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**AN ECOLOGICAL STUDY OF
THE INDIAN - MEAL MOTH
Plodia interpunctella (Hübner)
WITH EMPHASIS ON DIAPAUSE**

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The Indian-meal moth, *Plodia interpunctella* (Hübner), is an important pest of stored food products, especially dried fruits and nuts in California, and many other parts of the world. Many authors believe that this species will grow and breed continuously under favorable conditions. Some experimental data obtained in California, however, suggested that late in the season the insect may enter a facultative diapause as a mature larva. The present investigation has shown that this actually occurs.

The investigation indicated that throughout much of California diapause occurs in the fall, probably because temperature during incubation of the eggs is sufficiently high to induce diapause and later, during larval growth, sufficiently low to allow diapause to occur. Temperature acclimatization increased the cold-hardiness of both diapausing and nondiapausing individuals. However, diapausing larvae were more cold-hardy than nondiapausing larvae of the same strain.

Two strains of *Plodia interpunctella* were investigated in this study and it was found that they exhibited a marked difference in tendency to diapause.

AN ECOLOGICAL STUDY OF THE INDIAN-MEAL MOTH *Plodia interpunctella* (Hübner) WITH EMPHASIS ON DIAPAUSE¹

M. E. TZANAKAKIS²

INTRODUCTION

THE INDIAN-MEAL MOTH, *Plodia interpunctella* (Hübner), is an important pest of stored food products, particularly dried fruit and nuts, in California as well as in most parts of the world. Its biology and control have been the subject of considerable research, the results appearing in numerous papers. Most investigators believed that this insect, which may complete several generations per year, does not diapause, but grows and develops continuously throughout the year, if temperature is maintained at levels sufficiently high for growth. Recently Michelbacher (1953),³ interpreting the experimental data of Simmons *et al.* (1931), and Hamlin *et al.* (1931), and the fact that the Indian-meal moth seems to be able to survive the cold winters of Utah out-of-doors, suggested that this insect must overwinter as a mature larva in diapause. The present investigation, which is primarily ecological in nature, was undertaken at his suggestion. Its purpose was to establish whether diapause occurs in the Indian-meal moth, and, if it does, to attempt to determine the environmental factors involved. The experiments were carried out during the years 1957 and 1958.

The larva of the Indian-meal moth has been reported to feed preferably on the embryo and the softer parts of seeds as well as on dried fruit and nuts. The frass and webbing associated with this insect add to the damage caused by actual feeding. Because of pure food laws, extremely light infestations may result in losses of serious proportions. Among the numerous authors who have emphasized the destructiveness of this pest, Bioletti (1915) and Parker (1915) considered it as probably the most common and destructive of the insect pests of raisins and dried fruits in California. Lovett (1921) reported it as by far the most generally destructive of a variety of serious pests attacking stored food products in the northwestern United States. In Australia during the 1926-27 season, Myers (1928) found it to

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³ See "Literature Cited" for citations referred to in the text by author and date.

be the most important pest of raisins during storage and transit. Dean *et al.* (1936) reported it as one of the pests causing considerable trouble in flour mills. Michelbacher and Ortega (1958) mentioned the Indian-meal moth as one of the most important pests of nuts, cereal and cereal products, dried fruit, chocolate candies, and various other confections.

Plodia interpunctella is probably a native of the Old World. Today it is cosmopolitan, having been spread to all parts of the world by commerce. It has been collected or reported from most areas of North, Central, and South America, Europe, North, West, and South Africa, Asia, Japan, Australia, New Zealand, and many islands.

The Indian-meal moth was first described by Hübner (1811-1817) as *Tinea interpunctella*. Later Guénée (1845) placed it in the genus *Plodia*. Some early authors have described it also as: *Elucita interpunctalis* (Hübner, 1825), *Plodia interpunctalis* (Butler, 1879), *Phycis interpunctella* (Duponchel, 1836), *Phycita interpunctella* (Treitschke, 1832), *Myeloides interpunctella* (Zeller, 1839), *Ephestia interpunctella* (Herrich-Schäffer, 1849; Stainton, 1859; Frey, 1880), *Ephestia zae* (Clemens, 1860), *Ephestia interpunctalis* (Druce, 1896), *Ephestia elutella* (Frogatt, 1898), *Ephestia glycinivora* (Matsumura, 1917), *Tinea zae* (Fitch, 1856).

The systematics of this species have been reviewed by Richards and Thomson (1932) and by Heinrich (1956).

The following common names have been given to *Plodia interpunctella*: Indian-meal moth, pantry moth, meal-worm moth, peach worm, cloaked knothorn, compressed vegetable moth, Dörrobstmotte, kupferrote Dörrobstmotte, kupferfarbige Dörrobstmotte. "Indian-meal moth" is the most generally used of these names, and is the one which has been accepted in the official list of common names of insects by the Entomological Society of America.

MORPHOLOGICAL CHARACTERISTICS

The egg is white, grayish white, or yellowish white, 0.3 to 0.5 mm long, ovate, with a reticulate chorion.

The young, newly hatched larva is white, except for its head, and is about 1 mm long. When full grown, the larva is usually yellowish white, occasionally yellow, pinkish, or greenish white. Apparently the body color is influenced to some degree by the nature of the larval food. The head and prothoracic shield are brown. The anal segment bears a dorsal plate similar in color to the prothoracic shield.

The size of mature larvae as well as that of pupae and adults has been reported to vary, according to the food and rearing conditions during larval growth. There is also some variation between the size of the individuals of the same group. Usually, at the time full growth is attained, the larvae entering diapause are the largest. However, these larvae lose weight and become smaller during the period of diapause. Furthermore the females are generally larger than the males. Treherne (1921) gave the length of mature larvae as 12 mm, Hamlin *et al.* (1931) 9 to 19 mm with an average of 13 mm, Zacher (1938) 11 to 17 mm, Candura (from Zacher, 1938) 7 to 21 mm with an average of 12 to 14 mm. Zacher (1938) gave the weight of mature larvae as 14 to 30 mg, with an average of 25.3 mg.

In the present investigation, the weight of diapausing larvae of the "Berkeley" stock, reared on chicken mash, after they were held for three weeks at 25° C and 53 per cent R.H.⁴ was as follows:

	Number of larvae	Average weight per larva, in mg
Males	107	20.05
Females	148	23.95

The pupa is generally brown, the color changing from yellowish brown the first day, to dark brown, and finally, before emergence of the adult, to almost black. Hamlin *et al.* (1931) reported that the length of the pupa ranged from 6 to 11 mm. The weight of pupae, according to Zacher (1938) ranged from 9.8 to 13.2 mg for the males, and from 11.8 to 14.6 mg for the females.

During the present investigation it was determined that the size and weight of pupae varied with sex, age of pupae, and with food and temperature during the larval stage. Pupae from larvae reared on chicken mash, with or without raisins, and on walnut meat, were distinctly larger than those from larvae reared on raisins or on rolled barley (table 1). Pupae from larvae reared at 20° C were generally heavier than those from larvae reared at 25° or 30° C.

The adult is 5 to 10 mm long, and has an average wing expanse of about 16 mm. It is easily recognizable by its distinct coloration. The basal third of the fore wings is silvery white or gray with occasional minute dark spots. The outer portion is reddish bronze with irregular dark bands. The posterior wings, as well as the abdomen are silver gray. The thorax is somewhat darker. The females are easily distinguished by their genitalia and usually by their larger size and expanded abdomen.

Table 2 shows the time which elapsed, and the loss of weight which occurred from full-grown larva to adult, in two groups of individuals. As far as the duration of stages is concerned, it appears that in nondiapausing individuals there was no considerable difference between the sexes. However, when weight loss is considered, the difference between sexes was noticeable. The average loss of weight from full-grown larva to young pupa, percentagewise, was greater in the female; from young pupa to old pupa, and from old pupa to adult, it was greater in the male. The total loss of weight from mature larva to adult was greater in the male. This was mostly due to the loss that occurred during the final (imaginal) metamorphosis. In individuals of the "Fresno" stock, reared on chicken mash, this latter loss of weight, on an average, in the case of the male, was at least twice that of the female.

In the Berkeley stock, the larvae were reared on walnut meat, and the length of development and loss in weight were greatly influenced by diapause. Here, the time spent in the mature larval stage varied greatly among individuals, and so did the weight loss during that time. This accounted for a greater variation in the total weight loss from mature larva to adult. Yet, the loss of weight during the final metamorphosis did not vary greatly

⁴ Relative humidity.

between individuals of the same sex, and the range of values for one sex did not overlap that for the other.

