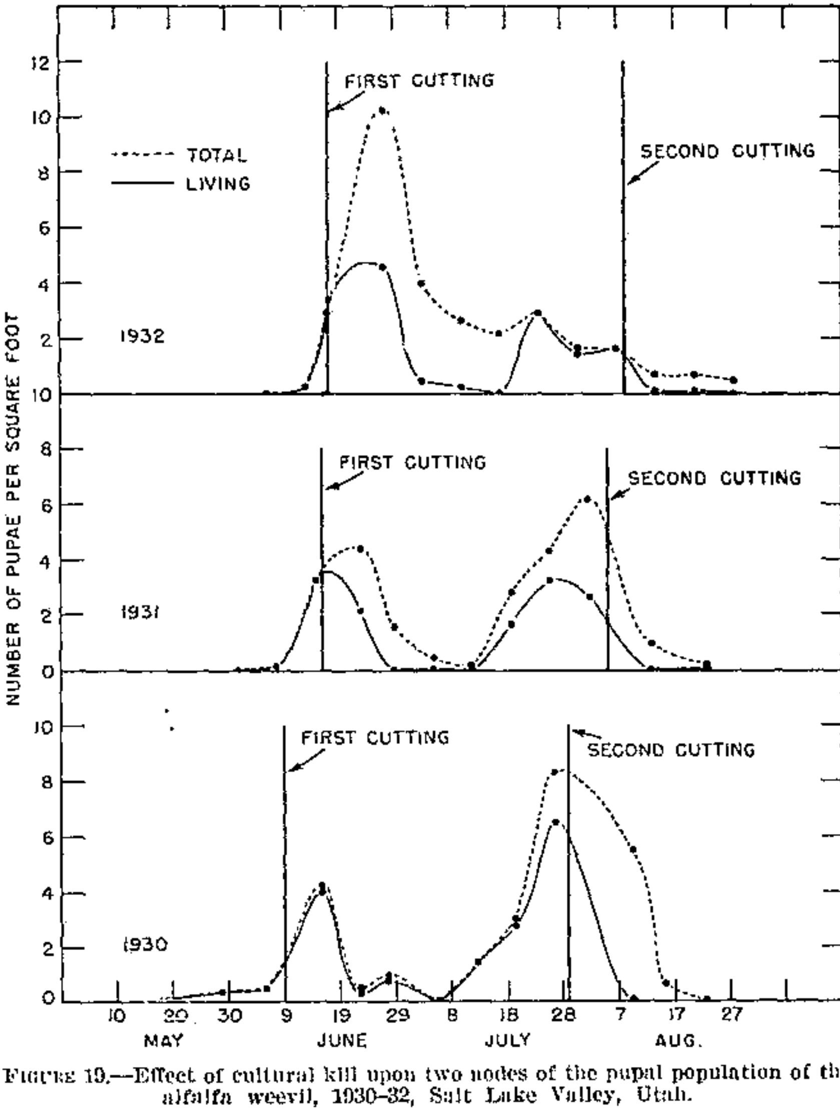

FIGURE 19.—Effect of cultural kill upon two nodes of the pupal population of the alfalfa weevil, 1930–32, Salt Lake Valley, Utah.

particularly the pupal stage, and thus attacking those first-crop individuals that escape parasitization by *Bathyplectes;* and (2) any species active in the second-crop period on either larvae or pupae, and thus impinging upon individuals that receive but scant attention from *Bathyplectes.*

FREE-LIVING PHASE

To understand fully the relation of *Bathyplectes* to the alfalfa weevil, it is necessary to know, in addition to the prevalence and effect of its endoparasitic phase, the abundance and condition of its free-living stages. Such supplementary information was gained by counting and dissecting the *Bathyplectes* cocoons obtained from the periodic field samplings.

The annual cycle of abundance of *Bathyplectes* living in cocoons is shown in table 22. Beginning with the last month of the first-crop period (mid-May to first cutting) in 1930, both the gross abundance and the abundance of viable *Bathyplectes* cocoons were at the low point of the cycle. During the second-crop period there was a great increase from parasitized weevil larvae that lived on the first growth of alfalfa. However, because of heavy mortality from stubblefield conditions, exaggerated by persistence of some old, overwintered cocoons, only about 38 percent of these larvae contained living individuals. During the remainder of the season the *Bathyplectes* adults parasitized only a small percentage of the negligible population of weevil larvae.

TABLE 22.—*Seasonal trends of abundance of primary (Bathyplectes curculionis) and secondary (Eupteromalus viridescens) parasites of the alfalfa weevil based upon averages in an area equaling eight 1-square-foot samples, 1930–32, Salt Lake Valley, Utah*

Season	Primary parasite		Secondary parasite	
	Total cocoons	Living individuals	Total cocoons	Living individuals
1930	*Number*	*Number*	*Number*	*Number*
Mid-May to cutting of first crop	68.00	5.00	11.50	0.33
Second-crop period	381.00	147.17	9.50	4.83
Third-crop period	248.00	53.00	17.83	10.00
1931				
Mid-February to mid-April	172.50	44.20	4.60	1.90
Mid-May to cutting of first crop	127.00	7.20	10.40	1.80
Second-crop period	306.86	85.86	35.57	23.29
Third-crop period	251.00	27.00	47.67	26.00
1932				
Mid-February to mid-April	210.50	19.80	25.20	5.80
Mid-May to cutting of first crop	137.40	2.00	6.80	1.80
Second-crop period	341.29	73.29	17.00	7.14
Third-crop period	251.33	38.67	13.67	7.67

After the second cutting near the end of July, at the peak of seasonal heat, the immobile *Bathyplectes* cocoons were again exposed to stubblefield conditions, and as a consequence the number of living parasites decreased by about two-thirds. The effect of the secondary parasite *Eupteromalus viridescens* is mingled with this heat kill, as will be shown later. No further appreciable reduction of living stages occurred during the fall, but by the following spring they had decreased to an average of 5.5 to the square foot, which represents approximately the number available for production of adults to oviposit in weevil larvae living on the first crop of 1931. Following emergence of the adult parasites in the spring the number of living individuals in cocoons again declined during the last month of the first-crop period. This low point of the cycle of the cocooned individuals coincides with the maximum parasitization among weevil larvae.

The cycle then repeats, rising to a new peak during the second-crop period of 1931 and then declining, because of summer kill after second harvest, winter mortality, and spring emergence of adults, to the low point during the precutting period of 1932.

Developmental changes in these cocoons, determined by dissection, outline the seasonal history of *Bathyplectes*. This parasite lives as a larva within its cocoon from early summer of one year to early spring of the succeeding year. The overwintered larvae begin pupating in the latter half of March, and by the middle of April the pupal stage predominates. Pupation is largely completed by the middle of May, and emergence of adult parasites reaches its peak the second week of May. The progeny of these adults, living within the weevil larvae until the latter have spun their cocoons, kill the hosts and quickly spin their own (*Bathyplectes*) cocoons.

The majority of the new parasite cocoons appear about 2 weeks after the first cutting, having been produced from weevil larvae that lived on the first alfalfa crop. In 1932 new cocoons appeared initially just before the first cutting. Ten days after this cutting (table 23) nearly half of the cocoons were new, and of these less than half were viable. At the next examination, 17 days after the cutting, the abundance of cocoons had increased by more than half, with nearly two-thirds of them new, but of these new cocoons only about one-third were viable. At neither of these examinations was an appreciable percentage of the old cocoons viable.

TABLE 23.—*Differential abundance and viability of cocoons of Bathyplectes curculionis after cutting of the first crop based upon averages in an area equaling eight 1-square-foot samples, 1932, Salt Lake Valley, Utah*

Interval after first cutting, days	Total cocoons	Old cocoons (1931 origin)		New cocoons (1932 origin)					
				Total	Viable	Transforming type		Wintering type	
		Total	Viable			Total	Viable	Total	Viable
	Number	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
10	278	155	0.65	123	43.1	58	15.5	65	67.7
17	457	167	0	300	36.3	62	1.6	238	45.4

The new *Bathyplectes* cocoons are dimorphic. In heavy-textured or wintering cocoons larvae live through the remainder of the summer and the next winter, pupating in the spring. Larvae in light-textured, or transforming, cocoons, on the contrary, pupate quickly and emerge as adults from shortly before to about 2 weeks after the first cutting. These adults are believed to be largely responsible for the limited parasitization of the few weevil larvae living upon the second growth of alfalfa.

The part played by these transforming individuals may be illustrated by the data for 1932. On June 13, 4 days before cutting, from a total of 122 cocoons only 3 contained living parasites, and 2 of these were new, both of the transforming type. Ten days after cutting the cocoons were almost equally of the transforming and wintering types, but less than one-sixth of the former were viable in contrast to two-thirds of the latter (table 23). Seventeen days after cutting the number of new cocoons had increased greatly, but the proportion that were of the transforming type had decreased to only one-fifth. The increase was thus due to formation of additional wintering cocoons. Not only were the transforming cocoons much less numerous, but also less than 2 percent of them were viable, by contrast with nearly half of the wintering cocoons. Transforming individuals had thus virtually disappeared within 2½ weeks after the first cutting, leaving only wintering cocoons to perpetuate the species.

SUPERPARASITIZATION

When the size relationship is such that but one parasite develops from a host, the matter of superparasitization has an important bearing upon the efficiency of the parasite. As pointed out by Fiske (*4*) and by Clausen, Jaynes and Gardner (*2*), if the hosts were parasitized on a purely fortuitous basis, there would be a tremendous waste of parasites in attaining a high percentage of parasitization. For example, in thus parasitizing 90 percent of the hosts there would be required approximately 2.1 parasite offspring per host, whereas if the female parasite were able to select unparasitized hosts the same percentage of parasitization would be reached when the ratio of parasites to hosts was only 0.9.

The very high percentages of parasitization established by *Bathyplectes*, particularly among fourth-instar weevils, at once suggest that the female avoids already parasitized larvae, but the fact remains that a fair amount of superparasitization is sometimes encountered, as illustrated in table 24.

Table 24 shows that superparasitization occurred in all instars. However, only 6.79 percent of the total, or 12.03 percent of those parasitized, contained more than one parasite. Does this extent of superparasitization indicate random deposition of eggs by the female *Bathyplectes*? The answer may be had by comparing observed distributions with theoretical ones calculated on the assumption of fortuity and involving like numbers of parasite offspring and weevil larvae. The chance distributions are readily determined by use of Poisson's distribution formula

$$e^{-m}\left(1, m, \frac{m^2}{2!}, \frac{m^3}{3!}, \frac{m^4}{4!}, \frac{m^5}{5!} \cdots\cdots\cdots \frac{m^x}{x!}\right),$$

TABLE 24.—*Superparasitization of alfalfa weevil larvae by Bathyplectes curculionis, first-crop period of 1931, Salt Lake Valley, Utah*

Number of parasites in a single weevil larva	Frequency in different instars				Total frequency	Percent of total
	First	Second	Third	Fourth		
0	999	504	197	77	1,867	43.56
1	240	619	668	601	2,128	49.65
2	10	68	124	35	237	5.53
3	0	6	21	13	40	.93
4	0	2	9	3	14	.33
5	0	0	0	0	0	0
Total	1,249	1,289	1,019	729	4,286	100.00

the successive terms of which give the theoretical proportion of larvae containing 0, 1, 2, 3, 4, 5. ________ *x* parasites. The results of calculations for each instar from a sampling of May 20, 1931, are shown in table 25.

Among first instars small discrepancies appear between observed and chance distributions, there being a small excess of single-parasitized larvae and deficiencies in the other classes. While the evidence here is not strong, it at least suggests that the female *Bathyplectes* may have some ability to select unparasitized larvae. Second instars, which have been longer exposed to parasitic attack and have a higher level of parasitization, also exhibit discrepancies, but the excess of larvae each containing a single parasite is so large as to leave little doubt concerning the ability of the female *Bathyplectes* to avoid larvae already parasitized. Finally, third and fourth instars show a great many more single-parasitized larvae than would be expected if parasite eggs were deposited at random.

The excesses in the different instars cannot be compared directly, because the total number of larvae is different in each case. Instead, use may be made of the ratio of the observed frequency to the number expected on the basis of chance to contain a single parasite (table 26). These ratios show that throughout the season and in all instars, with but two exceptions, the number of larvae containing a single parasite exceeds the number expected on the basis of fortuity.

