Some factors affecting the development of the eggs of the Mormon cricket (Anabrus simplex Hald)
by Orville B Hitchcock

A THESIS Submitted to the Graduate Committee in partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University

Abstract:
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Development in the Mormon cricket embryo continues throughout the winter regardless of the cold temperatures to which they are subjected.

These cold temperatures have a stimulating effect upon the developing embryo.

The data on egg development does not indicate the presence of a true diapause in this stage of the life cycle.

More oxygen was consumed per egg when they were alternated between 10° and 25°C. than when held at a constant temperature of 25°C.

When eggs were alternated between 10° and 25°C. there was a much higher per cent hatch than when they were held at a constant temperature of 25°C. In every case a higher per cent hatch was obtained in the 10° cabinet.

Crickets which were confined in their activities by pen, barrier, etc., failed to lay fertile eggs.

Within wide limits soil moisture conditions have very little effect upon hatching of Mormon cricket eggs.

SOME FACTORS AFFECTING THE DEVELOPMENT OF THE EGGS OF THE MORMON CRICKET (*Anabrus simplex* Hald)

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ABSTRACT

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INTRODUCTION

The Mormon cricket, Anabrus simplex (Hald), has been present in Montana for a great many years, but it was not until 1926 that it was recorded doing extensive damage to crops. Since that time serious outbreaks have occurred in practically all parts of the State, with the exception of the northeastern counties. These outbreaks have been so serious that it has been necessary for the Federal Government, State, counties, and individuals to expend large sums of money for equipment, materials, and labor in the protection of crops. Although the campaigns have been quite effective from a crop protection standpoint, more information concerning the effect of climate, parasites, and other factors would, undoubtedly, be of value in formulating a more effective control program.

Since practically no work has been done on the eggs of the Mormon cricket, studies on this stage of the life cycle were undertaken. The experiments were carried out in an attempt to obtain some definite information on the following points: (1) The presence or absence of a diapause period; (2) the effect of temperature on egg development; (3) the effect of moisture on hatching, and (4) general factors affecting fertility. Some definite information on the above factors may aid materially in predicting with some degree of accuracy, the possibility of the insect appearing in outbreak numbers. The occurrence of a diapause period during the egg stage might

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have considerable effect on the time of spring hatching. If such a period exists it is important to know when it occurs and what conditions are necessary to break it. If there is no diapause it is desirable to know how much accumulated temperature is necessary to develop and hatch the egg.

Some knowledge of the moisture conditions necessary for hatching is also of importance. It may be possible that an extremely wet or dry season might be unfavorable for emergence and that the numbers of crickets would be greatly reduced when the eggs are subjected to such conditions. There is also a possibility that the use of dust and artificial barriers may have some effect upon the fertility of the adults.

This paper embodies results of experiments which were carried out in an attempt to answer the above questions.

LITERATURE

Caruthers (7) states that a low temperature, though it interrupts the development of the Orthopteran embryo, acts as a stimulus which accelerates development as soon as the temperature is raised. He also found that in some species a temporary cooling seems to be a condition necessary for normal development, and eggs kept at a constant high temperature from the time of oviposition fail to develop.

Bodine (2) found that the rate of egg development in certain Orthoptera (grasshoppers) was affected by temperature and, that other factors being constant, the increment in rate seemed to increase in direct proportion to the increase in temperature within the normal limits of development. He also found that exposure to low temperatures produced an accelerative effect on subsequent development of eggs at constant temperatures.

Uvarov (17) explains that low temperatures produce an acceleration in the development of the Orthopteran embryo only when it is subjected to their action at a definite stage in its development. He states that in nature, most of the Acrididae begin development shortly after the eggs are laid. Development is then interrupted and only resumes again the next spring, when the temperature, after winter cooling, rises above the developmental zero. He further explains that this interruption of development, or embryonic diapause, cannot be explained by the action of low temperatures because, in many species of temperate regions, oviposition takes place quite early in autumn, or even in summer, and the diapause begins when temperatures are well above the developmental zero. Also, attempts to break the diapause in the laboratory by keeping eggs at high temperatures fail, at least, in the case of certain species. This, he says, is indicated by the fact that, in the case of some tropical species, the embryonic diapause coincides with the dry season, and the eggs hatch after the first rain.