Zacher (1938) reported that the "grown" larva is about twice as heavy as the pupa, and the pupa twice as heavy as the moth. Data obtained during the present investigation for nondiapausing individuals, reared on chicken mash at 20° C and 58 per cent R.H. in the dark, and held under the same conditions, showed an average weight ratio of 1.7 : 1.4 : 1, which differs considerably from the 4.2 : 2 : 1 ratio reported by Zacher. This, how-

TABLE 1
THE WEIGHT OF TWO-DAY-OLD PUPAE OF *PLODIA INTERPUNCTELLA*,
REARED AT 20°C AND 58 PER CENT R.H. ON VARIOUS FOOD MEDIA*

Stock	Larval food	Number pupae weighed	Sex	Av. wt per pupa in mg
Berkeley	Chicken mash with raisins.....	22	♂	15.14
Berkeley	Chicken mash with raisins.....	30	♀	19.01
Berkeley	Chicken mash.....	57	♀	16.13
Berkeley	Walnut meat.....	59	♂	14.13
Berkeley	Walnut meat.....	49	♀	19.53
Berkeley	Raisins.....	4	♂	9.55
Berkeley	Raisins.....	3	♀	10.13
Berkeley	Rolled barley.....	14	♂	10.58
Berkeley	Rolled barley.....	10	♀	12.12
Fresno	Chicken mash with raisins.....	150	♂	14.90
Fresno	Chicken mash with raisins.....	125	♀	19.16
Fresno	Chicken mash.....	210	♂	12.43
Fresno	Chicken mash.....	218	♀	17.27

* 1.5 gm. of food per larva.

ever, might be accounted for by differences in the sex ratio, food medium, temperature, humidity, time of weighing, and the occurrence of diapause.

GENERALIZED LIFE HISTORY

The larva is extraordinarily polyphagous. Richards and Thomson (1932) listed 83 different kinds of food on which it has been reported to feed, including dried fruits, nuts, grain and grain products, garden seeds, dried vegetables, herbarium specimens, dead insects, powdered milk, spices, cacao, chocolate, candies and other confections, biscuits, drugs, and the nest contents of honey bees and bumble bees. The adults will readily drink water, sirup, and similar liquid substances (Zacher, 1938).

As reported in the literature, the female lays from approximately 40 to 400 eggs, either directly on, or adjacent to the food material. The number of eggs per female depends upon a number of factors, such as temperature, food of the female while in the larval and adult stage, and on the size of the individual. In general the larger moths lay the most eggs. The oviposition period has been reported to be from one to 18 days. At room tempera-

TABLE 2

TIME AND WEIGHT-LOSS FROM MATURE LARVA TO ADULT, FOR INDIVIDUALS OF *PLODIA*, REARED AND HELD AT 20°C AND 58 PER CENT R.H. IN THE DARK

Stock	Number individuals	Weight in mg				Number of days					
		Mature larva		Young pupa*		Mature larva to pupa		Pupal stage		Adult longevity	
		Range	Average	Range	Average	Range	Average	Range	Average	Range	Average
Fresno.....	4 ♂	14.5-17.1	15.8	12.7-14.4	13.9	3-6	4.5	17-18	17.7	11-19	14.5
	7 ♀	19.8-25.8	23.4	17.0-20.8	19.5	4-6	4.6	14-18	16.4	10-16	13.7
Berkeley.....	1 ♂	17.7	16.2	5.0	22.0	14.0
	9 ♀	20.5-36.2	29.1	18.8-30.6	24.5	3-17	8.2	20-22	20.8	9-27	14.7
Berkeley.....	4 ♀†	24.8-44.1	34.3	15.2-26.2	21.1	56-148	98.2	21-25	23.3	8-12	9.5

Stock	Number individuals	Weight loss, expressed as per cent of weight of young pupa				Total loss (mature larva to adult)			
		Mature larva to young pupa		Young to old pupa†		Old pupa to adult§		Total loss (mature larva to adult)	
		Range	Average	Range	Average	Range	Average	Range	Average
Fresno.....	4 ♂	6.6-20.4	14.0	2.1-9.2	5.7	33.1-37.5	35.7	46.2-65.5	55.4
	7 ♀	16.5-24.0	20.3	2.1-5.8	3.4	14.3-19.8	16.1	34.8-56.6	39.8
Berkeley.....	1 ♂	9.3	9.2	29.0	47.5
	9 ♀	6.5-43.8	18.3	5.0-10.6	7.3	14.2-24.4	18.8	28.4-67.8	44.4
Berkeley.....	4 ♀†	47.2-86.9	62.3	5.3-8.3	6.7	22.8-25.7	24.0	78.8-115.6	93.0

* One day old.

† Two days before adult emergence.

‡ Diapausing.

§ The day of emergence.

tures, the majority of the eggs are laid in the first three or four days. The length of the incubation period depends mainly on temperature. At room temperature it varies from four to eight days. During the present work, at 25° C and 53 per cent R.H. it lasted four to five days.

Soon after hatching, the young larvae tend to disperse in search of food. At this stage, their small size enables their penetrating even containers that seem well sealed. In a few hours they establish themselves on the food material and start feeding. The larva always leaves a silken thread behind. Richards and Thomson (1932) found that the number of larval molts ranged from five to seven, even where larvae were reared under identical conditions. They also concluded that there was no relation between sex and the number of molts. Zacher (1938) estimated the number of molts as five. The duration of the larval stage varies according to the food, season, and other ecological conditions. This has been observed by a number of investigators, including Hamlin *et al.* (1931), and Zacher (1938). However, as demonstrated in the present investigation, one should distinguish between the duration of the feeding larval stages, and that of the mature (nonfeeding) larval stage. The latter depends considerably on the occurrence and duration of diapause. It is difficult to compare the results obtained by previous authors, because they did not make any distinction between the two periods.

Most larvae on reaching maturity leave the food medium, and wander about in search of a suitable place to spin a cocoon in which to pupate or to hibernate. This is usually a crack or other protected place, preferably in dark locations. A few larvae may spin their cocoons in the food medium, immediately below the surface. The cocoons spun by the pupating larvae can be distinguished from those made by the hibernating or diapausing larvae. The hibernaculum or hibernation cocoon is dense and completely closed, while the pupal cocoon is flimsy, rather loose, tapering, and opens anteriorly to provide for the exit of the adult.

Following the termination of hibernation, the larva opens a hole through the hibernaculum, and either spins its pupal cocoon inside, or comes out and constructs the pupal cocoon nearby. Although no specific experiments to this end have been carried out during the present investigation, observations by the author tend to indicate that the larva spins its pupal cocoon outside the hibernaculum only when the latter is not roomy enough to include the former. After spinning the pupal cocoon, the larva passes through a prepupal stage similar to that described by Waloff (1948) for *Ephestia elutella* Hübner. The duration of the pupal stage seems to depend mainly on the temperature during that stage and to be independent of the duration of the larval stage (Fraenkel and Blewett, 1946). The duration of the adult stage is dependent upon environmental factors, such as temperature and humidity, the occurrence of mating, and oviposition, and on whether the moths have the opportunity to drink water or other liquids.

According to observations made by the author and the information obtained from the literature, the life cycle, during periods of warm weather, may be completed in about four to six weeks. Under natural conditions indoors or out-of-doors, the number of generations per year varies. The information on this subject, as obtained from the literature, is given in table 3.