This steady increase is not due entirely to parental selection. Dissection records show that, beginning with second instars, the supernumerary parasites, especially the egg when a larva is also present, are frequently found dead and encysted. This condition is particularly noticeable among superparasitized third instars, and is observed less frequently in fourth instars. As a consequence of this loss of excess parasites, superparasitization is less among fourth than among third instars (table 26).

In first to third instars, however, before elimination of extra parasites is accomplished, the ratios represent approximately the selection exercised by *Bathyplectes* females and may therefore be called coefficients of selectivity. Since superparasitization was most prevalent

TABLE 25.—*Comparison of observed and calculated distribution of parasites among alfalfa weevil larvae of all instars, collected May 20, 1931, Salt Lake Valley, Utah*

Number of parasites in a single weevil larva	First instar			Second instar			Third instar			Fourth instar		
	Frequency		Deviation	Frequency		Deviation	Frequency		Deviation	Frequency		Deviation
	Observed	Calculated		Observed	Calculated		Observed	Calculated		Observed	Calculated	
0	157	158.9	−1.9	61	87.3	−26.3	8	44.8	−36.8	3	23.6	−20.6
1	32	28.4	+3.6	117	71.9	+45.1	114	52.0	+62.0	63	30.2	+32.8
2	1	2.5	−1.5	17	29.6	−12.6	15	30.2	−15.2	12	19.4	−7.4
3	0	.2	−.2	3	8.1	−5.1	2	11.7	−9.7	6	8.3	−2.3
4	0	------	------	1	1.7	−.7	4	3.4	+.6	1	2.7	−1.7
5	0	------	------	0	.3	−.3	0	.8	−.8	0	.7	−.7
Number of larvae	190.			199			143			85		
Mean number of parasites per larva	.1789			.8241			1.1608			1.2824		
e^{-m}	.8362			.4386			.3132			.2773		

TABLE 26.—*Ratio of observed to calculated frequency of occurrence of single-parasitized alfalfa weevil larvae and prevalence of superparasitization by Bathyplectes curculionis, first-crop period, 1931, Salt Lake Valley, Utah*

Sampling date	Ratio of observed to calculated frequency for indicated instar				Superparasitization of indicated instar			
	First	Second	Third	Fourth	First	Second	Third	Fourth
					Percent	*Percent*	*Percent*	*Percent*
Apr. 20	1.14				2.7			
Apr. 27	1.06	0.71			0	8.7		
May 4	1.16	1.10			1.0	6.1		
May 11	1.10	1.59	1.57		0	4.8	21.3	
May 20	1.13	1.63	2.19	2.09	.5	10.6	14.7	22.4
May 25	1.32	1.54	1.69	2.33	.5	7.6	26.9	8.4
June 1	1.14	1.56	1.81	2.28	1.0	5.8	17.5	8.7
June 8	1.10	1.41	1.76	2.34	0	1.6	9.5	2.0
June 15	.92	1.41	1.74	2.19	0	3.4	7.1	3.5
Average	1.13	1.37	1.79	2.25	.6	6.1	16.2	9.0

among third instars the average coefficient of selectivity for this instar clearly shows that *Bathyplectes* exercises a high degree of selectivity.

THE SECONDARY PARASITE EUPTEROMALUS VIRIDESCENS

A pteromalid that has been known for many years as an external parasite of cocooned larvae of *Bathyplectes curculionis* was identified in 1930 as *Eupteromalus viridescens* Walsh.[12] Its abundance and development throughout the year were determined in the course of dissecting the free-existing *Bathyplectes* cocoons taken in periodic field samplings. With these data it is possible to discover the role of *Eupteromalus* in the environmental complex of the weevil.

Eupteromalus viridescens passes the winter in the larval stage inside the cocoons of *Bathyplectes*, and some larvae are present through April. Pupation begins in March, and pupae occur throughout April and scatteringly in May. The first adults appear the third week of May. Pteromalid larvae reappear in the newly formed *Bathyplectes* cocoons about the middle of June and increase in abundance until the end of July. Pupation of these larvae begins about the middle of July and reaches its peak about the last week of that month. Adults emerge again the latter half of July and in August, eggs having been found early in August. Larvae predominate during the fall. The secondary parasite is thus indicated as having two generations annually.

The first-brood adults oviposit in the newly formed *Bathyplectes* cocoons, of both transforming and wintering types, in June and early

[12] Determined by A. B. Gahan, Division of Insect Identification, Bureau of Entomology and Plant Quarantine.

in July. The appearance of the second-brood adults overlaps the time of cutting the second crop and coincides with the formation of the negligible number of *Bathyplectes* cocoons derived from the small and lightly parasitized population of weevil larvae living upon the second growth of alfalfa. Second-brood adults oviposit in the few *Bathyplectes* cocoons then formed, and the increase in number of immature stages of the secondary at this time makes it reasonably certain that they attack members of the main group of earlier formed (June) *Bathyplectes* cocoons, from a portion of which they themselves bred, and which contain larvae throughout the summer and winter. The second brood of *Eupteromalus* adults is therefore important in further reducing the number of *Bathyplectes* larvae that have survived both stubblefield heat following the first cutting and hyperparasitization by the first generation of *Eupteromalus*.

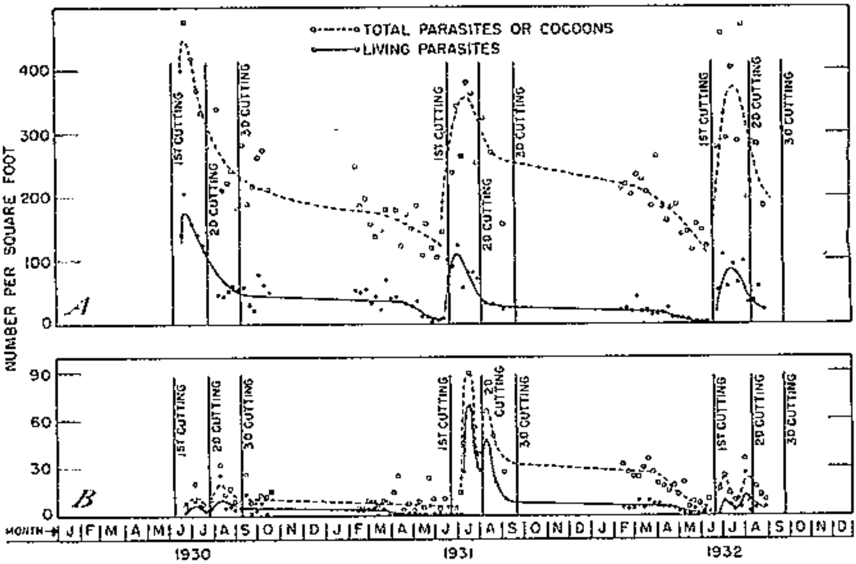

FIGURE 20.—Seasonal abundance of both (*A*) primary and (*B*) secondary parasites of the alfalfa weevil in relation to the cropping system, 1930–32, Salt Lake Valley, Utah. Vertical lines indicate time of cutting.

However, the heat following the second cutting, which kills many *Bathyplectes* larvae, likewise kills many larvae and pupae of the secondary parasite, the broods of which had already begun to overlap before the second cutting. It is therefore impossible to segregate and measure the kill of *Bathyplectes* larvae effected by the secondary, although the data provide a reasonably satisfactory understanding of the part played by it. Data on abundance and survival of *Eupteromalus* during significant periods of the year are summarized in table 22.

Understanding of the relation between primary and secondary parasites, and of their relation to the season and the cropping system, may be improved by a study of figure 20.

Estimation of the effect of *Eupteromalus* in curtailing the abundance of *Bathyplectes* is difficult, because the mortality from two generations of the secondary parasite is interwoven with the heat kill of the primary and the secondary following both first and second cuttings. The most conservative estimate may be had by dealing with the figures representing the end point of the process during the third-crop period, that is, by relating the number of living secondary parasites to the total number of living primaries and secondaries. This method of calculation shows that there was a 15.87-, 49.06-, and 16.55-percent infestation by the secondary for 1930, 1931, and 1932, respectively.

These figures do not take account of the dead pteromalids, which had, of course, killed their *Bathyplectes* hosts before they themselves died, or of the *Bathyplectes* larvae destroyed by secondaries that issued as the second brood of *Eupteromalus* adults. It is believed that the dead secondaries represent cocoons so situated in the field that their occupants, whether primary or secondary, would have been killed by the stubblefield heat, in which case the effect of the hyperparasitization would be neutralized.

The second objection has more validity, for when second-brood *Eupteromalus* adults emerged they left empty *Bathyplectes* cocoons, which thereafter could not be taken into account by the method of study employed. There was, then, actually some destruction of *Bathyplectes* larvae by the secondary parasite prior to the period to which the above percentages apply, but its extent is unknown. On the other hand, a goodly portion of the *Bathyplectes* so destroyed would, in the absence of the secondary, have succumbed to stubblefield heat following first cutting. Thus the best that can be done is to accept the above percentages as possibly slightly underestimating the extent of *Eupteromalus* hyperparasitization of *Bathyplectes curculionis* cocoons.

The percentages cited show that the mortality due to *Eupteromalus* varies widely in different years and suggest that the economic benefit of *Bathyplectes* would in consequence exhibit comparable fluctuation. The effect of drastic reduction of *Bathyplectes* is mitigated, however, because the beneficial action of this parasite depends upon its very high parasitization of the early weevil larvae, and the adult primary parasites produced the following spring are sufficiently numerous to parasitize almost completely the more advanced weevil larvae. Nevertheless, with continued growth of the population of weevil larvae, both in number and size, the reduction of *Bathyplectes* manifests itself in (1) an earlier decline in the parasitization of weevil larvae, (2) a more rapid drop in parasitization, and (3) a lower level of parasitization than would obtain with normal abundance of *Bathyplectes*. More concisely, the percentage of parasitization of fourth instars begins to decline when that stage is yet comparatively scarce, and the parasitization ultimately established among the smaller larvae is noticeably lowered.

The nearly complete parasitization of the earliest maturing weevil larvae is not unusual, however, and the lowered parasitization affecting the main group of smaller larvae is of no consequence, for they succumb to starvation during the stubble period following the first cutting. The important difference is that incomplete parasitization of mature larvae appears so early in the scheduled development of the weevil population that the unparasitized individuals may pupate and produce adult weevils before the alfalfa has reached the flower-bud stage of growth and cultural kill can be accomplished by harvesting it.

Such conditions make the time of cutting the first crop more critical, any delay after maturity being more than ordinarily penalized by the production of new-generation weevils. This is the net effect of drastic kill of *Bathyplectes* by *Eupteromalus*.

The foregoing information concerning *Eupteromalus* throws much light on a perplexing question which arose in 1932 and to which there was no answer at that time. In Salt Lake Valley during that season parasitization of weevil larvae by *Bathyplectes* declined earlier and more rapidly than usual, although in Weber Valley nearby it held up normally. In the latter locality when cocooning of weevil larvae had reached an average of 7 to the square foot parasitization of cocooned individuals by *Bathyplectes* was still 94.5 percent, whereas in Salt Lake Valley an average cocoon population only one-fourth as large showed only 82.7 percent parasitization.

Finally, this analysis of the influence of *Eupteromalus* illustrates well how a condition of the moment may have its antecedent factors deeply buried in the history of a biological complex. Thus the unusual abundance of weevils that menaced the alfalfa crop of Salt Lake Valley in the spring of 1933 was due partly to a curtailment of parasitization by *Bathyplectes* in 1932, which in turn arose from an unusual abundance of *Eupteromalus* in the summer of 1931.

Anaphes Pratensis, Egg Parasite

Two internal mymarid egg parasites, *Anaphes pratensis* Foerst. and *Anaphoidea luna* Gir., were liberated in alfalfa fields near Salt Lake City in 1925–28.[13] These two species were so similar in appearance that they could not be distinguished while the insects were alive, and therefore no attempt was made to handle their emergence and liberation separately. *Anaphes pratensis* was first recovered from several fields near Salt Lake City in the spring of 1926,[14] being taken from the eggs of both *Hypera postica* and *H. punctata*. There is no record of recovery of the other parasite, and apparently it has failed to establish itself.