Bodine (2) in his work on the oxygen requirements of developing Orthopteran eggs made the following observations. The embryo first goes through a rapid period of development and, after reaching a certain stage, it undergoes hibernation which is followed by an increase in activity or development as is shown by the oxygen consumption throughout these stages. He further states that such rhythm seems necessary for the normal development of the organism and that it is of interest to note that changes in the rate of oxygen consumption takes place in the early spring when the temperature is considerably below the so-called developmental zero. From this he concludes that, in the case of grasshopper eggs, temperature is not necessarily a limiting factor in controlling gas exchange during growth or normal development, and the morphological evidence indicates that definite development occurs during these periods even though the eggs are exposed to temperatures supposedly below those required for normal development. He also pointed out that eggs which had been exposed to 25°C., when subsequently returned to low temperatures, showed no marked decrease in rate of development despite the fact that they were exposed to extremely low temperatures. He further states that development, once started, seems independent, or at least, not correlated, with external temperatures, but eggs will not hatch at these low temperatures if left continually exposed to them. He concludes that some mechanism acts within the eggs which makes development, in a measure, independent of external temperatures.

Parker (11), in his work on the eggs of Melanoplus mexicanus mexicanus Saussure and Camnula pellucida Scudder, found that the eggs placed at constant high temperatures the day they were laid, hatched in an average of 26 days, while eggs placed at 0° immediately after they were laid and later placed at constant high temperatures, developed much more rapidly and hatched 11 days after being subjected to a constant high temperature. Eggs which were allowed partial development after being laid and then subjected to low temperatures showed an increase in rate of development when later returned to constant high temperatures. Eggs placed at alternating temperatures showed a great increase in rate of development over eggs held at constant temperatures.

Bodine (3), in his work on oxygen consumption of *Melanoplus differentialis*, kept at constant high temperatures from the time of laying until hatching, obtained the following results. There is a fairly rapid rising rate of oxygen consumption during the first three weeks of development which is followed by an equally rapid decrease to a minimum value. This relatively low rate of oxygen consumption continues over a period of time (diapause) at the end of which an increase in rate occurs and culminates in the hatching of the egg.

Burkholder (6), when working with single eggs of *Melanoplus differentialis*, found that, in general, cycles or rhythm changes in rate of oxygen consumption substantiate results obtained upon larger numbers of eggs by previous workers.

PROCEDURE

On October 24 a large number of eggs were collected from the field near Billings, brought into the laboratory and candled. Only those which showed development were selected for the experiment. The eggs were divided into five lots of 400 eggs each, placed in moist sand and numbered from 1 to 5. Lot 1 was placed at a constant temperature of 25°C. Lots 2 to 5 were cooled to varying low points in the following manner. Lot 2 was held at 10°C. for one day, 2°C. for one day, returned to 10°C., and placed at 25°C. on the sixth day. Lot 3 was similarly cooled to -5°C., raised to 10°C. and transferred to 25°C. on the sixth day. Lot 4 was cooled to -10°C. and lot 5 to -15°C. and then both were brought up to 25°C. On the sixth day all lots were at 25°C. constant temperature and 100% relative humidity.

The foregoing treatment is tabulated in table I:

TABLE I.-Temperatures to which Mormon cricket eggs were subjected in study of effect of cooling on egg development.

Lot 1		Lot 2		Lot 3		Lot 4		Lot 5	
Temp.	Days	Temp.	Days	Temp.	Days	Temp.	Days	Temp.	Days
25°	7	10°	1	10°	1	10°	1	10°	1
		2	1	2	1	2	1	2	1
		10	4	-5	1	-5	1	-5	1
		25	1	10	3	-10	1	-10	1
				25	1	10	2	-15	1
						25	1	10	1
								25	1

On the seventh day each lot was redivided into two lots of 200 eggs each. One of these was kept at 25° constant temperature and the other alternated for one day intervals between 25°C. and 10°C.