During the present investigation the time required from hatching to adult

TABLE 3
NUMBER OF GENERATIONS OF *PLODIA INTERPUNCTELLA* IN DIFFERENT PARTS OF THE WORLD, AS REPORTED BY VARIOUS AUTHORS

Country	Larval food	Number generations per year	Environmental conditions	Author
United States	————	6, 7, or more	In a heated atmosphere	Chittenden (1895)
United States	————	4-5	In a moderately cool granary	Chittenden (1897)
United States	Peanuts	4-7	Under good conditions of temperature.....	Popenoe (1911)
United States	————	4-6 or 7	According to temperature	Dean (1913)
United States	————	4-6	In heated buildings.....	Metcalf and Flint (1951)
United States (California) ..	Prunes	4	In heated buildings.....	Hamlin <i>et al.</i> (1931)
United States (California) ..	Raisins, figs	5	In heated buildings.....	Hamlin <i>et al.</i> (1931)
United States (California) ..	Figs	5	In heated buildings.....	Simmons <i>et al.</i> (1931)
United States (California) ..	Walnuts	7-8	Under favorable conditions	Michelbacher and Ortega (1958)
Australia.....	Raisins	2	————	Myers (1928)
England.....	Dried fruit	1 or 2	In unheated warehouses...	Potter (1935)
Germany.....	————	2	In unheated granaries.....	Zacher (1938)

emergence of nondiapausing individuals reared on chicken mash at various temperatures was as follows:

At degrees C	Per cent R.H.	Days
35	41	24-31
30	45	22-27
25	53	28-33
20	58	51-59

Hibernation

Very little is known concerning the overwintering habits of *Plodia interpunctella* out-of-doors, and there was no agreement by early authors on how this insect spends the winter indoors. Bioletti (1915) believed it probable that *Plodia interpunctella* passed the winter in the pupal stage, although he indicated that in warm situations the larvae also may survive. However, most investigators, including Popenoe (1911), Parker (1915), Essig (1920), Myers (1928), Hamlin *et al.* (1931), Simmons *et al.* (1931), Zacher (1938), Michelbacher (1953), and Gray (1956) are of the opinion that, in temperate regions, the insect hibernates as a full-grown larva. Lovett (1921), who conducted his investigations in Oregon, reported that all stages of the insect could be found throughout the winter. However, in central California, a region generally warmer than Oregon, Hamlin *et al.* (1931), Simmons *et al.* (1931), and Parker (1915) failed to observe any adult activity during the winter.

According to Treherne (1921), in British Columbia, larvae believed to be codling moth but later identified as *Plodia interpunctella* had been received at the experiment station on many occasions. They had been taken frequently under burlap bands on apple trees in codling moth quarantined areas, occasionally in apple fruit on the trees, but most commonly in dry cull apples remaining in the orchard, and in apple refuse in packing houses.

In the spring of 1941 in the vicinity of Bakersfield, California, Linsley and McSwain (1942) found three out of 759 nests of *Anthophora linsleyi* Timberlake examined to be infested with larvae of *Plodia interpunctella*. According to McSwain,⁵ larvae of *Plodia interpunctella* are able to maintain themselves during the winter in the nests of *Anthophora* bees in California.

Michelbacher (1953) reported, after Bohart, that in Utah, the nests of bumble bees almost always become infested with *Plodia interpunctella* toward the end of the season. Further observations of Dr. G. E. Bohart (*in litt.* August 4, 1958) tend to indicate that *Plodia interpunctella* is able to overwinter in old bumble bee nests constructed in seat cushions in an automobile junk yard in Utah.

DIAPAUSE (Summary of literature)

Diapause⁶ is a state of arrested development, which is common in hibernating or aestivating insects and other arthropods. Although it is most common among the Arthropoda, diapause is also known to occur among other groups of animals (Porifera, Cladocera, Crustacea, Aves, Mammalia), and among plants (seeds, bulbs, buds of perennial plants).

The term "diapause" was first used by Wheeler (1893) for a stage in the embryogenesis of *Xiphidium ensiferum* Scudder. Later Henneguy (1904) used it in the sense of a condition of arrested growth in an insect. In his "diapause" Henneguy included all forms of arrested growth, even those caused by the immediate effect of cold (cold torpor). This broad meaning was adopted by many subsequent authors. Shelford (1929), however, suggested that the term "diapause" should be used only when development or activity is arrested spontaneously, and the term "quiescence" when the arrest is directly controlled by unfavorable conditions. Roubaud (1930) used the terms "true diapause" and "pseudodiapause" in a similar sense.

Although the terms "diapause" and "quiescence" literally do not differ, they have been adopted by most of the modern investigators and reviewers to distinguish between two different phenomena. Quiescence thus represents a state of arrested development which is caused by unfavorable environmental conditions such as cold, heat, or drought, and which ends as soon as the environment becomes favorable again. An insect in diapause, on the other hand, will not resume development when placed under favorable conditions. Certain physiological processes have to be completed before such an insect is able to resume development. In general, we may say that diapause is temporarily irreversible, whereas quiescence is immediately reversible, and that certain physiological mechanisms are involved in the case of diapause, which are absent in the case of quiescence.

An insect in diapause is characterized by reduced metabolism, and often by increased resistance to adverse climatic conditions, such as cold, heat, or drought. Diapause usually occurs at that stage of the life cycle of an organism, which is the most resistant to the rigors of the climate, and at the time of the year which precedes the unfavorable season. A diapausing insect thus manages to maintain itself successfully during the unfavorable season

⁵ Personal communication.

⁶ δίαπαισις = rest, cessation.

of the year, and to resume its development and active life when the environment becomes favorable again.

An insect, depending upon the characteristics of the species, may enter diapause during the egg, larval, nymphal, pupal, or adult stage. In the immature stages diapause represents an arrest of growth or development; in the adult, it is expressed as a lack of growth of the reproductive organs, particularly the ovaries.

Diapause can be distinguished typically into obligate and facultative. It is obligate when it occurs in every individual of every generation, irrespective of the environmental conditions (*Melanoplus mexicanus mexicanus* Saussure). Species possessing an obligate diapause are known as "univoltine" and have one or less generation per year. In species with a facultative diapause (multivoltine) there are typically more than one generation per year, and some generations in which few or no individuals enter diapause are followed by a generation in which most or all of the individuals enter diapause (*Platyedra gossypiella* Saunders). In such species the occurrence of diapause depends largely on the environment. Several insect species possess a type of diapause intermediate between obligate and facultative. Furthermore, strains or races of the same species occupying different environments may differ in the type of their diapause [*Pyrausta nubilalis* (Hübner), *Ephestia elutella* Hübner].

The importance of hormones in controlling the phenomenon of diapause has been demonstrated by many investigators. A detailed coverage of the ecological, phenological, and physiological aspects of diapause is not within the scope of the present work. For such a detailed treatment, the reader is referred to the recent reviews by Bonnemaison (1945), Andrewartha (1952), Andrewartha and Birch (1954), and Lees (1955, 1956). Only the most important environmental factors that induce and interrupt diapause are considered in the following brief discussion.

Induction of Diapause. In multivoltine species, the occurrence of diapause is induced by the environment. The individuals of every generation retain the capacity of entering diapause, but will not do so unless they are exposed to certain environmental factors at the proper time. These factors exert their action prior to the onset of diapause. The factors that have been proved to be of major importance in inducing diapause in multivoltine species are photoperiod and temperature. Other factors, such as quantity and quality of food may also affect the tendency of an individual to diapause; their action, however, as determinants in the majority of species studied, has been of minor role.

Photoperiod should be considered as the most important inducing factor, and would be expected to be so, because day length is the most reliable indicator of the season. It is well known that for a given species and region, diapause occurs in a certain season of the year. In the cases reported, the critical factor was the length of the photoperiod, or scotoperiod, and not the intensity of light, provided the latter was above a certain minimum which varied with the species. In some species the photoperiod is more important than the scotoperiod; in others the reverse is true; and in others diapause is induced only within a certain range of values for photoperiod and scotoperiod.

The effect of photoperiod, no matter how pronounced, is seldom independent of temperature. Even if light conditions are favorable, diapause will not occur unless the temperature is within a suitable range. The critical range of temperatures varies according to the species. As a rule, high temperatures prevent, and low temperatures favor diapause. There are, however, examples like that of *Bombyx mori* (Linnaeus), (Kogure, 1933) where high temperatures induce diapause, and that of *Grapholitha molesta* Busck (Dickson, 1949) where both high and low temperatures prevented diapause, while medium ones induced it. Cases in which temperature by itself can induce diapause have also been reported, as in a strain of *Ephestia elutella* isolated by Basden (Waloff, 1949).

Duration and Termination of Diapause. If an insect in diapause is kept under temperatures high enough for morphogenesis, it may ultimately die without developing, or develop in a prolonged and irregular manner, or resume development normally after a lapse of time. If, on the other hand, an insect in diapause is exposed first to low temperatures for a sufficient period, then to higher temperatures favoring morphogenesis, it will usually in a short time resume normal development.