Incubation of all eggs taken in the periodic samplings resulted in the finding, in 1930, of a few weevil eggs that had bright red circular spots in them. These eggs all came from litter, and each later produced an adult *Anaphes pratensis*. To determine the importance of this parasite, all eggs obtained from the periodic samplings of 1931 were incubated. No parasites issued from eggs deposited in growing alfalfa stems, and in eggs taken from litter parasitization appeared

[13] Mymarid egg parasites were also liberated in the Salt Lake Valley in 1911, 1912, and 1913. At that time they were called *Anaphoidea luna*, but in the light of later work it seems probable that *Anaphes pratensis* was also involved in these liberations.

[14] Unpublished notes by T. R. Chamberlin, Bureau of Entomology and Plant Quarantine.

initially near the end of April, reached a maximum the third week of May, and stopped after the first of June (table 27).

TABLE 27.—*Parasitization of alfalfa weevil eggs in litter by Anaphes pratensis, first-crop period, 1931, Salt Lake Valley, Utah*

Sampling date	Weevil eggs		Sampling date	Weevil eggs	
	Total	Parasitized		Total	Parasitized
	Number	*Percent*		*Number*	*Percent*
Apr. 13	473	0	May 25	552	2.72
Apr. 20	1,124	0	June 1	632	2.85
Apr. 27	1,287	.70	June 8	387	0
May 4	1,629	1.17	June 15	231	0
May 11	1,633	.80	June 16 [1]		
May 20	1,257	3.34			

[1] First crop cut.

This parasite was also reared from the larger eggs of the clover leaf weevil (*Hypera punctata*) taken in the periodic samples and from each of which two parasites ordinarily issue. The fact that parasitization by *Anaphes* does not appear in eggs of the alfalfa weevil until those of the clover leaf weevil have become scarce indicates that the former species serves merely as an alternate host. *Anaphes* is therefore an inconsequential factor in the control of the alfalfa weevil under conditions obtaining in Salt Lake Valley.

METEOROLOGICAL FACTORS

The temperature data, measured and recorded as stated on page 10, provide an opportunity for determining the relation between weevil increase and temperature, and for establishing a simple conception of the seasonal trend of heat which may be used to study the effect of thermal aberrations upon weevil activities in a given season.

WEEVIL INCREASE AND TEMPERATURE

The first objective may be attained by cumulating the day-degrees above 50° F. from the beginning of the season up to the date of each census of the weevil population, and plotting against these cumulative values the average abundance of immature weevils (fig. 21). Use of these temperature units has the effect of spacing the observations in proportion to the average temperatures of each sampling interval, whereas a time unit, by implying equal effectiveness of each day in promoting growth of the immature population, would obscure such differences.

The graphs show that early in the season increase of the immature population proceeds in proportion to the temperature, as measured by cumulative day-degrees in excess of 50° F. This trend continues until 3 to 4 weeks before cutting of the first alfalfa crop. The rela-

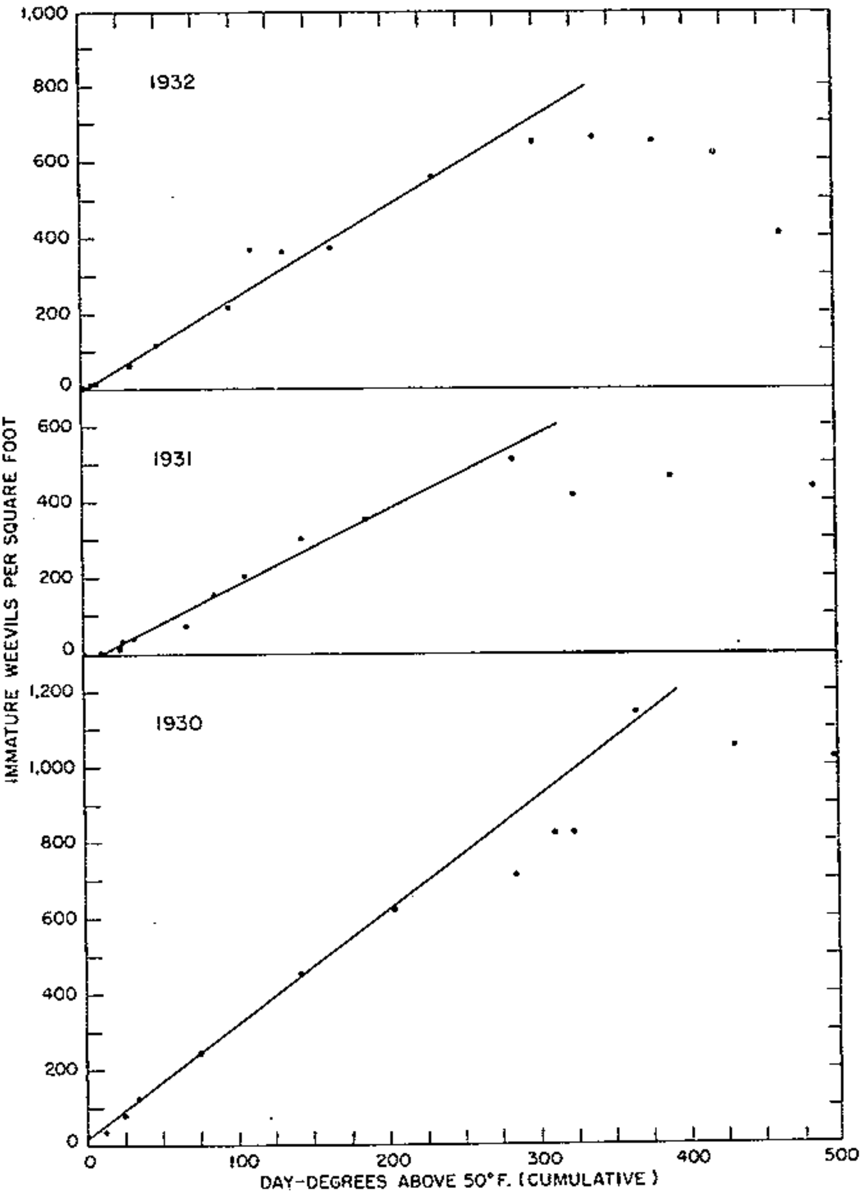

FIGURE 21.—Relation between immature alfalfa weevil population and day-degrees above 50° F. early in the season, 1930-32, Salt Lake Valley, Utah.

tionship means that the biological processes underlying egg laying are governed by temperature, because increase of the immature population depends entirely upon oviposition. However, it may not be construed as an exact measure of ovipositional activity, because any mortality affecting the immature stages would depress the rate of increase. The quantitative relationship therefore applies only to the net rate of increase of the immature weevil population.

The rates of increase are shown by the slopes of the trend lines (fig. 21) and, as determined by graphical differentiation, were 3.04, 2.00, and 2.40 progeny per day-degree in 1930, 1931, and 1932, respectively. These rates, however, also reflect the variable abundance of parent weevils in the different seasons. Consequently, a comparable basis was provided by dividing each rate by one-half the number of adult weevils present at the beginning of the season, thus adjusting the rate of increase to the basis of a single female weevil. When so computed, the respective rates were 1.13, 2.67, and 1.68 progeny per female per day-degree, representing the variation in the reproductive ratio in the differing seasons. The general average rate of 1.83 will serve as an approximate measure of the relation between weevil increase and temperature.

The last two to four points in the graphs, which represent intervals of 3 to 4 weeks before the first cutting, depart widely from the lines of relationship just discussed. Not only is the rate of increase not maintained, but there is finally an actual decrease in the total number of progeny before any individuals have progressed to the adult stage. The decrease is a reflection of mortality in some component of the immature population, and the records indicate that it occurred among newly hatched larvae. The death of the tiny larvae is believed to result from a scarcity of suitable food at this season, as the plants mature and the terminal buds harden, and also from heat and drought.

Seasonal Trend of Heat

The seasonal trend of heat was studied by summing the day-degrees above 50° F. for each week of the 6-year period 1928-33, and plotting the weekly sums against the weeks of the year, as shown in figure 22. Despite the capriciousness of the individual seasons, the ensemble was found to form a clear-cut pattern, and suggested that the seasonal trend might be described by the normal distribution which, calculated in the usual fashion (see p. 20), gave the theoretical distribution of effective heat shown in table 28.

The smooth curve derived from the calculated distribution, also shown in figure 22, admirably represents the pattern of the empirical curves. The theoretical distribution will therefore serve as a standard of comparison for detecting accurately and rapidly the peculiarities of a given season, the effects of which may then be studied in the trends of the various components of the alfalfa weevil complex. This base curve for Salt Lake Valley, the area in which the ecology of the alfalfa weevil is best known, may also be useful in pointing out differences in seasonal heat of other weevil-infested localities and in indicating the probable effects of such differences upon weevil activities.

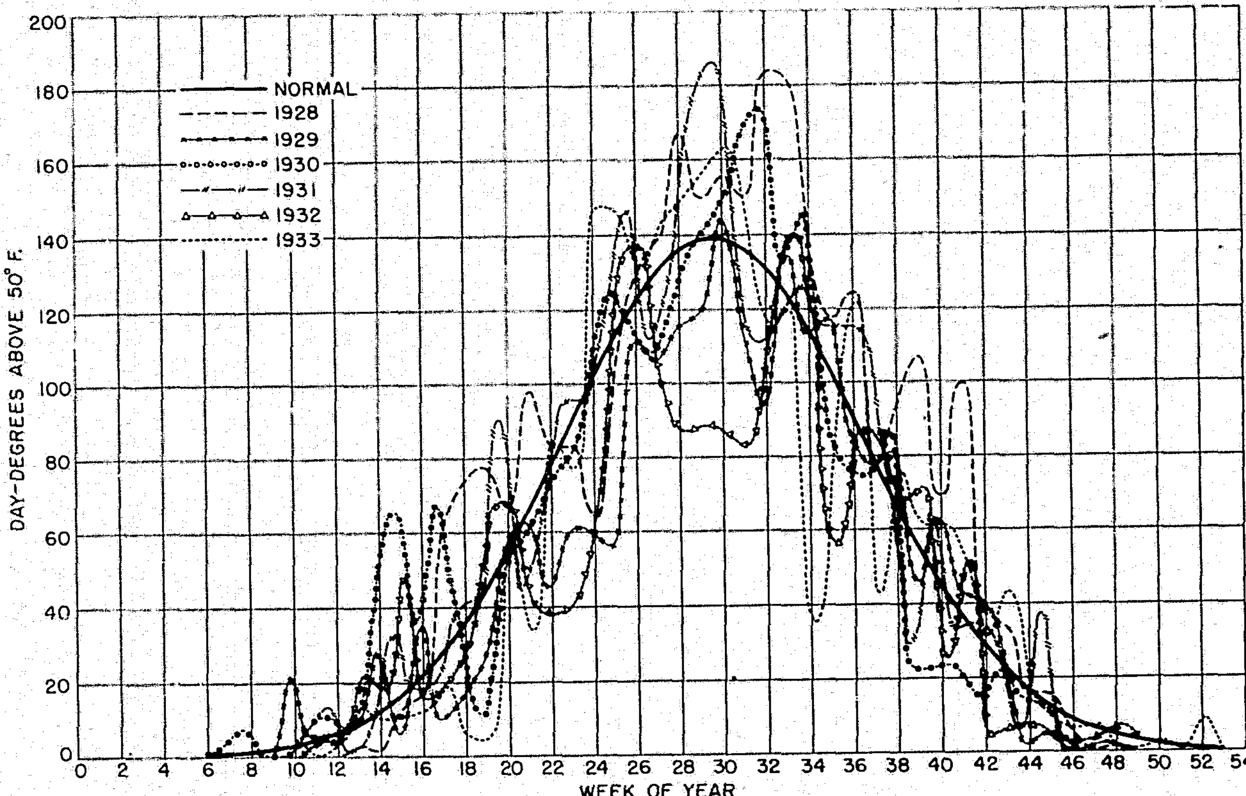

FIGURE 22.—Temperature distribution in Salt Lake Valley, Utah, based on weekly day-degrees above 50° F., observed trend of heat in 1928-33 and normal-distribution curve.