Eggs were collected from the same area in the field at intervals of approximately two weeks throughout the winter. These were candled and selected in the same manner as the above eggs. They were divided into two lots of 200 each and placed in moist sand. One lot was held at a constant temperature of 25°C. and the other alternated between 25°C. and 10°C. as previously described. Eggs were collected on the following dates: Nov. 8, Nov. 22, Dec. 6, Dec. 21, Jan. 7, and Jan. 23.

As soon as the first eggs collected on October 24 were subjected to the above treatment, 20 eggs were taken from each lot and placed in a Barcroft differential manometer and the rate of oxygen consumption determined. Eggs which were collected later in the field were also run in the manometer immediately after being brought into the laboratory. Twenty eggs from each lot were run again at intervals of approximately 30 days.

This procedure was continued throughout the experimental period.

STIMULATING EFFECT OF LOW TEMPERATURES

The most satisfactory way to express the accumulative effect of temperatures is by means of degree hours. Other methods have been used but they do not give an accurate comparison between different lots. A degree hour is defined as the product of the temperature, (in degrees Centigrade) times the number of hours at which the eggs were exposed to such temperature. In this way all changes in temperature can be expressed on a common basis.

Cricket eggs which had not yet been exposed to cold temperatures in the field were collected. The eggs were brought into the laboratory and were subjected to varying low temperatures as shown in Table I. They were held at a constant temperature of 25°C. until no further hatching took place. The eggs which were not exposed to low temperatures required the greatest number of degree hours to complete the hatching. When the eggs were subjected to low temperature there was a very noticeable stimulating effect. The greatest stimulation took place in the eggs which were lowered to -10°. These required 10,207 degree hours less than those which had had no previous cold treatment. When the eggs were lowered to -15° there was a retarding effect. It took 5,550 more degree hours for the eggs to hatch than those which had been lowered to -10°. Thus it will be seen that lowering the temperature to -10° decreased the number of degree hours by approximately 10,000 when compared with untreated eggs. As the temperature was lowered from approximately 25°C. to 5°C. there was a gradual decrease in hatching time. From 5° to -10°C. a rapid decrease took place but when lowered to -15° there was a marked increase in the degree hours necessary to hatch the eggs. These data are tabulated in Table II and shown graphically in figure 1.

TABLE II.-Degree hours necessary to hatch eggs collected October 24 after being subjected to the varying temperatures given in Table I.

	Eggs held at a constant temperature of 25°C after treatment		Eggs subjected to alternating temperatures of 10°C and 25°C after treatment	
Lot No.	Degree hours per egg	% Hatch	Degree hours per egg	% Hatch
1	35,257	10.5	24,908	59.0
2	30,000	11.5	23,404	42.5
3	26,250	8.0	22,245	50.0
4	25,050	7.5	20,165	54.5
5	30,600	2.0	23,857	43.5
Average	31,101	7.9	22,915	49.9