For the termination of diapause, therefore, and the resumption of normal development, certain physiological processes must be completed. For these processes Andrewartha (1952) coined the term "diapause development." Schneiderman and Horwitz (1958) used the term "diapause ending processes" in a similar sense. This latter term will be used in the present work. The term "breaking of diapause" will be used in the present work, when referring to the completion or end of the diapause-ending processes.

After diapause has been broken, the insect will remain in a state of quiescence, if temperature remains below the threshold for morphogenesis. If temperature becomes high enough for morphogenesis, development will be resumed immediately. The range of temperatures favorable for the diapause-ending processes differs with the species. The optimum for the majority of the species reported upon, has been above 0° C, but below 15° C. The temperature ranges for morphogenesis and for the diapause-ending processes may overlap, but the optima are distinctly different.

The duration of diapause differs greatly with the species. Under natural conditions, it may last from a relatively short period to more than a year. In some species, as in *Eurydema ornatum* Linnaeus, only a few days at the proper temperature are necessary to break diapause. In other species, such as *Carpocapsa pomonella* (Linnaeus), several months at the proper temperature may be necessary. Furthermore, attention should be called to the fact that the duration of diapause may vary greatly among different individuals of the same species. Thus, Yothers and Carlson (1941) reported that healthy hibernating codling moth larvae may fail to transform the season following hibernation, and may, under certain conditions, transform to moths two seasons later. Boyce (1934) observed that biennial-generation individuals represented a relatively high percentage of a population of the walnut husk fly (*Rhagoletis completa* Cress), and furthermore that a portion did not emerge until the third or even the fourth year after pupation.

With some, but not all species, low temperature for a sufficient period is the most reliable means of ending diapause. In other species, photoperiod is

the principal factor determining the duration and termination of diapause. Wounding, and exposure to fumigants and other chemical substances have been reported to break diapause in some species. Such artificial methods, however, generally have not proved to be very effective.

The absorption of water is for many species necessary for the resumption of development after diapause has been broken. Water, however, or high atmospheric humidity does not seem to initiate the diapause-ending processes.

Diapause in the Indian-meal Moth. The distinction between "diapause" and "quiescence" in their modern meaning is fairly recent (Shelford, 1929). Popenoe (1911) reported that *Plodia interpunctella* overwinters as a full-grown larva in a state of quiescence. By this he probably meant a fairly inactive condition. Most authors, however, have been of the opinion that in heated buildings or wherever temperature is sufficiently high for growth, and other conditions are favorable, feeding and breeding go on throughout the winter. Potter (1935) stated that in warehouses in London *Plodia interpunctella* has a life history similar to that of *Ephestia elutella*. The latter species is known to enter diapause as a full-grown larva in that area (Waloff and Richards, 1946; Richards and Waloff, 1946). This indicates the possibility of the occurrence of diapause also in *Plodia interpunctella* in England.

In spite of the rather voluminous literature on *Plodia interpunctella*, it is only in the papers by Hamlin *et al.* (1931), and Simmons *et al.* (1931) that experimental data are presented, that indicate the occurrence of a facultative diapause in this species. Hamlin *et al.* (1931) though not suspecting or mentioning diapause, separated the larvae into "transforming" and "wintering" groups (table 4). On the basis of our present knowledge we would place them in nondiapausing and diapausing categories. The data in table 4 show that with the advancement of the season, starting with larvae hatched about the middle of July, the percentage of individuals entering diapause increased. The data of Simmons *et al.* (1931) gave a similar picture.

As far as can be determined, Michelbacher (1953) was the first to correctly interpret the data of Hamlin *et al.* and Simmons *et al.*, to relate them with observations of other workers and of his own, and to conclude that *Plodia interpunctella* enters diapause under certain conditions.

EXPERIMENTAL METHODS

Rearing Method. In most cases the insects were reared in one-pint, squat, wide-mouthed, glass Mason jars with screw caps. A circular sheet of Whatman No. 1 filter paper was substituted for the removable metal cap. Usually 66 or 70 larvae were reared in each jar, on 99 or 105 grams of rearing medium respectively. Thus 1.5 grams of food-medium were available per larva. The depth of the rearing medium was approximately 3.5 cm for chicken mash and walnut meat, 2.7 cm for raisins, and 4.4 cm for rolled barley.

In a few cases rearing took place in 25 by 50 mm glass shell vials. Three larvae were reared in each vial, on 4.5 grams of food-medium. The vials were covered with fine Dacron organdy.

As a rule, first instar larvae, within 24 hours from hatching, were transferred by means of a very fine camel hair brush, from the incubation jars to the rearing jars or vials. In a few cases an open shell vial containing the

eggs was placed on the food-medium. Upon hatching, the young larvae crawled out of the vial into the medium. Two strips of white corrugated paper, about 30 cm long and 2 cm wide, were added to each jar to provide quarters for pupation. Oviposition and incubation, depending on the purpose of each experiment, took place in shell vials or in jars similar to those used for rearing. Whenever it was desirable to have a uniform representation of a group rather than of a pair of parents, the eggs of several pairs of moths were used, and aliquots of the eggs of each pair were placed in each jar of a given experiment. Depending on the purpose of each experiment, incubation took place at 20° C, 25° C, or 30° C.

TABLE 4
DEVELOPMENTAL PERIOD OF THE INDIAN-MEAL MOTH ON RAISINS,
FRESNO, CALIFORNIA, 1925-1927*

Date eggs hatched	Total larvae	Transforming individuals			Wintering individuals		
		Larvae	Days of larval life		Larvae	Days of larval life	
			Range	Av.		Range	Average
Sept. 25-26, 1925.....	114	0	114	162-227	183.1
April 14-17, 1926.....	20	20	28-56	39.9	0
June 9, 1926.....	16	16	21-61	36.2	0
July 14, 1926.....	23	22	29-74	44.1	1	282	282.0
Aug. 20-21, 1926.....	16	5	34-48	40.4	11	231-267	249.1
October 16, 1926.....	14	0	14	159-188	172.6

* After Hamlin *et al.* (1931).

All containers were carefully cleaned and subjected to high temperature before re-use. No microbial disease or predatory or other undesirable organisms were noticed in the insect cultures during the investigation.

Rearing, as well as most of the studies, was carried out in the Insectary of the Department of Entomology and Parasitology of the University of California at Berkeley.

According to the purpose of each experiment, the insects were reared and kept in constant temperature cabinets (incubators), or in desiccators, or in heated rooms, or out-of-doors. As a rule, tests involving fairly large numbers of insects reared in jars were conducted in incubators. Those involving a small number of insects reared in vials, were carried out inside desiccators, placed in the incubators. A saturated solution of calcium nitrate $\text{Ca}(\text{NO}_3)_2$ maintained the following relative humidity in the desiccators:

Desiccator temperature °C	Per cent R.H.
5	71 ± 2
10	70 ± 4
15	64 ± 3
20	58 ± 2
25	53 ± 3
30	48 ± 3

The relative humidity maintained in the incubators was as follows:

Incubator temperature °C	Per cent R.H.
10	71 ± 6
15	73 ± 7
20	58 ± 8
25	50 ± 8

The relative humidity was measured by a Serdex hygrometer and the readings corrected by comparison with those of a sling-type, wet-dry bulb psychrometer.

The temperatures in the constant temperature cabinets were accurate within $\pm 1^\circ$ C. Temperature and relative humidity outside the incubators were measured by hygrothermographs.

Under controlled conditions, the light was provided by a 15 W Sylvania tungsten bulb. The light intensity was measured by a Weston Model 756 illumination meter, and ranged, depending on the position of the jars, from 2 to 8 f.c. (foot candle), with an average of 3.6 f.c.

Rearing Media. Several rearing media (food-media) were used during the present work. Each will be referred to by the bold-faced phrases shown below.

1. **Chicken Mash.** This consisted of a freshly prepared mixture of 7 parts (by volume) of chicken mash, $\frac{1}{2}$ part of glycerine, and $\frac{1}{2}$ part of honey. The mash was furnished by the Poultry Husbandry Department of the University of California. Its composition was as follows:

Pounds	Pounds		
corn	300	liver and glandular meal	20
wheat	135	limestone, ground	15
barley	100	bone meal	12
alfalfa meal	40	salt	5
wheat bran	150	MnSO ₄ , technical	0.5
fish meal	100	fortified fish oil	2.5
soybean oil meal	100	riboflavin	1 gr
dried whey	25		

**Analysis
(approximate)**

	Per cent
Protein	20
Calcium	1.6
Phosphorus	0.8

2. **Chicken Mash With Raisins.** This rearing medium was prepared by mixing 8 parts by volume of mixture no. 1 with 1 part of Zante currants (small, black, seedless raisins).