TABLE 28.—*Calculated temperature distribution for Salt Lake Valley, Utah*

Week of year	Plus or minus deviation from origin (29.5 week of year) (x)	Calculated day-degrees above 50° F. (y)	Week of year	Plus or minus deviation from origin (29.5 week of year) (x)	Calculated day-degrees above 50° F. (y)
29.5	0	139.29	18 and 41	11.5	36.18
29 and 30	.5	138.94	17 and 42	12.5	28.33
28 and 31	1.5	136.13	16 and 43	13.5	21.74
27 and 32	2.5	130.70	15 and 44	14.5	16.34
26 and 33	3.5	122.74	14 and 45	15.5	12.03
25 and 34	4.5	113.31	13 and 46	16.5	8.69
24 and 35	5.5	102.33	12 and 47	17.5	6.14
23 and 36	6.5	90.55	11 and 48	18.5	4.25
22 and 37	7.5	78.51	10 and 49	19.5	2.89
21 and 38	8.5	66.69	9 and 50	20.5	1.92
20 and 39	9.5	55.52	8 and 51	21.5	1.25
19 and 40	10.5	45.28	7 and 52	22.5	.80

The normal-distribution curve is not the only one capable of describing the trend of seasonal heat. Other mathematical curves that might be used are the Gram-Charlier and the Fourier. The latter is a periodic curve based upon a series of sines and cosines of multiples of the independent variable (i. e., the weeks of the year), the generalized equation being

$$y=A_0+(A_1 \sin x+B_1 \cos x)+(A_2 \sin 2x+B_2 \cos 2x)+ \ldots\ldots +)$$

Because of its periodic nature the Fourier curve best accords with the seasonal cycle of temperature, but since the physical meaning of the several terms in the equation is not known, the curve is valuable only for its descriptive ability.

The normal distribution, in addition to describing the trend, measures the dispersion about the mean ordinate in terms of the standard deviation, which may be useful in characterizing temperature distributions of different areas, as σ was employed in studying egg populations of different areas. The normal curve also has the advantage of simplicity of calculation. A freehand curve would describe the trend as well as any other except that each person would draw it somewhat differently. Mathematical curves are free from this objection, and as long as they adequately describe the data their use seems preferable.

The utility of this heat yardstick, when used with a knowledge of weevil trends and cropping practices, may be shown by comparing the measured temperature distribution of each year with the calculated distribution. These comparisons are shown in figures 23 and 24, and demonstrate that large departures from the trend may

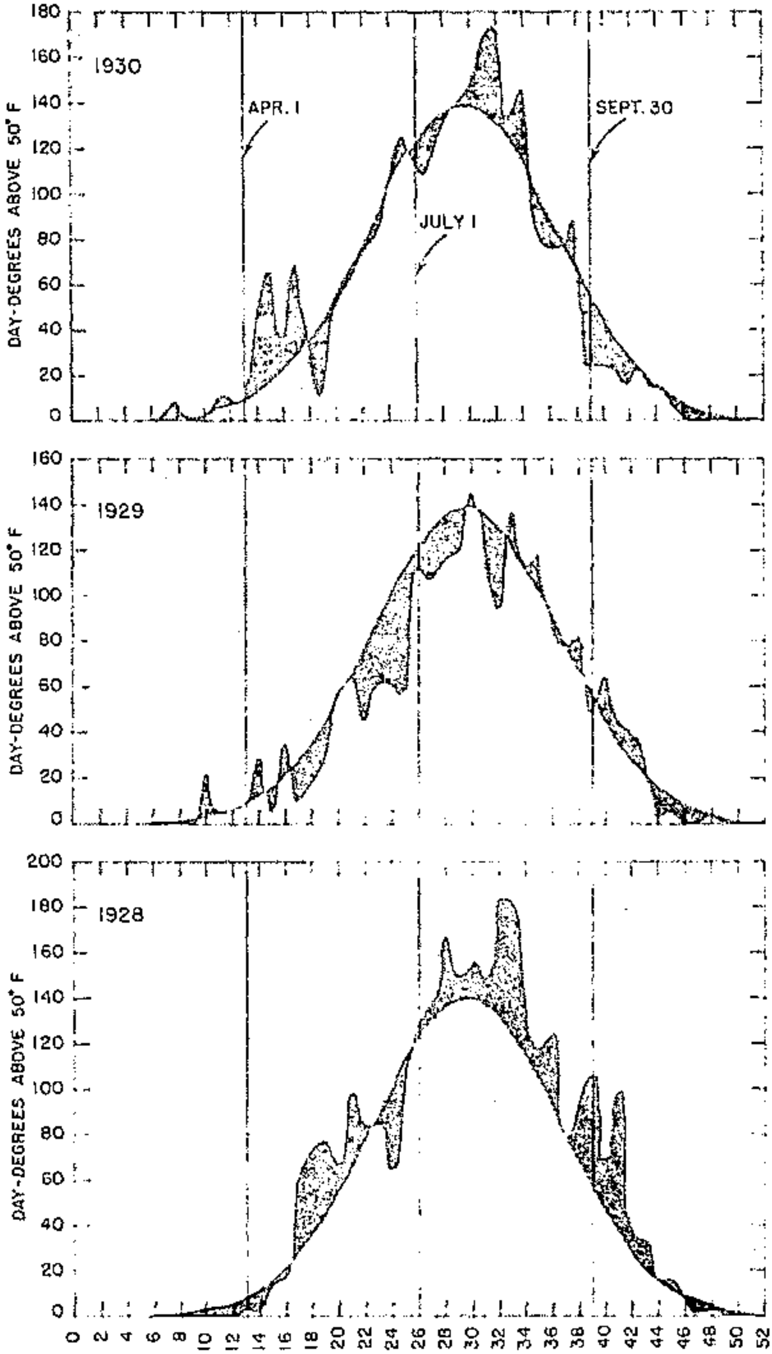

FIGURE 23.—Departures from normal temperature distribution, 1928–30, Salt Lake Valley, Utah.

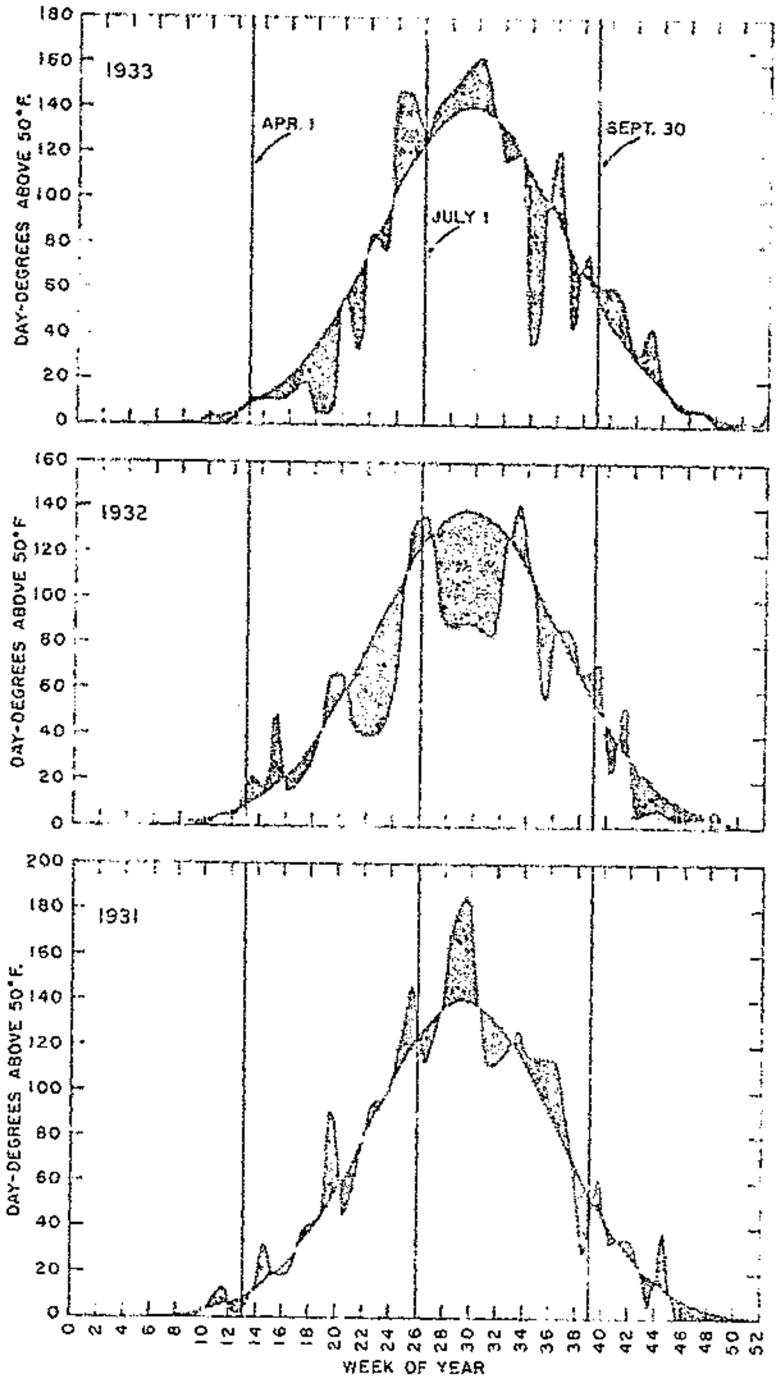

FIGURE 24.- Departures from normal temperature distribution, 1931-33, Salt Lake Valley, Utah.

occur at any season of the year. For example, in 1928 there was a considerable excess of heat throughout the year, whereas in 1929 there was a general deficiency of heat. However, since the immature population has completed its damage and produced the succeeding generation of weevils by early August, those deviations from the up slope of the curve are far more important in the present study.

In 1930 springlike weather began early and there was an excess of heat during April, the principal effect of which fell upon the adult weevils, as reflected in the earliness of the egg population shown in figure 8. Approximately normal heat during June and July resulted in a good kill of the immature stages after the first and second cuttings (pp. 28 and 30).

During the spring and early summer of 1931 the actual temperature distribution followed the base curve remarkably closely, producing no exceptional features in the egg and larval populations or in the kill of immature stages following cuttings. The principal aberration of the year was an extremely hot period in July, which was attended by unusually high mortality of cocooned individuals that had developed on the second crop (p. 35). Moreover, it was during this period that the population of new-generation weevils, produced from the early node of pupae, declined severely (p. —).

The 1932 season, after a fair excess of heat in April, shows large deficiencies from the last week of May to the third week of June and again during July and early in August. These cool periods, coinciding with the first and second cuttings, reduced the usual severe cultural kill which supplements the biological kill by the *Bathyplectes* parasite. As a consequence the production of sufficient new-generation adult weevils to threaten damage to the first crop of 1933 was foreshadowed as a general condition in Salt Lake Valley. The earlier and more rapid decline of parasitization by *Bathyplectes*, occasioned by the hyperparasite *Eupteromalus viridescens* during the preceding season, also contributed to the production of these adults.

In the fall of 1932 a survey of Salt Lake Valley based on 24 fields showed 4 fields with weevils too scarce to produce damage in any event, 12 with weevils of pivotal abundance, and 8 with weevils so plentiful as virtually to assure damage to the first alfalfa crop in 1933. The pivotal fields are shifted into the damage or damage-free class mainly through the effect of the spring weather, first on oviposition and then on incubation (p. 12). With normal spring weather they may be expected to combine with those of the damage class and provide an outlook for damage of approximately five-sixths of the alfalfa acreage in 1933.

Deficient heat, such as obtains in late, cold springs, or deficient moisture coupled with excessive heat, which abbreviates the spring season, tends to prevent damage in the pivotal fields, the one by retarding weevil activities, particularly incubation and larval growth, sufficiently to allow the crop to reach the flower-bud stage before the larval population reaches damaging proportions, and the other by curtailing oviposition commensurately with the brevity of the spring season. Under such conditions only about one-third of the acreage would have been subjected to weevil damage in 1933.

The spring of 1933 was late and cool, and oviposition was retarded, but a large egg population accumulated because of the abundance of adult weevils and delayed hatching. The abrupt change to summer heat therefore concentrated heavy populations of small larvae on the first crop, quickly stopping its growth by destroying the growing tips. The alfalfa growth had been little retarded by the backward weather, however, and was nearly ready to cut. Owing to these spring weather conditions it was possible to harvest a good crop before the larvae reached their most injurious phase.[15] Possibly somewhat more than one-third of the fields were damaged because of needless delay in cutting, but under more nearly normal conditions the injury would have been far more general.