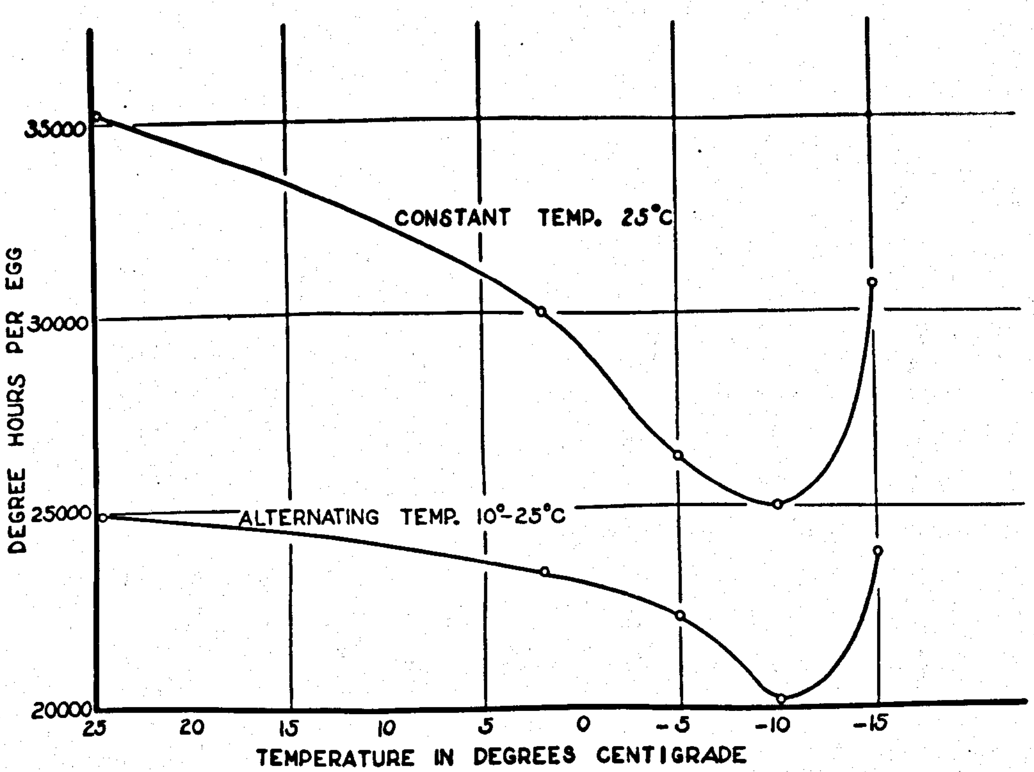

Figure 1.

EFFECT OF ALTERNATING TEMPERATURES

The eggs were treated as shown in Table I and were then subjected to alternating temperatures of 10° and 25°C. for equal periods of 24 hours. Twenty four thousand nine hundred and eight (24,908) degree hours were necessary to hatch eggs which were not subjected to cold temperatures. As in the previous experiment, the greatest stimulation took place at -10°. At this temperature only 20,165 degree hours were necessary to hatch the eggs. Again a retarding effect was produced in the eggs which were lowered to -15° and 23,857 degree hours were required to hatch them. A comparison between the eggs not subjected to low temperatures and those lowered to -10° show that approximately 4,700 degree hours more were necessary to hatch the eggs which had had no previous treatment. It also took 3,692 degree hours more to hatch the eggs which were lowered to -15° than those which were subjected to -10°. Again there was a gradual decrease in degree hours necessary to hatch the eggs as the temperature was lowered from approximately 25° to -2°. From -2° to -10° there was a rapid decrease and from -10° to -15° there was a rapid increase in the degree hours required for hatching. These data are recorded in Table II and shown graphically in figure 1.

A comparison of the eggs which were held at a constant temperature of 25° and those which were alternated between 10° and 25° show that there is a very definite acceleration produced by the alternating temperatures. An average of 31,101 degree hours was necessary to hatch the eggs at a constant temperature. Those which were alternated averaged only 22,915, or 8,186 degree hours less.

EFFECT OF FIELD TEMPERATURES

The eggs which were used in these experiments were collected at two-week intervals from October 24 to January 23. All experiments were run at a constant temperature of 25°C. The various lots showed a subsequent decrease in the number of degree hours necessary for hatching. Thirty-five thousand two hundred and fifty seven (35,257) degree hours were required to hatch eggs collected on October 24. Those that were brought in from the field at subsequent intervals of approximately two weeks showed a steady decrease in the number of degree hours required for hatching. The last lot of eggs which were collected on January 23 required only 6,371 degree hours. This was 28,886 less than were necessary for the eggs which were brought in on October 24. See Table III and figure 2.

EFFECT OF ALTERNATING TEMPERATURES ON FIELD EGGS

Eggs were collected as in the previous experiment and alternated between 10° and 25°. They, also, showed a large decrease in the number of degree hours necessary for hatching. The eggs that were brought in from the field on October 24 hatched in 24,908 degree hours. There was a rapid decrease in the number of degree hours necessary to hatch the eggs which were collected at later dates. Only 6,320 were required for those that were brought in on January 23. This was 18,588 less than were required for the eggs collected on October 24 approximately three months earlier. See Table III and figure 2.