3. **Raisins.** Thompson seedless raisins produced in California. They were of unknown age, purchased at a local grocery in 2-pound plastic bags.

4. **Walnut Meat.** Current year nut meats of the Payne variety, which were kept refrigerated until the day of use.

5. **Rolled Barley.** This product, used dry, was of unknown age and origin.

The above media, except the walnut meat, were subjected to high temperature, before use, in order, if infested, to render them free from undesirable arthropods.

Insect Stock. The original stock of *Plodia interpunctella* was furnished for the investigation in January, 1957, from the Stored-Product Insects Laboratory of the U. S. Department of Agriculture at Fresno, California. This stock, which constitutes the material referred to as "Fresno" stock, had been reared, prior to January, 1957, for many generations, at room temperature, on a mixture of chicken mash, honey, glycerine, and raisins, similar to the mixture used in the present investigation.

In October, 1957, over 100 larvae were obtained from infested walnuts in a home at Berkeley, California. The progeny of these individuals are designated as "Berkeley" stock.

Definitions of Terms Used In the Present Work

Larval Stage. The period from hatching to pupation. It thus includes the feeding (immature) larval stages, the wandering stage, the "spun-up" stage, and the prepupal stage.

Mature Larval Stage or Full-grown Larval Stage. The larval stage as defined above, exclusive of the feeding larval stages. It is the stage spent in the last larval instar, after feeding has stopped.

Diapausing Larva. A mature larva which failed to pupate within three weeks after reaching mature larval stage when held at 25° C and 53 per cent R.H. During the present investigation it was observed that, with the exception of a few larvae which pupated in the third week, the majority of full-grown larvae, if nondiapausing, pupated within two weeks, when held at 25° C and 53 per cent R.H. To minimize the disadvantages of adopting this somewhat arbitrary criterion, the intensity of diapause, as defined here, was also recorded whenever necessary and possible.

Intensity of Diapause. The intensity or profundity of diapause is measured as the number of days, in excess of three weeks, that a mature larva spent in diapause at 25° C and 53 per cent R.H.

Per Cent of Diapause or Amount of Diapause. The number of diapausing larvae in a given group is expressed as per cent of total number of mature larvae in that group. The per cent of diapause thus represents the incidence of diapause in a group of larvae.

OCCURRENCE AND DURATION OF DIAPAUSE

It was demonstrated during the present investigation that a facultative diapause does occur in *Plodia interpunctella*. It was also noticed that different strains of this species may differ in their tendency to diapause. Thus, no larvae of the Fresno stock entered diapause, when exposed to conditions that produced diapause in up to 28 per cent of the larvae of the Berkeley stock. Also, conditions that caused 100 per cent diapause in the Berkeley stock, resulted in only 12 per cent diapause in the Fresno stock. For this reason, the Berkeley stock, which had a greater tendency to diapause, was mostly used in the experiments in which diapause was investigated.

Exposure of the diapausing larvae to low temperatures was not necessary for the termination of diapause. Diapausing larvae held continuously at 15°, 20°, and 25° C, pupated normally after a lapse of time which varied with the temperature, and with the intensity (profundity) of diapause of each individual. Not only was pupation under these conditions normal, but also

the pupae (except those held at 15° C), developed into healthy adults capable of normal reproduction. Thus, in the present investigation, the duration of diapause varied considerably within and between different temperatures. For example, at 20° C and 58 per cent R.H. it ranged from several to 191 days, and at 25° C and 53 per cent R.H. from a few to 112 days.

TABLE 5

THE DIFFERENCE IN THE DURATION OF DIAPAUSE IN THE BERKELEY STOCK, WHERE ONE GROUP OF LARVAE WAS HELD CONTINUOUSLY AT 20°C AND 58 PER CENT R.H., AND THE OTHER TRANSFERRED AFTER THE 47TH DAY OF DIAPAUSE TO 25°C AND 53 PER CENT R.H.

Held continuously at 20° C		Transferred to 25° C the 47th day	
Number and sex	Duration of diapause in days	Number and sex	Duration of diapause in days
1 ♀	90	1 ♂	81
1 ♀	117	2 ♂ ♀	83
1 ♀	131	2 ♀ ♀	88
1 ♂	133	3 ♂ ♀ ♀	90
1 ♂	135	1 ♂	92
1 ♀	137	1 ♀	99
1 ♂	143	1 ♂	100
1 ♀	149	1 ♂	109
1 ♀	155	1 ♀	128
1 ♂	168
1 ♂	174
1 ♀	184
1 ♀	191
13 (5 ♂ 8 ♀)		13 (6 ♂ 7 ♀)	
Average.....	146.7	Average.....	93.9

In a group of 96 larvae of the Berkeley stock reared on chicken mash at 20° C and 58 per cent R.H., 37 pupated within 43 days from hatching, 33 in from 44 to 50 days, and 26 entered diapause. The 26 diapausing larvae were held for 47 days at 20° C, after which time one half were transferred to 25° C, and the other half left at 20° C. The duration of diapause of each of these 26 larvae is shown in table 5. It is seen that the duration of diapause in the group held continuously at 20° C was considerably longer (90 to 191 days with an average of about 147 days) than in the group that was transferred to 25° C after the 47th day of diapause (81 to 128 days with an average of about 94 days). If the first 47 days of diapause, when both groups were held at the same temperature, is subtracted, and only the diapause period when the two groups were held at different temperatures is taken into account, the difference in the duration of diapause becomes more striking. The approximate average duration of diapause in the group held at 20° C becomes 104 days, whereas in the group held at 25° C it is 51 days, or only half as long.

In another experiment, diapausing larvae held for 16 weeks at 20° C and 58 per cent R.H. were divided into two equal groups. One group was con-

tinued at the same conditions, while the other was transferred to 25° C and 53 per cent R.H. The duration of diapause in excess of 16 weeks, for these two groups, is given in table 6. In general the period of diapause was reduced by the higher temperature.

A third experiment was conducted in which two groups of diapausing larvae, upon reaching larval maturity, were placed at 15° C and 20° C,

TABLE 6
THE INFLUENCE OF TEMPERATURE ON THE
LENGTH OF DIAPAUSE, AFTER THE LARVAE
HAD SPENT 16 WEEKS IN DIAPAUSE AT
20° C AND 58 PER CENT R.H.

Number of larvae	Holding temperature beyond the 16th week	Additional days in diapause beyond the 16th week	
		Range	Average
30	20° C	4-89	38.4
31	25° C	9-112	15.2

TABLE 7
THE INFLUENCE OF TEMPERATURE ON THE DURATION OF
DIAPAUSE IN LARVAE REARED AT 20° C AND
58 PER CENT R.H.

Number of larvae	Per cent mortality during experiment	Temperature during diapause	Duration of diapause in days	
			Range	Average
44	6.8	15° C	15-193	118.9
44	2.3	20° C	26-101	61.5

respectively. The results, which are similar to those obtained in table 6, are given in table 7.

The data presented in tables 5, 6, and 7, which are substantiated by additional observations during the present investigation, show that, within the range of developmental temperatures studied, the higher the temperature during diapause, the shorter the duration of diapause.

No investigation was conducted on the influence of light on the duration of diapause. However, observations were made that furnished some information on this subject. This occurred in an experiment where two groups of larvae were held under two different light conditions. These larvae, of the Berkeley stock, were reared on walnut meat, at room temperature. Upon maturity they were transferred to out-of-doors, where one group was continuously exposed to subdued daylight of a natural photoperiod from April 19, to September 12, 1958. The other group was placed in continuous darkness. Pupation was recorded at approximately weekly intervals. Sixteen larvae diapaused in each group. The duration of diapause in these two groups is presented in table 8. It can be seen that there was practically no difference in the duration of diapause between the two groups.

DURATION OF LARVAL GROWTH AND INCIDENCE OF DIAPAUSE

It has often been reported that individuals which are destined to diapause, grow slower than those which are not. According to Andrewartha (1952), the correlation between diapause and slower growth seems to hold irrespective of whether diapause has been determined in the first place by photoperiod, genetic constitution, maternal physiology, or other causes. This, according to the same author, indicates a consistent difference between the diapausing and nondiapausing individuals with respect to the metabolism of the food.