Precipitation, by its variable frequency and incidence during the season, has important effects upon the weevil population, influencing egg laying, hatching, and kill of larvae following crop cutting. These effects are to a large extent integrated by temperatures measured at ground level, but there are some indications that precipitation may also have independent effects. For example, the three observations in 1930 lying below the line of relationship between immature population and seasonal heat (fig. 21) occurred during a rainy period of 4 weeks' duration. Since the same three observations are below the trend line in the egg-population curve (fig. 8), the depressing effect of precipitation appears to have affected the ovipositional activities of adults. In field studies of this type, however, it has not been possible to differentiate between the two effects.

The annual trend of precipitation in Salt Lake Valley, based upon 22 years' records of the Weather Bureau taken at Midvale, Utah, has been constructed by plotting the average value for each week and smoothing by means of a freehand curve. By superimposing the actual precipitation curve for a given year upon this annual trend, it is possible to see its peculiarities at a glance. This curve is also useful in studying normal differences of precipitation in different parts of the weevil-infested area. Figure 25 shows that in northern Utah

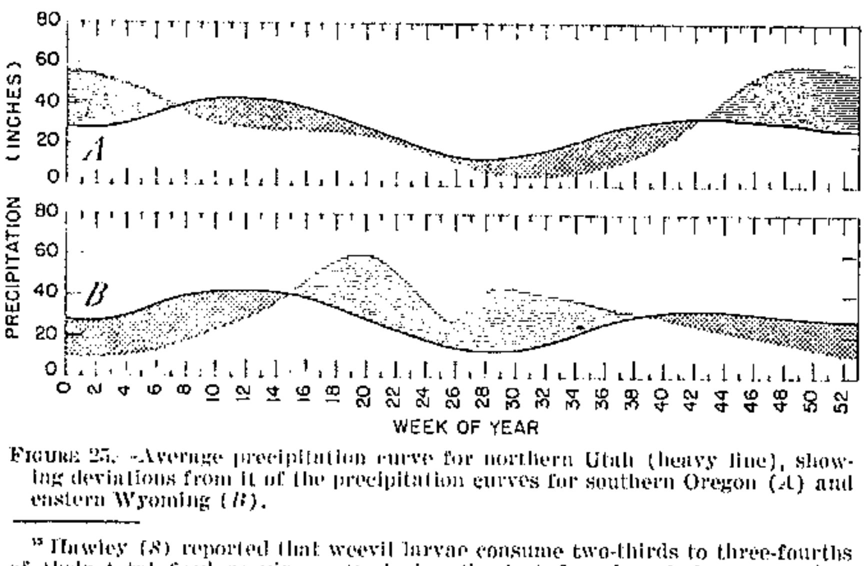

FIGURE 25.—Average precipitation curve for northern Utah (heavy line), showing deviations from it of the precipitation curves for southern Oregon (*A*) and eastern Wyoming (*B*).

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[15] Hawley (*8*) reported that weevil larvae consume two-thirds to three-fourths of their total food requirements during the last few days before cocooning, i. e., during the fourth instar.

precipitation is highest in the spring and lowest in midsummer, that in eastern Wyoming it is less in fall and winter and greater in spring and summer than in northern Utah, and that in southern Oregon the differences are of opposite character to those in Wyoming.

CULTURAL FACTORS

Cultural factors chiefly important in the alfalfa weevil problem include density of stand, soil fertility, cutting, irrigation, harvesting practices, and clean culture.

Stand and Fertility

In view of the demonstrated relation between weevil increase and temperature, the different larval instars might be expected to show the same proportionate representation in neighboring fields having similar soils and exposed to the same weather conditions. That this is not true is shown by results obtained in seven fields in Salt Lake Valley during 1932. The spring breeding base of weevils in these fields ranged from 2.1 to 8.1 per square foot. A few fourth instars appeared in all fields the second week of May. The number increased during the remainder of the month and became increasingly out of proportion to the abundance of parent weevils. The results at the end of May are shown in figure 26. In general, the number of fourth instars

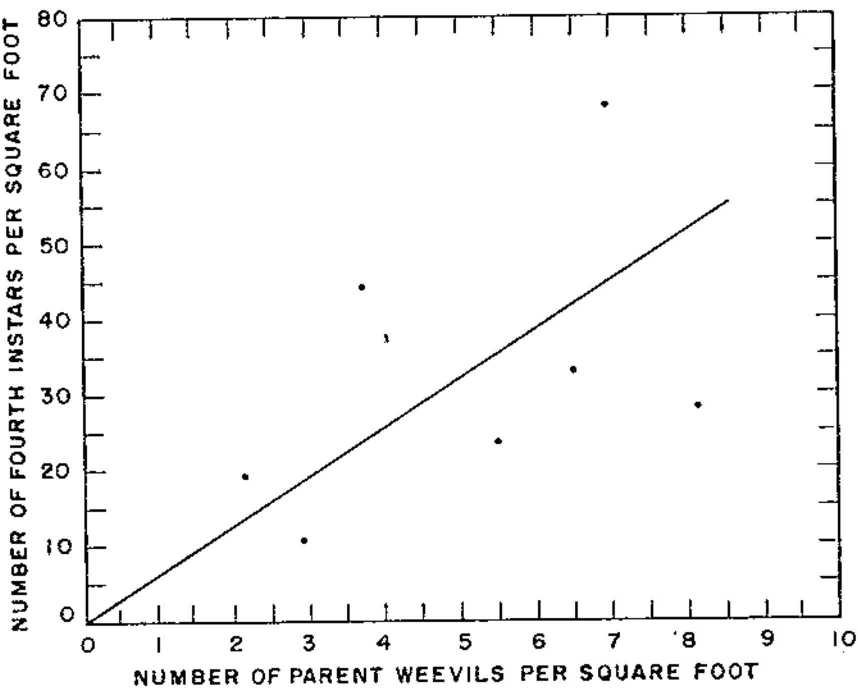

FIGURE 26.—Number of maturing alfalfa weevil larvae produced by the end of May in seven fields having varying populations of parent weevils, 1932, Salt Lake Valley, Utah.

increased with the number of parent weevils, but the great amount of scatter of the dots about the freehand curve clearly indicates the operation of other factors.

The fields at this time showed pronounced differences in density of alfalfa growth, and therefore in the degree of shade afforded the field surface. Naturally, the sun's rays reached and warmed the ground more in poorly shaded than in well-shaded fields. Consequently, more rapid development of the weevil population would be expected in the less dense growths. An attempt was made to obtain a rough measure of stand density by clipping and weighing the vegetation in randomly selected 1-square-foot areas. The average weight of green material for the different fields ranged from 6.67 to 10.38 ounces to the square foot. The higher figure, however, was considerably inflated by the presence of orchard grass, which was in head and added much to the weight but contributed little shade.

The relation between the average number of fourth instars per parent weevil and the average green weight of vegetation in the seven fields under study is shown in figure 27. The number of fourth instars per parent weevil is shown to have decreased roughly 2.5 for each increase of 1 ounce of vegetation, between the limits of 6.5 and 9.5 ounces. This graph, however, should not be projected with a view to determining limits, for as complete shading is approached an increase in vegetation would not continue to give proportionate inhibition to larval growth.

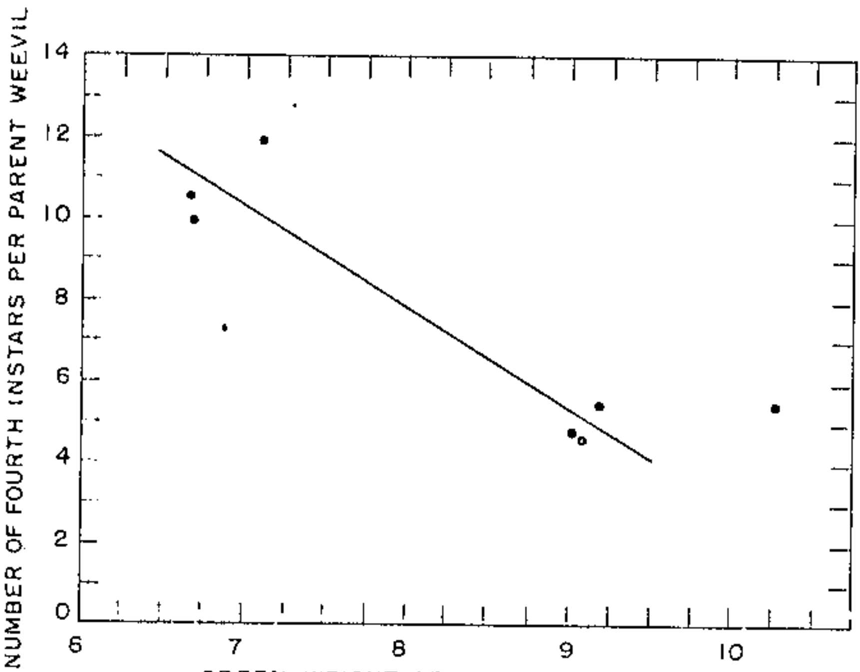

FIGURE 27.—Relation between number of maturing larvae per parent weevil and density of alfalfa growth, 1932, Salt Lake Valley, Utah.

During the following year an attempt was made to measure directly the effect of stand upon temperature by establishing thermographs in selected fields to record the temperature 4 feet above the ground and at ground level. The fields were selected to represent the usual range of stand density, were of the same soil type, and were not more than a mile apart. The stands were of different age because density of stand is usually a function of its age. In these fields stand density was measured in terms of the area covered by alfalfa crowns when the spring growth was 5 inches high. The data in table 29 show that the study fields covered the range of variation satisfactorily.

TABLE 29.—*Alfalfa coverage of 3 fields, spring of 1933, Salt Lake Valley, Utah*

Stand	Age of stand	Average area covered by alfalfa crowns in 1 square yard [1]	
	Years	*Square feet*	*Percent*
Thin	7	1.73±0.25	19.2
Average	3	4.28± .08	47.6
Thick	2	6.16± .12	68.4

[1] Average of nine 1-square-yard areas.

The thermographs were installed on May 15, and the comparison of temperature for the first-crop period is based upon the interval to June 8, when the crop was cut in one of the fields. The results, given in table 30, show that the thin stand allowed approximately 30 percent, and the thick stand 11 percent, more heat to reach the ground than did the average stand. Contrary to expectation, the vigorous growth of the older stand of average density shaded the ground more thoroughly than did the thick, younger stand composed of slender, seedlinglike plants. These percentages would undoubtedly vary considerably according to the season and the weather, but they demonstrate the important effect of stand and growth upon the amount of heat reaching ground level, where the majority of alfalfa weevil eggs are deposited. Furthermore, the temperature of the air over the thin stand was higher than that over the average stand, the 9 percent excess doubtless reflecting the greater heat at ground level. There was no appreciable difference in this respect between the thick and the average stands.

During the second-crop period the same sort of differences obtained (table 30). The average daily heat at ground level amounted to approximately 13 percent more in the thin stand than in the average stand. Comparison of the thick and average stands during this period is not entirely satisfactory, because the former was irrigated more frequently and was cut a week earlier. Nevertheless, the heat at ground level in the young, thick stand was on an average about 3 percent greater, and statistical analysis indicates that this difference is not accidental. The average number of day-degrees recorded in the air above the thin stand was 7 percent greater than that over the average stand, while the difference in air heat above the thick and the average stands has no significance.

TABLE 30.—*Comparison of heat in thin, average, and thick alfalfa stands during first- and second-crop periods, 1933, Salt Lake Valley, Utah*

Stand	Age of stand	Average heat units above 50° F.			
		First-crop period		Second-crop period	
		Ground	Air	Ground	Air
	Years	*Day-degrees*	*Day-degrees*	*Day-degrees*	*Day-degrees*
Thin	7	9. 17	11. 73	23. 94	26. 23
Average	3	7. 07	10. 68	21. 14	24. 41
Thick	2	7. 83	10. 75	21. 77	23. 99
Difference between thin and average		+2. 10	+1. 05	+2. 80	+1. 82
Difference between thick and average		+. 76	+. 07	+. 63	—. 42

Density of stand is thus shown to have an important influence upon the amount of heat reaching the lower levels in an alfalfa field where the early weevil eggs are laid. Both hatching and larval development proceed faster in thin stands. Furthermore, it is considered that all the differences in heat at ground level shown in this work underestimate the actual differences, because the shade necessary for proper operation of the thermometric element also moderated the temperature of the surrounding area.