TABLE III.-Degree hours necessary to hatch eggs collected at different periods during the winter from October 24 to January 23.

	Eggs held at a constant temperature of 25°C		Eggs subjected to alternating temperatures of 10°C and 25°C	
Date collected	Degree hours per egg	% Hatch	Degree hours per egg	% Hatch
Oct. 24	35,257	10.5	24,908	59.0
Nov. 8	21,646	13.0	16,403	46.5
Nov. 22	18,600	3.5	16,422	54.5
Dec. 6	13,266	4.5	11,054	64.5
Dec. 21	7,658	8.5	6,751	62.5
Jan. 7	8,400	11.5	7,509	68.0
Jan. 23	6,371	10.5	6,320	90.5
Average	15,885	8.8	12,766	63.6

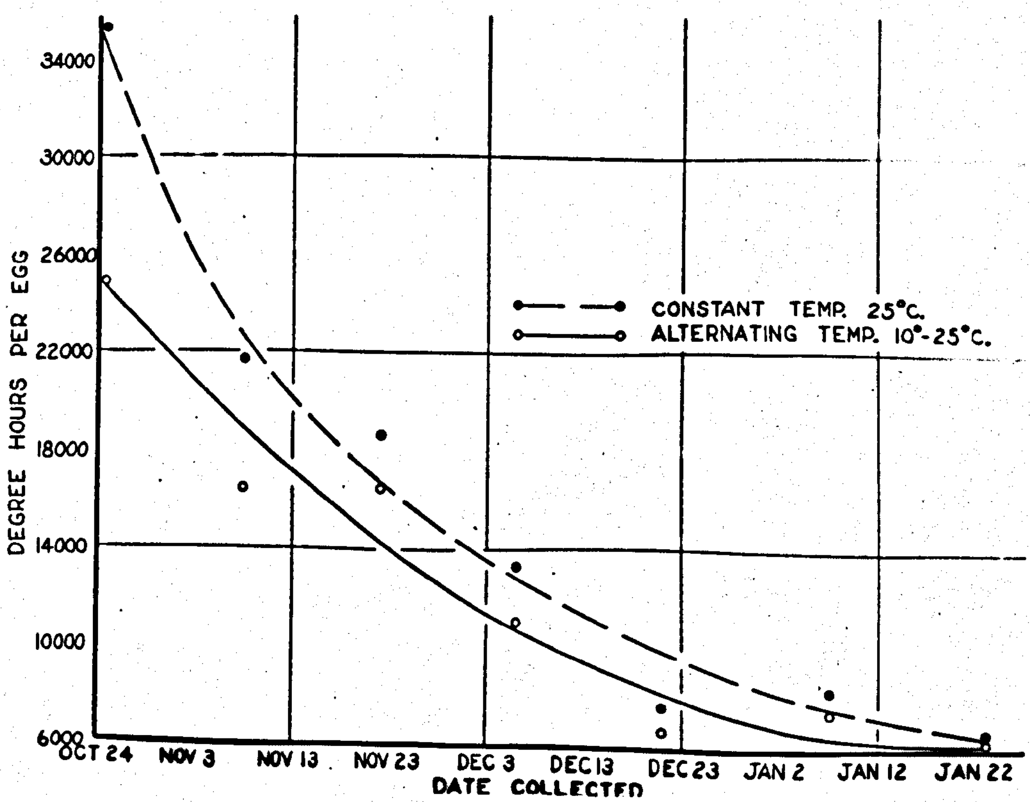

Figure 2.