TABLE 8
THE DURATION OF DIAPAUSE IN 32 DIAPAUSING LARVAE
OF THE BERKELEY STOCK HELD OUT-OF-DOORS
UNDER TWO DIFFERENT LIGHT CONDITIONS*

Light conditions during diapause	Duration of diapause in days	
	Range	Average
Natural photoperiod.....	55-156	104.3
Continuous darkness.....	61-156	105.2

* Out-of-door period April 19 to September 12.

No experiments were conducted during the present investigation to this end. However, in the course of other experiments, data were recorded on the duration of growth of diapausing and nondiapausing groups of larvae of the Berkeley stock. The larvae in question were from experiments in which some groups were exposed to conditions conducive to diapause, while others were not. In all cases the individuals of any series were from the same parents. All the larvae were reared on chicken mash, at 20° C and 58 per cent R.H. Observations were made at three-day intervals. The information in regard to duration of larval growth is presented in table 9. The larvae of groups "a" were held, during incubation, under conditions not conducive to diapause, while those of groups "b" were subjected to conditions conducive to diapause. It can be seen that within any series, as well as on a total average, the duration of larval growth in groups where no or little diapause occurred, was shorter than in groups where all or the majority of the larvae entered diapause. Too much emphasis cannot be placed on this situation because there were cases where nondiapausing larvae had, on an average, a longer duration of growth than diapausing ones. For example, the average duration of larval growth in the diapausing groups of series VII, VIII, IX, and X was shorter than in the nondiapausing group of series IV. Also, there was a rather wide overlapping in the ranges of duration of larval growth between diapausing and nondiapausing groups.

Further, information on the relation that exists between duration of larval growth and the incidence of diapause can be obtained by a study of the differences in the per cent of diapause between the earlier and later maturing larvae of a given group. Such information on 21 groups of larvae is given in table 10. The larvae in each series were divided into two, three, or four

groups, according to the duration of larval growth. The experimental method employed was the same as in the groups presented in table 9. The information in table 10 is not presented in the same manner for all the 21 series. In the first 10 series (I–X) the percentage (proportion) of larvae that was arbitrarily included in either the faster-growing “a,” or the slower-growing “b” group of each series, varied, but always included at least 13.3 per cent of the total. In the remaining 11 series (XI–XXI), the data of the few slowest-growing larvae of each series are shown separately as “c” in the grouping.⁷

It is seen that in the first seven series (I–VII), the percentage of larvae entering diapause was constantly higher in the groups containing the slower-growing larvae. In the following three series (VIII–X), the reverse is true, although the differences were distinctly smaller. In the remaining 11 series (XI–XXI), the percentage of diapause in the fastest-growing larvae was generally lower than in the next slower-growing intermediate group of larvae. Furthermore, in four out of these 11 series (XI–XIV), the per cent of

TABLE 9
DIFFERENCES IN THE DURATION OF LARVAL GROWTH
BETWEEN NONDIAPAUSING (GROUP A) AND DIAPAUS-
ING (GROUP B) *PLODIA* LARVAE, REARED AT 20°C
AND 58 PER CENT R.H.

Series	Group	Number of larvae	Per cent diapause	Duration of larval growth, in days*	
				Range	Average
I.....	a	39	0	28-40	33.1
	b	59	72.9	31-49	36.9
II.....	a	39	0	28-40	31.8
	b	55	92.7	28-49	38.4
III.....	a	41	2.4	25-46	28.7
	b	56	94.6	28-49	34.0
IV.....	a	69	0	28-40	33.7
	b	43	69.8	27-48	35.9
V.....	a	59	0	27-42	31.1
	b	53	90.5	32-44	36.2
VI.....	a	65	7.7	27-42	32.5
	b	66	100.0	31-39	37.1
VII.....	a	64	0	25-43	31.6
	b	55	94.6	26-41	31.8
VIII.....	a	36	0	24-30	26.3
	b	78	91.1	28-52	32.3
IX.....	a	71	0	21-30	25.7
	b	55	98.3	27-39	30.9
X.....	a	93	0	27-36	30.6
	b	45	88.9	30-39	33.3

* From hatching to mature larva.

⁷ These few larvae represented less than 13 per cent of the total larvae of each series.

TABLE 10
 THE RELATION BETWEEN DURATION OF LARVAL GROWTH AND INCIDENCE OF DIAPAUSE IN VARIOUS GROUPS OF *PLODIA* LARVAE REARED AT 20°C AND 58 PER CENT R.H.

Series	Group	Number of larvae	Duration of larval growth in days	Per cent diapause
I.....	a	54	28-35	0
	b	42	36-42	64.3
II.....	a	6	28-30	0
	b	34	31-42	94.1
III.....	a	45	23-26	8.9
	b	12	27-29	83.3
IV.....	a	65	24-30	15.4
	b	10	31-45	20.0
V.....	a	45	23-26	4.4
	b	14	27-41	71.4
VI.....	a	30	≤28	6.7
	b	28	29-34	57.2
VII.....	a	21	31-34	42.8
	b	33	35-37	78.7
	c	12	38-40	100.0
VIII.....	a	46	26-32	95.6
	b	9	33-41	88.9
IX.....	a	35	30-33	94.3
	b	10	34-39	70.0
X.....	a	38	27-30	100.0
	b	17	31-39	94.1
XI.....	a	17	32-41	8.5
	b	10	42-46	40.0
	c	4	47-51	100.0
XII.....	a	23	28-37	13.5
	b	27	38-43	55.5
	c	2	44-46	100.0
XIII.....	a	22	29-32	13.6
	b	30	33-35	86.7
	c	1	39-41	100.0
XIV.....	a	14	30-33	7.1
	b	22	34-39	86.4
	c	2	40-42	100.0
XV.....	a	43	31-37	72.1
	b	14	38-43	78.6
	c	2	44-49	50.0
XVI.....	a	38	28-34	71.1
	b	18	35-37	100.0
	c	3	38-46	100.0
	d	2	47-70	50.0

TABLE 10—Continued

Series	Group	Number of larvae	Duration of larval growth in days	Per cent diapause
XVII.....	a	51	≤28	2.0
	b	28	29-37	39.3
	c	2	38-40	100.0
	d	2	41-43	0
XVIII.....	a	27	26-29	0
	b	31	30-35	29.0
	c	3	36-41	0
	d	2	42-44	0
XIX.....	a	36	26-29	5.6
	b	21	30-35	4.8
	c	1	36-38	0
XX.....	a	62	28-31	92.0
	b	14	32-43	100.0
	c	2	44-52	0
XXI.....	a	47	28-34	38.3
	b	22	35-40	36.4
	c	2	41-43	0

diapause was the highest in the slowest growing larvae. However, in the last seven series (XV-XXI), the slowest growing larvae showed less diapause than other faster growing larvae of their series. It should be noted that these few slower-growing larvae looked healthy and developed into normal adults.

In spite of the fact that the number of larvae in groups c and d of most series was very small, the data of table 10 seem to indicate that when some diapause occurs in a group of larvae, the larvae with accelerated growth have little tendency to diapause, those with an intermediate speed of growth have a stronger tendency to diapause, and the slowest-growing individuals may or may not diapause.

Although more detailed evidence would be desirable, the data presented seem to indicate that at least in the case of *Plodia* larvae, the generally accepted view that diapausing individuals grow more slowly than nondiapausing ones is not always true.

INDUCTION OF DIAPAUSE

The Relation of Temperature to Induction of Diapause

It was mentioned earlier that, generally, in insects that spend the cold season of the year in diapause, high temperatures tend to prevent diapause, while rather low temperatures favor its occurrence. Further, it was noted, temperatures below those favoring rapid growth and development usually were a requisite for the occurrence of facultative diapause.

Influence of Temperature During Larval Growth. During the present investigation it was determined that a constant temperature of 20° C during larval growth fell within the range of temperatures favorable for diapause in *Plodia interpunctella*, whereas constant temperatures of 25° C or higher did not. For this reason a temperature of 20° C was adopted as the

TABLE 11
EFFECT OF VARIOUS EXPOSURES TO LOW TEMPERATURES DURING
LARVAL GROWTH ON INDUCING DIAPAUSE IN *PLODIA*
LARVAE OF THE BERKELEY STOCK*

Number of individuals	Temperature during larval growth, ° C	Per cent mortality during larval growth	Diapause		
			Per cent	Intensity in days	
				Range	Average
51	20° continuously.....	12.1	2.0	4	4
49	20° the first 5 days, 15° the last 2 days, of each week..	8.2	4.1	5	5
48	20° the first 5 days, 10° the last 2 days, of each week..	11.1	0
46	20° the first 6 days, 10° the last day, of each week.....	17.8	0

* Parent generation and incubation at 20° C larvae reared on chicken mash in the dark.

standard rearing temperature during larval growth, in all experiments in which the effect of various factors on the induction of diapause was investigated.