Soil fertility is also a prime factor in producing shade, as was illustrated by an extreme case encountered in 1932. A certain field, although having an exceedingly dense stand, was experimentally determined to be deficient in phosphorus. The alfalfa grew very slowly and by the middle of May was only 6 inches high as compared with 12 inches in the valley generally. Because of this short growth a large proportion of the field surface was exposed to the sun's rays while representative fields were rather thoroughly shaded. As a result the weevil population developed faster, the number of fourth instars per parent weevil averaging 8.2 on May 20 when it was only 0.7 in the other fields.

Apart from its bearing upon weevil development, density of alfalfa has much to do with severity of weevil damage. In fields having a sparse covering large larvae come upon the crop at an earlier stage of its growth than they do in fields having a normal vegetative cover. Moreover, the damage appears to be much more severe simply because of the smaller amount of foliage. Thus, whereas approximately two parent weevils to the square foot are required in Salt Lake Valley to damage the crop in an average alfalfa field with normal spring weather, a field having sparse alfalfa cover may be damaged by the progeny of fewer weevils. For example, the field mentioned above as having extremely poor growth because of phosphorus deficiency suffered severe weevil damage in 1932 despite the fact that the breeding base was only 1.33±0.17 weevils per square foot.

These studies show that stand and fertility profoundly modify the usual trends shown by the periodic population studies. Whereas the weevil's schedule of development and the trend of parasitization in an average alfalfa field are such that few new-generation adults are produced if the first crop is cut at the flower-bud stage, these relations are disturbed in fields of sparse growth by the accelerated development of immature stages. On the other hand, dense shade retards the weevil's schedule with respect to crop maturity, and points to the conclusion that the first step in combating the alfalfa weevil is maintenance of a dense stand in vigorous growing condition.

Cutting and Irrigation

Timely cutting of the first and second alfalfa crops removes the food supply of the larvae and, except in rainy haying seasons, increases the temperature of the field surface. The drastic cultural kill usually effected is important in preventing damage by the alfalfa weevil.

Irrigation greatly lowers the temperature of the field and the cooling effect lasts for several days. To illustrate, in Wyoming Sweetman (*15*) found that the mean temperature from 8 a. m. to 5 p. m. on May 30 was 90° F. on dry soil, whereas 6 feet away on soil irrigated the preceding day it was only 68°. Therefore, to avoid reduction in cultural kill of immature weevil stages, no water should be applied for 7 to 10 days after cutting. The alfalfa plants, however, need an irrigation to bring the second crop along promptly. Both these desiderata are attained by the practice, common in Utah today, of applying an irrigation for the benefit of the new growth approximately 1 week before the first cutting.

Harvesting Practices

Many larvae congregate beneath haycocks to escape the stubble-field heat. Temporary shelter thus afforded is of little value to the species if the hay is hauled from the field as soon as cured, but delay in removing hay permits some individuals to reach the adult stage and thus diminishes the cultural kill.

The protective influence of haycocks may be illustrated by data obtained 4 days after the second cutting in 1930. Paired samples of 10 cocoons each taken from 27 randomly chosen positions, one sample from the open space and the other from beneath the nearest haycock, show essentially the same composition in the 2 series (table 31). In each stage, however, the percentage of living individuals is much lower among the cocoons taken from open areas of the field, and in each series the adult stage showed the highest proportion alive, and the larval stage least. Nearly 3 times as many weevils survived in cocoons beneath haycocks as in those between haycocks.

The haycocks covered one-eighth of the field area, and the gross abundance of cocoons beneath them was approximately twice that in the open field. In view of the differential survival in these situations, however, nearly half the living cocoons existed beneath the haycocks. The hay was left on the field much longer than necessary for curing; in fact, the new growth was well started before the hay was hauled, and the positions of the cocks were outlined in the third alfalfa growth, first by saucerlike areas of shorter growth and later by blossomless circular areas. Although no further examinations were

TABLE 31.—*Alfalfa weevil stages and living individuals in 540 cocoons taken equally between and beneath haycocks 4 days after the second cutting, 1930, Salt Lake Valley, Utah*

Stage	Cocoons containing living or dead individuals		Individuals alive in cocoons	
	Between cocks	Beneath cocks	Between cocks	Beneath cocks
Weevils:	*Percent*	*Percent*	*Percent*	*Percent*
Larvae	21. 1	20. 0	3. 5	22. 2
Pupae	61. 1	64. 8	15. 1	43. 4
Adults	14. 8	13. 0	27. 5	60. 0
All stages			14. 1	40. 4
Parasites	3. 0	2. 2	12. 5	66. 7

made, there can be little doubt that the mortality differential increased and the delayed hauling augmented the population of new-generation weevils. Prompt removal of hay is necessary to gain the greatest benefit from the cultural kill following cutting.

The raking and cocking of hay concentrates immature weevils within haycocks, and many of them are carried with the hay into the haystack. Hawley (*8*) shows that considerable percentages of large larvae, spun larvae, and pupae complete their development and emerge as adults in the haystack, but since newly issued weevils feed rapidly soon after emergence and would have no fresh food available in the haystack, the development of these individuals is considered of minor importance.

CLEAN CULTURE

In view of the likelihood that adult weevils wintering in border waste areas migrate back to the field in the spring, burning over these areas, as recommended by Titus (*16*), would reduce the ultimate spring breeding base. The benefit thus gained, however, must be weighed against increased erosion and the loss of cover for beneficial birds and other forms of animal life.

ECOLOGICAL INTERPRETATION

The results of the analytical studies may now be combined to show the successive influences affecting a weevil population throughout the season. Afterwards the ecological perspective thus obtained will be applied to the factors involved in the gradual transition of the weevil problem during the past quarter-century.

GRAPHIC SEASONAL SUMMARIES

The relationship between all phases of the weevil population for the seasons 1930, 1931, and 1932 has been portrayed graphically in figures 28, 29, and 30. Each stage of the population has been plotted as the average number of individuals to the square foot of field sur-

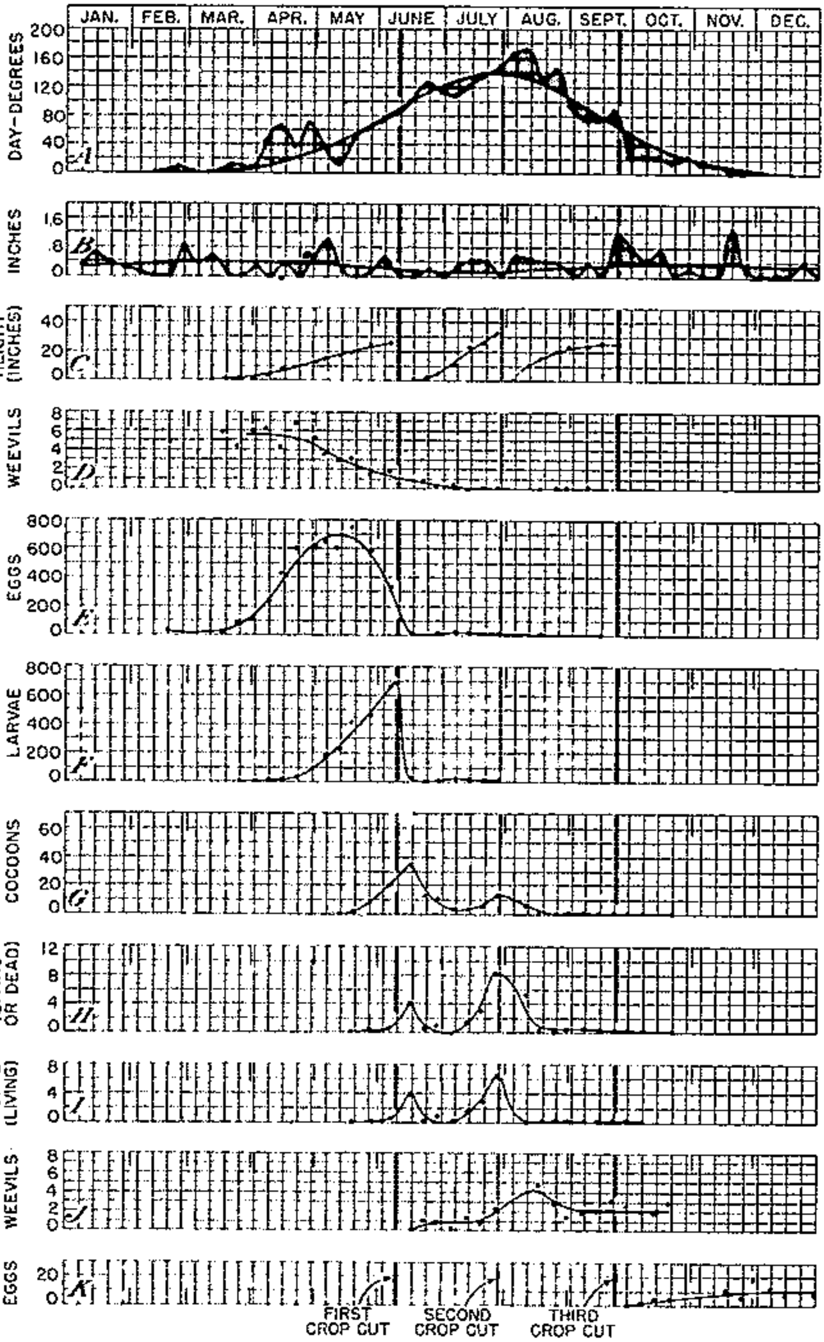

FIGURE 28.—Weekly census of an alfalfa weevil population, showing the background of temperature, precipitation, and cropping system, Salt Lake Valley, Utah, 1930: *A*, Departures from normal temperature distribution; *B*, departures from the average precipitation curve; *C*, cropping system; *D*, overwintered adult weevils; *E*, egg population; *F*, larval population; *G*, weevil cocoons containing parasite cocoons, weevil pupae, or larvae; *H*, weevil pupae living or dead; *I*, living pupae; *J*, new-generation adult weevils; *K*, first eggs laid by new adults. The heavy vertical lines indicate cutting dates. Data relating to the weevil population are averages per square foot of field surface.