OXYGEN CONSUMPTION

A comparison of the rate of oxygen consumption of eggs held at a constant temperature of 25°C. and those alternated between 10° and 25°C. show that the alternating temperatures have a stimulating effect on the eggs. All of these eggs were subjected to the varying temperature conditions shown in Table I. Those held at 25°C. had an average rate of oxygen consumption of 2.310×10^{-3}cc. of O_2 per egg for a 2-hour period. The eggs which were subjected to the alternating temperatures consumed 2.487×10^{-3}cc. or $.177 \times 10^{-3}$cc. more per egg. Likewise the eggs collected from the field throughout the winter and alternated between 10° and 25°C. consumed $.519 \times 10^{-3}$ cc. of O_2 more than those which were held at the constant temperature. This increase in oxygen consumed indicates greater embryonic activity and is in line with previous data which shows stimulation in the eggs which were alternated between 10° and 25°C. Twenty eggs were placed in the manometer for each experiment and since the eggs are small it is obvious that relatively small amounts of oxygen would be consumed. The Barcroft differential manometer is an extremely sensitive instrument and capable of measuring accurately such small quantities.

TABLE IV.-Average amount of oxygen consumed (cc.x10^{-3}) per cricket egg in a 2-hour period.

Eggs subjected to low temperatures outlined in Table I.			Periodical collections from the field		
Lot. No.	Constant 25°	Alternating 10 and 25°	Date collected	Constant 25°	Alternating 10 and 25°
	cc.O_2x10^{-3} per egg	cc.O_2x10^{-3} per egg		cc.O_2x10^{-3} per egg	cc.O_2x10^{-3} per egg
1	3.189	2.082	Oct. 24	3.189	2.082
2	1.813	3.037	Nov. 8	3.057	3.629
3	2.069	2.183	Nov. 22	2.570	3.166
4	2.056	2.355	Dec. 6	2.708	3.686
5	2.425	2.781	Dec. 21	1.721	3.137
			Jan. 7	2.786	3.440
Average	2.310	2.487	Average	2.671	3.190

DIAPAUSE

The data obtained from field eggs show that regardless of low temperatures, the eggs continue to develop throughout the winter. They even seem to be stimulated by the low temperatures to which they are subjected. In the late fall the presence of what appears to be a fully developed embryo has led to the belief that a true diapause exists during this period of the insect's life cycle. The supposition has been that the diapause period begins in the fall before cold weather sets in and that it lasts until the weather warms up in the spring.

There seems to be some disagreement among biologists as to what really constitutes a diapause and what causes it to take place. It may be considered as a definite inherent characteristic possessed by the individuals, or it may be the result of external ecological factors. In any event the presumption is that all physiological functions are at a minimum. Unfortunately this is based usually on visual observations and does not often include reactions of a chemical nature which may be essential for the further development of the organism. A study of the existing literature on diapause will substantiate the preceding statements. Henneguy (10) defined diapause as a cessation of activity, embryonic or otherwise, and not necessarily conditioned by temperature. Uvarov (16) states that diapause should be restricted to cases in which activity or development is arrested spontaneously. When activity or development is interrupted by the direct influence of unfavorable conditions, and resumed as soon as the conditions become favorable, a quiescent stage results which cannot be classified as diapause. He further states that diapause may occur in any stage of development of an insect and embryonic diapauses are exemplified by the eggs of grasshoppers. Boyce (5) in his work on the diapause phenomenon of insects defines diapause as a state of spontaneously arrested development brought about directly by physiological factors. He suggests that some of the causes of diapause may be dryness, cold, heat, hydrogen ion concentration, enzymes, hormones, and Roubands hypothesis of uremic poisoning. Slifer (13), working on the eggs of Melanoplus differentialis, found that the eggs develop at 25°C. for a three-weeks' period at which time they cease development and enter a true diapause. During this diapause no mitotic spindles are found and development seems completely arrested.