Dropping temperature during larval growth was tried as a means of inducing diapause in *Plodia* larvae. Some of the temperatures and various combinations of temperatures in °C, that were tested, were as follows:

25° continuously, throughout larval growth.

25° first two weeks, 15° for the remainder of larval growth.

25° first 11 days, 20° next three days, 15° for the remainder of larval growth.

25° first week, 20° second week, 15° for the remainder of larval growth.

25° first week, 20° second week, 15° third week, 10° for the remainder of larval growth.

20° continuously, throughout larval growth.

20° first three weeks, 15° for the remainder of larval growth.

20° first two weeks, 15° for the remainder of larval growth.

15° continuously throughout larval growth.

The above situations were not able to induce diapause, when the eggs had been incubated at 20° C. However, when the eggs were held at temperatures of 25° C or higher, some diapause resulted from all of the above temperatures and temperature combinations, except the one where larval growth took place at 25° C.

In order to study the effect of relatively short exposures to mildly low temperatures during larval growth on inducing diapause, the following experiment was conducted. Larvae of the Berkeley stock, from eggs that had been incubated at 20° C were reared continuously at 20° C or exposed to lower temperatures for one or two days per week. The rearing temperatures and the results are given in table 11. The data showed that no diapause was induced in larvae reared at 20° C and exposed for one or two days per week to 10° C. However, a slight amount of diapause occurred in larvae reared continuously at 20° or reared at 20° and exposed to 15° for two days per week, during their larval growth. It is interesting to note that where diapause took place, it was of a very weak intensity. Because of the very weak

intensity, combined with the very low percentage of diapause in these two groups of larvae, it can be concluded that the incidence of diapause was practically nil. Under the conditions of the experiment, the results demonstrated that rather short exposures to mildly low temperatures during larval growth at 20° C were not inductive to diapause.

Influence of Temperature During Incubation. Because the various combinations of temperature during larval growth failed to prove effective in inducing diapause, attention was focused upon the stages that precede hatching, namely the incubation period, and the parent generation stages. In one experiment, larvae of the Berkeley stock were reared under three different temperatures, 20° C, 25° C, and 30° C. Upon pupation those reared at each temperature were divided into three equal groups. Each of these latter groups was subsequently held, throughout the pupal and adult stage, as well as during the incubation period of the progeny, at either 20°, 25°, or 30° C. The progeny of each group, upon hatching, were transferred to and held during larval growth at 20° C and 58 per cent R.H. under either continuous darkness or a photoperiod of 12 hours light per day. The information obtained is given in table 12. It is seen that temperature, from parent pupation to hatching of progeny, seemed to be quite important in determining the incidence of diapause in the progeny. A temperature of 30° C caused a rather high percentage of the larvae to enter a profound diapause; 25° C resulted in a smaller percentage and less profound diapause, and 20° C induced no diapause at all. This effect was most pronounced in the progeny reared in continuous darkness. In general, the higher the temperature during the period from parent pupation to hatching of progeny, the higher the percentage and the intensity of diapause in the progeny.

The above experiment established the importance of temperature that preceded hatching on the induction of diapause in *Plodia* larvae. In order to determine at what particular stage, within the pupation-to-hatching period, high temperature exerts its influence, the following experiment was conducted: The pupal stage and the adult stage of the parents, and the egg stage of the progeny, were each held at 20° and 30° C and in all possible combinations of these two temperatures. The larvae (progeny) upon hatching were placed at 20° C and 58 per cent R.H. and held during larval growth either continuously under a photoperiod of 12 hours of light per day, or under the above photoperiod for the first two weeks of larval growth, and in continuous darkness for the rest of that period. The results of this experiment are given in table 13. The information shows that temperature was influential only during the incubation period, and not during the parent generation. Thus, by incubating the eggs at 30° C and rearing the larvae at 20° C it was possible to induce a high per cent of diapause. However, if the larvae were reared at 25° C, instead of 20° C, diapause did not occur, no matter how high the temperature during the incubation period. It seems, therefore, that the diapause-inducing effect of high temperature during incubation is destroyed if temperature is maintained at a high level throughout larval growth.

Although, as in the preceding experiment, photoperiod during larval growth seemed to have some influence on diapause, discussion of this is given in the section on photoperiod, which follows.

TABLE 12

THE EFFECT OF TEMPERATURE DURING THE PARENT GENERATION AND PRIOR TO HATCHING ON THE INDUCTION OF DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK REARED AT 20°C AND 58 PER CENT R.H. UNDER TWO DIFFERENT LIGHT CONDITIONS

Parents		Progeny									
Temperature during larval stage, °C	Temperature from parent pupa to hatching of progeny, °C	Continuous darkness					12 hrs light per day				
		Number of individuals	Per cent mortality during larval growth	Diapause		Number of individuals	Per cent mortality during larval growth	Per cent	Diapause		Average
				Per cent	Intensity in days				Per cent	Intensity in days	
20	20	64	8.6	0	67	4.3	0
20	25	57	0.7	28.0	3-106	21.6	72	0	1.4	4	4.0
20	30	55	12.7	94.6	22-128	75.5	63	0	14.3	43->122	>93
25	20	36	12.0	0	51	2.0	0	0
25	25	57	0	24.6	6-135	41.2	58	4.9	5.2	6-54	24.0
25	30	78	0	91.1	3->137	>77	71	9.0	36.6	5->134	>80
30	20	71	6.6	0	93	0	0
30	25	75	1.3	16.0	6->143	>83	70	5.4	7.1	7-22	12.4
30	30	55	6.8	98.3	21->143	>78	45	13.4	88.9	7->141	>90

TABLE 13

THE EFFECT OF TEMPERATURE FROM PUPATION OF PARENTS TO HATCHING, ON INDUCING DIAPAUSE IN *PLODIA*
LARVAE OF THE BERKELEY STOCK REARED AT 20°C AND 58 PER CENT R.H. UNDER TWO
DIFFERENT LIGHT CONDITIONS*

Parents		Progeny											
Temperature, °C		Light conditions during larval development											
Pupa	Adult	Incubation temperature, °C	12 hrs. light per day					12 hrs. light per day first 2 weeks. Continuous darkness remainder of time					
			Number of individuals	Per cent mortality during larval growth	Diapause		Per cent	Number of individuals	Per cent mortality during larval growth	Diapause		Per cent	Average
Range	Intensity in days	Range			Intensity in days	Range				Intensity in days			
20	20	20	69	8.0	0	71	5.3	7.0	6-45	22.8
20	20	30	43	21.8	69.8	3->47	>40	>40	36	34.5	91.7	26->44	>42
20	30	20	59	15.7	0	59	15.7	0
20	30	30	53	13.1	56.6	7->50	>43	>43	53	13.1	90.5	3->47	>43
30	20	20	67	4.3	3.0	9-34	21.5	21.5	66	5.7	15.2	6->54	>23
30	20	30	38	13.6	57.9	13->51	>45	>45	36	12.2	94.4	32->51	>49
30	30	20	63	6.0	3.2	29->50	>39	>39	65	3.0	7.7	10-54	16.0
30	30	30	66	12.0	71.2	51->60	>56	>56	66	12.0	100.0	43->57	>54

* Parent larvae reared at 30° C and 80 per cent R.H. in the dark.

TABLE 14

THE INFLUENCE OF HOLDING CONDITIONS FROM PARENT PUPATION TO HATCHING, AND OF VARIOUS LIGHT CONDITIONS DURING LARVAL GROWTH ON THE INDUCTION OF DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK WHEN THE LARVAE WERE REARED AT 20°C AND 58 PER CENT R.H.