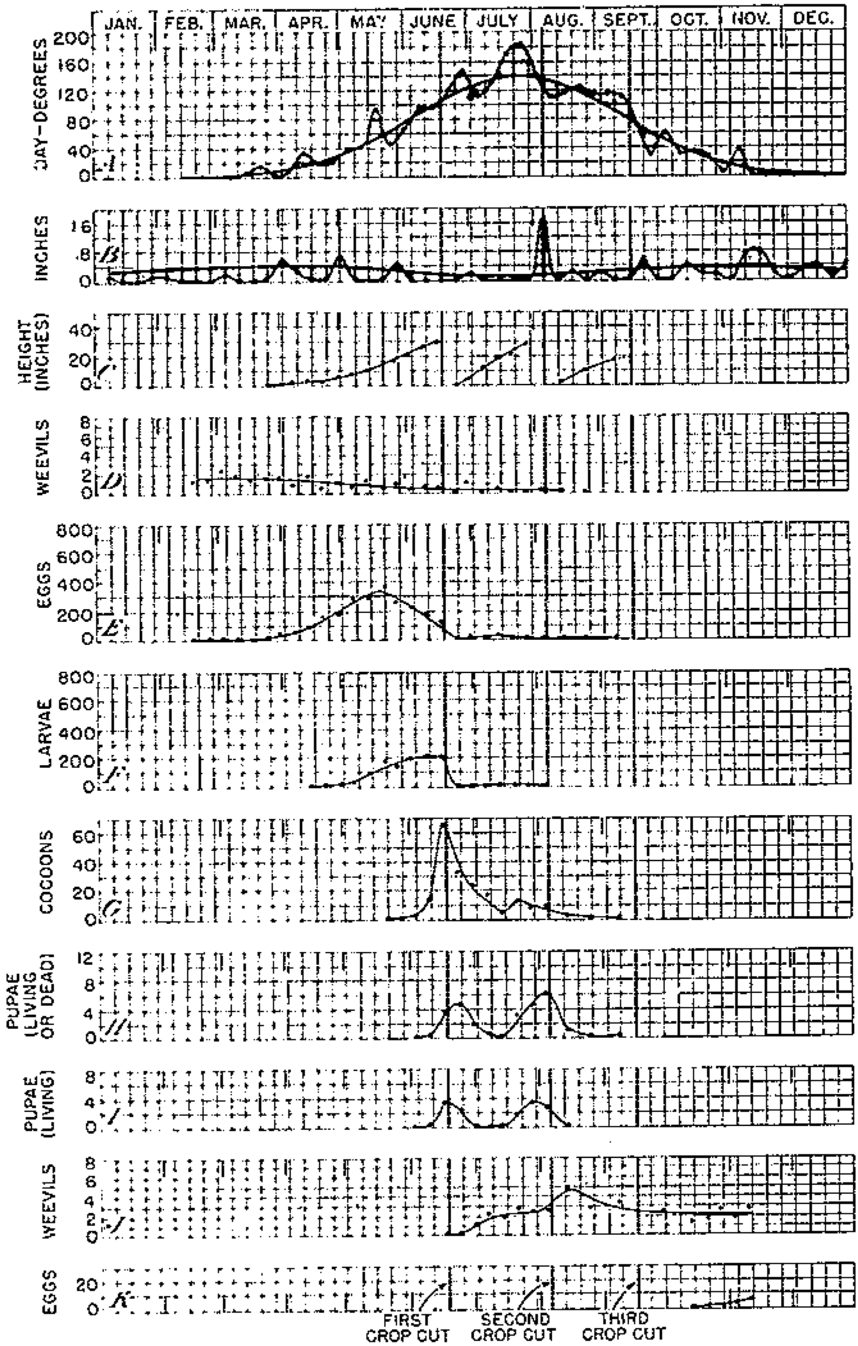

FIGURE 20.—Weekly census of an alfalfa weevil population, showing the background of temperature, precipitation, and cropping system, Salt Lake Valley, Utah, 1931: *A*, Departure from normal temperature distribution; *B*, departures from the average precipitation curve; *C*, cropping system; *D*, overwintered adult weevils; *E*, egg population; *F*, larval population; *G*, weevil cocoons containing parasite cocoons, weevil pupae, or larvae; *H*, weevil pupae living or dead; *I*, living pupae; *J*, new-generation adult weevils; *K*, first eggs laid by new adults. The heavy vertical lines indicate cutting dates. Data relating to the weevil population are averages per square foot of field surface.

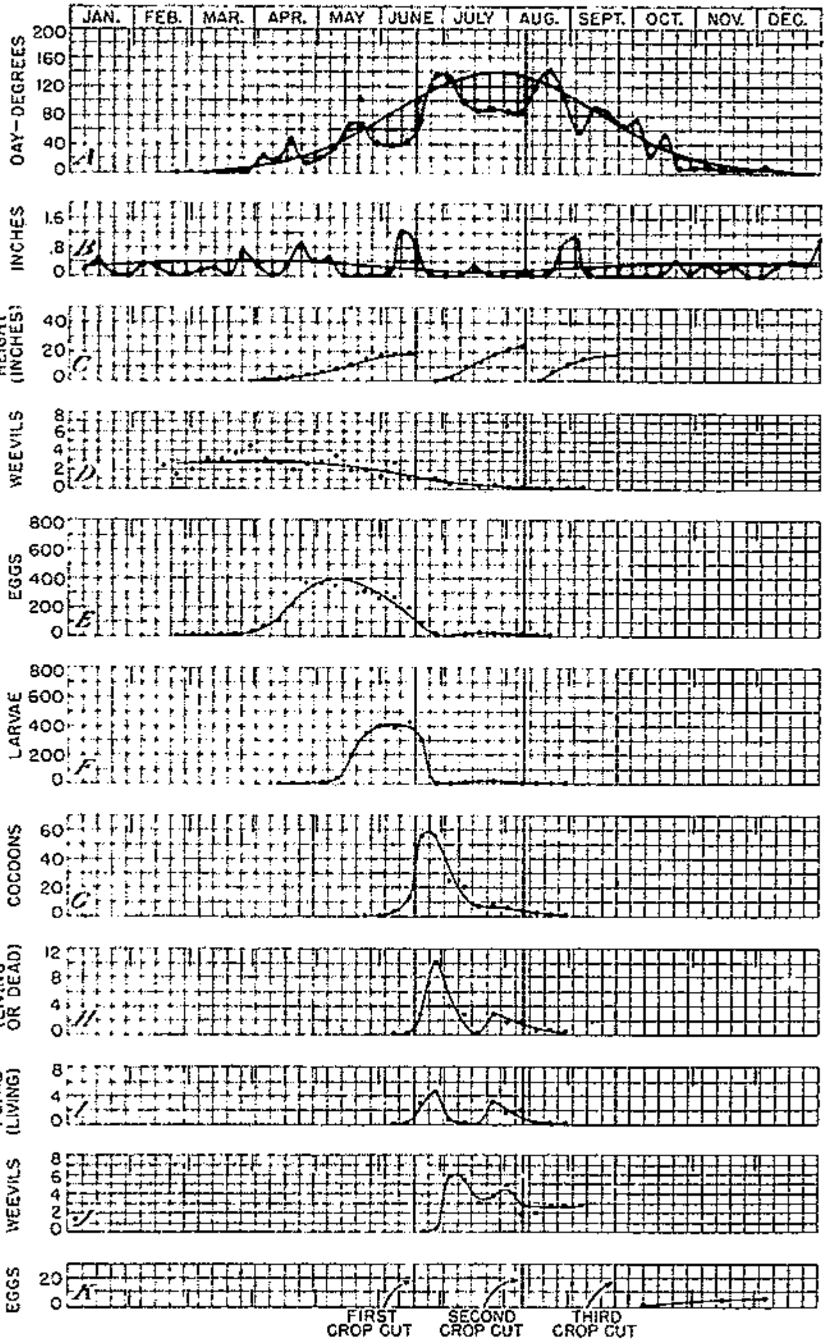

FIGURE 30.—Weekly census of an alfalfa weevil population, showing the background of temperature, precipitation, and cropping system, Salt Lake Valley, Utah, 1932: *A*, Departures from normal temperature distribution; *B*, departures from the average precipitation curve; *C*, cropping system; *D*, overwintered adult weevils; *E*, egg population; *F*, larval population; *G*, weevil cocoons containing parasite cocoons, weevil pupae, or larvae; *H*, weevil pupae living or dead; *I*, living pupae; *J*, new-generation adult weevils; *K*, first eggs laid by new adults. The heavy vertical lines indicate cutting dates. Data relating to the weevil population are averages per square foot of field surface.

face, with the seasonal trends represented by freehand curves. The accurate scaling of these figures will enable the reader to study the part played by time of cutting, parasitization, and weather in causing fluctuations in weevil abundance from year to year.

Graphs of the weevil populations bring out plainly that in all 3 years the egg population consisted of two parts, a huge one before the first cutting and a tiny one during the second-crop period. These divisions are preserved in the larval population and in the gross cocoon population, but in the latter there is less difference in the magnitude of the two parts. If the parasitized cocoons are excluded, the weevil cocoons of the second division deriving from the few eggs in the second-crop period may outnumber those originating from the main egg population. This result arises from the unequal incidence of parasitization by *Bathyplectes*. Destruction of pupae by adverse conditions of the stubblefield causes further reduction and nearly equalizes the number of living pupae originating from the unequal portions of the egg population. The extent to which the late node of pupae contributes to the new generation of adults reveals the true importance of the numerically insignificant second-crop weevil population.

The conception of the weevil's ecology established by this fundamental study, and shown in the graphic summaries, provides an understanding of the shift from constantly recurring economic loss recorded during early years to the present-day wide fluctuations in damage from year to year, from area to area in the same year, and even from field to field in the same area, which would otherwise be extremely confusing.

The research establishing these points was undertaken and developed without knowledge of certain field samplings made earlier by the staff of the alfalfa weevil laboratory. In 1913, beginning on May 5, weekly field counts were made from 0.0001 acre, but weather conditions were noted only in general terms, parasitization by the then recently introduced *Bathyplectes* was not determined, and the effect of cultural practices received a minimum of attention. That study was abandoned after 1 year, and an unpublished report by P. B. Miles shows that it was not possible to distinguish between normal trends and aberrations therefrom.

In the light of the data summarized in the present paper, the study by Miles appears to have been an excellent piece of work for that epoch in entomological research. In fact, the results suggest a number of conditions which the intensive ecological studies inaugurated in 1929 have established as generalities—namely, the decline and disappearance of overwintered adult weevils in late summer, the occurrence of the principal egg peak about the middle of May and of a small number of eggs during the second-crop period, the existence of first- and second-crop divisions of larvae and cocoons, and the appearance of new-generation adults during the summer as well as the beginning of their egg laying in the fall.

Time of Cutting and Maturity of the First Alfalfa Crop

In the early years of the appearance of the alfalfa weevil in Utah, as mentioned by the early writers (*16*, *17*, *18*), the second growth of alfalfa was held back and suffered serious damage from larvae that had been living on the first crop. This retardation of the second crop was stated as nearly equal to the usual length of the second-crop period, frequently preventing the cutting of a third crop (*17*). No injury approaching this in extent has been encountered in the present investigation, and now that the data on the weevil populations, parasitization, weather, and the relation of time of cutting to weevil increase under present-day conditions have been reviewed, it will be helpful to examine into the causes of the absence of this type of damage.

Chamberlin (*1*) noted that retardation of the second crop had ceased in the several years immediately preceding 1924. Although the improvement was generally credited to the introduction and multiplication of *Bathyplectes curculionis*, Chamberlin accounted for much of it by a change in the character of the seasons. Thus, he says, in the early period of severe retardation of the second crop the warm, dry weather in late winter and early spring gave the weevil an early start, and damp, cool weather at harvest time reduced the kill of larvae; whereas in the later period cool, wet spring seasons benefited the alfalfa but slackened egg laying and larval growth, and hot, dry harvest weather killed so many larvae that no treatment was necessary to protect the second growth of alfalfa.

The cool, wet weather at harvest would certainly reduce the heat kill of larvae living on the first crop when it was cut. Since Chamberlin wrote, however, there have been several such seasons without general recurrence of severe damage to the second crop. Some additional factors must therefore have operated in the early years, and one of them appears to have been the cutting of the first crop at a much more advanced stage of growth than is the custom today in Salt Lake Valley.

Many individuals familiar with alfalfa culture in this valley during the past 25 to 40 years state that before the first World War the first crop was in full bloom when cut, and that the cutting occurred in the first half of July. However, alfalfa ceases rapid growth several weeks earlier, produces flower buds and begins blossoming, and sends out vegetative buds from the base of flowering stalks. These basal buds develop simultaneously with continued flowering and are well-developed shoots when the older growth is in full bloom.

Under the earlier system of belated cutting the entire larval population was thrown upon these young shoots, so that the second crop was held back. Present practice, however, is to cut the first crop long before full bloom obtains, when the basal buds are small. Consequently, pending development of shoots from these buds, the field is practically devoid of larval food and the first three instars, as well as many fourth instars, have not completed their feeding and thus succumb to starvation. Those fourth instars that have completed feeding are not subject to starvation but may either succumb to heat or live to spin their cocoons. These mature larvae are the ones that chiefly benefit from a wet harvest season and so increase the number of adult weevils that will form the breeding base for the succeeding season. In other words, late cutting of each alfalfa crop provides a continuous supply of vegetation, whereas early cutting, by providing an interval in which there is no food, places the immature larvae under the stress of starvation.

The manner in which these several factors work together was well illustrated during the cool, rainy period of 1932, when seven experimental fields in Salt Lake Valley were cut as early as was consistent with the production of good-quality hay. Second-crop buds were mere dots at the base of growing stalks at the time of cutting, and despite the moderate temperatures smaller larvae did not survive long enough to eat the new shoots that grew from those buds. Many fourth instars did survive, and checked the second growth to a slight extent, but they were virtually all gone within 2 weeks after cutting. A result such as this in a cool, wet haying season is in sharp contrast with results under former practice which called for holding back the second crop for a period approximating the usual length of the second-crop period—6 to 8 weeks. There can be little doubt that earlier cutting and the consequent starvation of immature larvae accounts for much of the difference.

Further support for this conclusion may be had by viewing the early conditions reported by Titus (*16*), in the light of the mechanism which now operates. His charts, relating to conditions in Salt Lake Valley, show that time of cutting, particularly the first crop, was formerly much less uniform than at present, the peak of the first cutting occurring about July 15 in 1909 and June 21 in 1910. Moreover, he states that the latter was an exceptionally early season.