Faure (9) explains that the eggs of Locusta pardalina lie dormant in dry soil for many months and that they may be expected to hatch about ten days after the first rain in warm weather. He found that eggs one to fourteen days old will hatch if moisture is added. If no moisture is added and the eggs are left dry they will remain in diapause as long as three years. Moisture, in his opinion, seems to be the factor controlling diapause in this case. Bodine (3) states that diapause in the eggs of *Melanoplus differentialis* is, within limits, independent of temperature above developmental zero for its occurrence, but relatively dependent on temperatures above developmental zero for its duration. Low temperatures 10° to 0°C. destroy the diapause factor in these eggs. Bodine (4) states that the so-called diapause factors can be thought of in several ways, either as chemical, physico-chemical or perhaps physiological genetic factors present in more or less constant amounts in the egg at the time of laying. These diapause factors in the egg of *M. differentalis* during the course of three weeks' development increase either in potency or amount until they reach a certain threshold value, at which time they inhibit all developmental processes. When kept at a constant high temperature these factors gradually lose their potency or strength, and after a period of time developmental factors gain an upper hand and normal development ensues. Low temperatures will, however, destroy the diapause factors and when eggs subjected to low temperatures are then put at high temperatures, normal development will immediately begin.

Slifer (14) found that the grasshopper embryo twenty days old begins a long embryonic diapause and by comparing embryos eight days or a month older superficially, at least, there is no further development. If such embryos are fixed, sectioned, stained, and examined microscopically they will be found to contain few or no dividing cells. Embryos less than three week of age, on the other hand, display great numbers of mitotic figures. There is also no change in the position of the mebryo during the diapause period.

Richards (12) states that diapause in distinction to hibernation is an inherent obligatory characteristic which may be independent of temperature for its occurrence, though its duration is affected by temperature and other factors. It is manifested as a retardation or cessation of growth, mitosis, metabolism, and movements. It occurs at different stages in different species but almost always at a particular developmental stage in any one species.

If diapause involves a great reduction in physiological activity then the data obtained indicate that such a condition apparently does not exist in Mormon cricket eggs during the period in which observations were made. This is deduced from the data obtained from eggs collected at approximately two-week intervals from October 24 to January 23. There was a successive decrease in degree hours necessary to hatch the eggs in the laboratory for each collection as the winter progressed. This explains that there was continuous physiological activity in the embryo during this period.

PER CENT HATCH

Temperature conditions have a marked effect upon the percentage of Mormon cricket eggs which hatch. This may be seen by making a comparison of eggs which were held at a constant temperature of 25°C. with those which were subjected to alternating temperatures of 10° and 25°C. (Table II). In the case of the eggs which were collected October 24 and subjected to the varying low temperatures, as shown in Table I, a much higher per cent hatch was obtained in those subjected to the alternating temperatures (49.9%), than the eggs held at the constant temperature (7.9%).

This was also true of the eggs which were collected from the field at intervals throughout the winter. In this case 63.6% of those subjected to the alternating temperatures hatched as compared with 8.8% at constant temperature. See Table III.

This is further proof of the stimulating effect of alternating temperatures.

TEMPERATURES PRODUCING MAXIMUM HATCH

When cricket eggs are alternated for 24 hour periods between 25°C. to 10°C., a large percentage of the hatch occurs on the days when they are subjected to the lower temperature. Of the eggs collected October 24 and treated according to Table I, 61.03% of them hatched in the 10° cabinet, while only 38.96% of them hatched in the 25° cabinet.

This was also true of the eggs which were collected at intervals throughout the winter. The per cent hatch for these groups of eggs were 77.62% at 10° and only 22.38% at 25°. See Table V.

TABLE V.-Per cent hatch at the different temperatures during alternation.

Eggs subjected to varying low temperatures			Field Eggs		
Lot. No.	% hatch at 10°C.	% hatch at 25°C.	Date collected	% hatch at 10°C.	% hatch at 25°C.
1	54.43	45.57	Oct. 24	54.43	45.57
2	63.93	36.07	Nov. 8	72.32	27.78
3	61.66	38.34	Nov. 22	66.66	33.34
4	58.82	41.18	Dec. 6	84.42	15.58
5	66.33	33.67	Dec. 21	90.40	9.60
			Jan. 7	80.14	19.86
			Jan. 21	95.02	4.98
Average	61.03	38.96	Average	77.62	22.38