Titus does not mention the extent of flowering at the time of first cutting, but some of his photographs indicate that the second growth was well started while the hay crop was still in cocks on the field. The charts also show that the larval population reached its peak before the first cutting; the peak is now reached only in fields where cutting is considerably delayed. Titus also states that the larvae were nearly full grown when the first crop was cut: in fields cut according to current practice the second instars, and sometimes the first or third instars, are most numerous, and full-grown larvae are only just becoming moderately abundant at the time of first harvest.

In addition Titus shows that cocooning began about the middle of May in 1909, as it does at present, but reports that the abundance of cocoons increases over a period of about 2 months, whereas now the first crop is cut less than a month after the first cocoons appear.

This evidence seems to show conclusively that the trend toward earlier cutting was an important factor in reducing larval damage to the young second growth. The destruction of the larval population has the added benefit of supplementing the parasitization by *Bathyplectes* earlier in the season before the appearance of many unparasitized maturing larvae, and so reduces the production of new-generation weevils that will form the basis of the attack on the first growth the following year.

Earlier cutting has enabled farmers to harvest more crops annually. Titus has stated in conversation that in the early period, when damage to the second crop was severe, the third crop was only a partial one, which frequently was not cut but used for fall pasturage. A system is now in use whereby three crops are harvested and a partial fourth crop is pastured in the fall. The tendency to advance the cuttings is continuing, as some of the farmers in Salt Lake Valley are now harvesting four crops annually. The same process has been at work in other sections of Utah, but the progress has been very uneven. In Weber Valley, for example, during the past two decades farmers have changed from a predominantly two-crop system to one under which three cuttings are the rule. On the contrary, in Heber Valley, which is higher and has a shorter season than Salt Lake Valley, the two-crop system is still followed for the most part. Weevil injury is much more prevalent in Heber Valley.

These changes appear to have coincided with the growth of the dairy industry. According to C. R. Richards, county agricultural agent in Morgan County, Utah, this was the case in Weber Valley. Development of hay grading and the price differential commanded by the better grades have also undoubtedly been important factors. The recommendation by Titus (*16*, *17*) that the first growth be removed as soon as serious injury occurred likewise probably helped in the gradual advancement of first cutting time.

In addition to this modification of the cropping system, there has been a tendency to improve stands through more frequent replanting. In the early period of severe weevil damage fields were kept in alfalfa from 10 to 30 years, or even longer (*16*). At present, in Salt Lake Valley and other diversified cropping areas, fields are usually kept in alfalfa less than 7 years, and the Extension Service in Utah recommends plowing them under after 4 or 5 years. In fact, this practice has become almost imperative if a good stand is to be maintained, owing to the prevalence of bacterial wilt and, in limited areas, of the alfalfa stem nematode. However, there is still a tendency, particularly in the cattle-raising sections of the Intermountain States where hay is the main crop, to let fields remain in alfalfa too long, and when plowed up to replant to alfalfa too soon.

The retardation of the second crop in the Rogue River Valley, Oreg., was of the same type as that occurring in the rainy haying season of 1932 in Salt Lake Valley. In that season in Rogue River Valley almost all the smaller larvae were dead within a week after cutting, but rainy weather protected a goodly number of fourth instars from heat kill, and they subsisted on the young shoots of the second-crop which were present when the first crop was cut. Even so, the second crop was retarded only about 2 weeks, and three crops were harvested.

In the extremely early season of 1934, there was an unusual delay of the second crop in a Rogue River Valley field in which the first harvest was greatly belated. The larval population reached its peak the last week of April, caused some damage to the spring growth, and declined nearly to zero before harvest. The first crop had ceased growing by the first week of May, however, and as the second-growth shoots appeared they were fed upon by the declining larval population. These shoots were 2 to 3 inches tall by May 21, and were clipped with the first harvest on June 8. Ten days later more new shoots started, and the usual three crops were harvested in a season that might have produced four cuttings. The immature weevil population having run its course before first cutting, the second and third crops were nearly devoid of any immature stages of the alfalfa weevil.

In 1933 and 1935, in Rogue River Valley, the larval population declined to insignificant numbers after the first cutting, the second crop came on normally, and there were small egg and larval populations during the second-crop period, as usually obtains in Salt Lake Valley. Although *Bathyplectes curculionis* was liberated in the spring of 1934, it did not begin to be a significant factor until 1936.

SUMMARY

The alfalfa weevil (*Hypera postica* (Gyll.)), an Old World species, was first observed near Salt Lake City, Utah, in 1904, and has since spread throughout Utah and into 10 other Western States. Economic damage is confined to alfalfa and is brought about by the feeding of the larvae on the terminal buds and leaves of the plant.

To gain an understanding of the environmental complex affecting the abundance of the alfalfa weevil, it was essential that the insect be studied under natural field conditions where the effects of cultural, climatological, and biological factors influencing its development could be observed and measured. Since earlier work had indicated the impracticability of employing the usual methods of study for this purpose, a plan was developed which involved weekly samplings, in a representative alfalfa field in Salt Lake Valley, Utah, of the entire weevil population and the immobile stages of its parasites. These periodic samplings were carried on for the years 1930, 1931, and 1932 and were supplemented by special studies in other fields, both in this valley and in other areas.

The resulting data present a series of cross sections of the weevil complex, showing the incidence, varying magnitude, and interrelationship of the various elements of the populations against the changing background of weather, crop growth, and harvest.

The alfalfa weevil spends the winter in the adult stage, and these adults die out by the end of the following summer. The main peak of eggs comes on the first crop, and oviposition proceeds most rapidly when the daily temperatures are oscillating about 50° F. Early eggs are laid in broken, dead alfalfa and weed stems lying on the ground, and as the alfalfa begins to grow the eggs are increasingly deposited in living stems. Egg clusters average 8.3 in litter and 9.5 in growing stems, with respective ranges of 1 to 45 and 1 to 33.

The egg population may be described by the normal-distribution curve, which permits characterization in terms of the mean of the oviposition season and its standard deviation, the mean indicating the date on which the major portion of the egg population is centered, and the standard deviation (σ) indicating the concentration of the egg population. A highly concentrated egg population results in a massed attack of the larvae on the alfalfa, causing more severe damage than if the same number of larvae spread their attack over a longer period; hence, σ provides an index of the injuriousness of the alfalfa weevil, a given adult population representing less potential damage when a high value of σ is obtained.

Hatching in volume begins about the first of May in Salt Lake Valley. The larval population grows rapidly until interrupted by first-crop cutting, usually early in June. Starvation due to removal of the food supply and the lethal action of the sun's rays result in the death of nearly all larvae of the first three instars and a high percentage of the fourth instars. Hatching of the few eggs laid soon after first harvest produces a small larval population on the second crop.

Cocooning ordinarily begins the middle of May, proceeds slowly during the succeeding 2 weeks, and reaches a peak with the cutting

of the first crop in June. Thereafter the number of cocoons decreases until near the end of the second-crop period, when cocooning of the few second-crop larvae produces a small secondary peak, or at least a break in the downward trend.

Adult weevils of the new generation may derive mostly from the larval population living on the first growth of alfalfa, or from the very small second-crop larval population, or about equally from both. The number of adults in alfalfa fields declines each year during July and August, and large numbers are subsequently found in waste areas around the edges of the fields, where they spend the winter. A small percentage of the female weevils remaining in the field reach sexual maturity early in the fall, and these females may deposit a few eggs before winter. None of the females that move to the field borders reach sexual maturity until the following spring. Small numbers of weevils overwinter in and around haystacks and contribute to the carry-over of the species.

The principal parasite of the alfalfa weevil in the United States is *Bathyplectes curculionis* (Thoms.). It attacks all instars, but the percentage of parasitization increases to the highest level among fourth instars. The lower parasitization of the first three instars is inconsequential, because they succumb to stubblefield conditions following the first harvest. There is also a seasonal trend, parasitization rising to the highest level in mid-May, declining somewhat by early June, and dropping to very low levels during the second-crop period in July. In consequence of these two trends parasitization of fourth instars usually remains high until the first growth of alfalfa reaches the flower-bud stage. Parasitization by *Bathyplectes* is ineffective during the second-crop period.

By maintaining almost perfect parasitization early in the season, *Bathyplectes* delays the appearance of individuals capable of producing adult weevils until the cultural kill can be accomplished by cutting the first crop. Acting together these factors reduce the number of pupae deriving from the large first-crop larval population to the level of those resulting from the much smaller second-crop larval population. The second-crop larvae are lightly parasitized, and a large number of new-generation adults may be produced if cutting of the second crop is not also properly timed.

Bathyplectes lives as a larva within its cocoon from early summer of one year to early spring of the next. Pupation begins in March and is largely completed by mid-May. Emergence of the adult parasites reaches a peak the second week of May, and the progeny, living within the weevil larvae until the latter have spun their cocoons, kill the host and spin their own cocoons. These parasite cocoons are dimorphic, and are most abundant about 2 weeks after the first crop is cut. Larvae in light-textured cocoons pupate quickly and emerge as adults the same season; those in heavy-textured cocoons pupate the following spring.

Superparasitization of weevil larvae is common, but comparison of the observed frequency of superparasitized larvae with the theoretical frequency calculated from the Poisson series indicates that the adult parasite exercises a high degree of selectivity. *Bathyplectes* is thus an efficient parasite, effecting a high percentage of parasitization with a low ratio of parasites to hosts.

The pteromalid *Eupteromalus viridescens* Walsh, a parasite of cocooned larvae of *Bathyplectes curculionis*, passes the winter in the larval stage, pupates from March to May, and issues as an adult the latter part of May. *Eupteromalus* larvae appear in the newly formed *Bathyplectes* cocoons in mid-June, pupate in July, and begin emerging as adults about the first of August. Larvae predominate again during the all. Thus two generations annually are indicated.

Mortality inflicted by the secondary parasite fluctuates widely, but the effectiveness of *Bathyplectes* is not correspondingly affected, since the remaining *Bathyplectes* are usually sufficiently numerous to maintain a high level of parasitization among the early-maturing weevil larvae. Nevertheless, exceptional abundance of *Eupteromalus* may materially increase the production of weevils.

The introduced egg parasite *Anaphes pratensis* Foerst, is of no practical importance, since it parasitizes an insignificant percentage of eggs deposited in litter and none of those in growing alfalfa stems.

Analysis of the temperature data reveals a straight-line relationship between weevil increase and the seasonal heat, and describes the seasonal trend of heat by the normal-distribution curve, which may be used to study the effect of thermal aberrations upon weevil activities and for comparison of different seasons and areas.

A thick stand and vigorous growth of alfalfa, by shading the ground more thoroughly, retards the development of the immature weevil population. Thinness of stand may to some extent be compensated by vigorous growth. Apart from its bearing upon weevil development, the density of alfalfa growth has much to do with the severity of weevil damage. Hence, fewer weevils are required to produce crop damage in a field of sparse growth than in a field with good stand and vigorous growth.

Timely cutting of the first and second crops, by removing the food supply of larvae and exposing them to the lethal action of the sun's rays, effects a drastic reduction of the immature weevils.

Irrigation during growth of the crop retards development of the weevil by lowering the temperature of the field, but it is necessary to suspend irrigation for at least 1 week following harvest in order to produce high temperatures and increase the cultural kill.

Raking and cocking concentrates many larvae in the haycocks, and others congregate beneath them to escape stubblefield heat. This protection is of little value to the species if the hay is promptly removed from the field, but delay increases the number of individuals reaching the a ult stage.

These studies have provided an insight into the environmental complex of the alfalfa weevil. The mechanism limiting production of adults from the enormous first-crop larval population is found to be a delicately balanced relationship, involving almost perfect parasitization by *Bathyplectes* of the early maturing larvae, coupled with early cutting which destroys the younger, more lightly parasitized larvae. Parasitization among second-crop larvae is negligible, and the number of adults maturing from this smaller larval population depends almost entirely upon time of cutting.

Both the nature and the extent of damage by the alfalfa weevil have changed since its introduction into this country. Early writers record the most serious damage as resulting from larvae feeding on the second-crop buds and delaying growth, sometimes for so long that only two crops could be harvested. During recent years the principal damage has been confined to the first crop. This change has coincided with general improvement of alfalfa stands, the introduction and widespread establishment of the larval parasite *Bathyplectes curculionis*, and the gradual advancement of the first cutting date.

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