Conditions from pupation of parents to hatching*	Num-ber of indi-viduals	Illumination during larval growth	Diapause			Per cent mortality during larval growth
			Per cent	Intensity on days		
				Range	Average	
20° C, 58% R.H., darkness.....	41	Continuous darkness.....	2.4	21	21	14.6
20° C, 58% R.H., darkness.....	39	12 hrs. light first two weeks, Darkness rest of time.....	0	18.7
20° C, 58% R.H., darkness.....	39	12 hrs. light per day.....	0	7.1
30° C, 45% R.H., darkness.....	56	Continuous darkness.....	94.6	10->80	>62	3.4
30° C, 45% R.H., darkness.....	55	12 hrs. light first two weeks, Darkness rest of time.....	92.7	16->77	>62	6.8
30° C, 45% R.H., darkness.....	52	12 hrs. light per day.....	38.5	8->72	>68	10.4
30° C, 80% R.H., darkness.....	70	Continuous darkness.....	95.7	16->80	>68	0
30° C, 80% R.H., darkness.....	62	12 hrs. light first two weeks, Darkness rest of time.....	79.0	6->80	>68	4.6
30° C, 80% R.H., darkness.....	59	12 hrs. light per day.....	72.9	13->77	>73	15.7

* Parent larvae reared at 20° C, and 58 per cent R.H. in the dark.

The Relation of Photoperiod to Induction of Diapause

Influence of Photoperiod During Larval Growth. It was often observed, in the present investigation, that the percentage of larvae entering diapause tended to be higher in groups reared in the dark. To secure additional information on this subject a number of experiments were conducted.

In the first of these, groups of larvae from eggs incubated at 20° C and

TABLE 15

THE EFFECT OF VARIOUS LIGHT CONDITIONS DURING LARVAL GROWTH ON THE INDUCTION OF DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK, FROM EGGS INCUBATED AT A TEMPERATURE UNFAVORABLE FOR DIAPAUSE*

Number individuals	Photoperiod during larval growth (Hours of light per day)	Diapause			Per cent mortality during larval growth
		Per cent	Intensity in days		
			Range	Average	
57	12 hrs during first 2 weeks, 8 hrs third week, 0 hrs fourth to fifth week.....	1.8	9	9	12.3
67	12 hrs during first 2 weeks, 8 hrs third to fifth week.....	9.0	3-50	22.8	5.6
64	12 hrs during first 2 weeks, 0 hrs third to fifth week.....	0	7.2
59	12 hrs during first 4 weeks, 8 hrs fifth week.....	0	10.6
59	12 hrs during first 4 weeks, 0 hrs fifth week.....	0	4.8
66	12 hrs during first 3 weeks, 8 hrs fourth to fifth week.....	1.5	52	52	7.0
56	12 hrs during first 3 weeks, 0 hrs fourth to fifth week.....	0	9.7
61	12 hrs continuously (control).....	0	9.0
64	8 hrs during first 2 weeks, 0 hrs third to fifth week.....	0	7.2
59	8 hrs during first 4 weeks, 0 hrs fifth week.....	5.1	22-95	52.3	9.2
54	8 hrs continuously (control).....	1.9	13	13	10.0
65	0 hrs continuously (control).....	3.1	9-12	10.5	5.8

* The larvae were reared at 20° C and 58 per cent R.H.

30° C were reared at 20° C under three different conditions of light. Information on the experimental procedure and the results are shown in table 14. The percentage of diapause that resulted from each of the combinations tested showed that: 1) When both the incubation temperature and the rearing temperature were 20° C (a combination not favoring diapause), light conditions exerted no visible effect in inducing diapause. 2) When the incubation temperature was 30° C and the larval rearing temperature 20° C (a combination inducing diapause), the per cent of diapause varied with the light conditions. In general, continuous darkness throughout larval growth, or at least during the latter half of it, was more inductive to diapause than a photoperiod of 12 hours light per day throughout larval development. It should be noted that a 12-hour photoperiod during the first half of larval growth had little effect upon discouraging diapause, if the latter half of larval development was in total darkness. These conclusions are further sub-

TABLE 16

EFFECT OF LIGHT CONDITIONS PRIOR TO HATCHING ON INDUCING DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK REARED AT 20°C AND 58 PER CENT R.H. UNDER TWO DIFFERENT LIGHT CONDITIONS

Light conditions preceding hatching*		Light conditions during larval growth of progeny							
		Continuous darkness			12 hrs light per day				
From hatching to pupation of parents	From parent pupation to hatching of progeny	Number of individuals	Per cent mortality during larval growth	Diapause		Per cent mortality during larval growth	Diapause		
				Per cent	Intensity in days		Per cent	Intensity in days	
				Range	Average			Average	
Continuous darkness . . .	Continuous darkness . . .	58	4.9	8.6	6-9	6.7	3.3	16-78	47.0
Continuous darkness . . .	Natural photoperiod . . .	35	5.4	5.7	8-109	58.5	2.1	9	9.0
Natural photoperiod . . .	Continuous darkness . . .	44	0	4.6	19-46	32.5	6.8	9-67	38.0
Natural photoperiod . . .	Natural photoperiod . . .	59	7.8	20.4	3-31	13.3	6.9	3-58	19.0

* At a room temperature averaging 22° C. during the period June 1 to July 18, 1958.

stantiated by the data presented in tables 12 and 13. The information given in these tables clearly shows that the photoperiod during larval growth exerted an influence on the per cent of diapause. It seems, therefore, that light, particularly during the latter part of larval growth tends to discourage diapause in *Plodia* larvae.

In another experiment on the influence of light on inducing diapause, a wider range of light conditions was investigated. In this experiment, larvae that had no tendency to diapause (held at 20° C during incubation) were reared on chicken mash at 20° C and 58 per cent R.H., under varying light conditions. The light conditions and the results obtained are shown in table 15. In six of the light conditions investigated, no diapause whatsoever occurred, while in the other six, only an occasional larva diapaused. In all cases the intensity of diapause was of a low level. The information given in the table supports the conclusion that none of the light conditions tried induced diapause to any considerable extent in larvae that had no tendency to diapause.

The data presented in tables 14 and 15 and the additional information obtained during the course of the present investigation showed that light conditions during larval growth had little influence on diapause, unless the insects were reared under temperature conditions favorable for diapause. However, where temperature conditions favored diapause, photoperiod exerted a pronounced effect. Darkness, particularly during the latter half of larval growth, was the condition most favorable to diapause. It would then appear that while light in itself was unable to induce diapause, it was able to reduce the tendency of this occurring.

Influence of Photoperiod Prior to Hatching. The influence of light conditions prior to hatching on inducing diapause was studied very little during the present investigation. In the only experiment that was conducted to this end, two groups of larvae (parent generation) were held during larval growth at room temperature. One group was exposed to daylight of a natural photoperiod and the other was held in continuous darkness. Upon pupation each group was divided into two smaller groups, one of which was exposed to the natural photoperiod and the other held in the dark through the hatching of progeny. Upon hatching, the larvae of each group were transferred to 20° C where they were held under two different light conditions throughout the larval growth, as shown in table 16. The data obtained from this experiment show that the percentage of diapausing larvae was generally very low, except the group that was exposed continuously to natural photoperiod from hatching of parents to hatching of progeny and where the larvae (progeny) were reared in the dark. However, the per cent of diapause in this group can probably be accounted for by the variable incubation temperature which averaged 22° C. If we also take into consideration the generally low intensity of diapause in most groups, we may reasonably accept the fact that there was no clear evidence of diapause induction in favor of any of the four light conditions tested. Further investigation, however, will be needed before any reliable conclusion can be reached with regard to the influence of photoperiod prior to hatching, and particularly in the incubation period, during which temperature proved to be so important in inducing diapause.

BREAKING OF DIAPAUSE

The breaking or termination of diapause in insects has been the subject of numerous papers. The environmental factors of importance in connection with the breaking of diapause in insects have been discussed earlier in the section on diapause. The influence on *Plodia interpunctella* of some of these factors, including low and high temperatures, wounding, and respinning of hibernaculum, was investigated.

Exposure to Mildly Low Temperatures. It was demonstrated earlier that exposure to low temperatures was not necessary for the normal termination of diapause in the Indian-meal moth. An experiment, however, was conducted

TABLE 17

THE EFFECT OF EXPOSURE TO 10° AND 20°C FOR 14 WEEKS ON BREAKING DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK

Number of diapausing larvae	Treatment	Number of individuals surviving treatment	Number of days spent in diapause at 25° C following treatment	
			Range	Average
34	10° C for 14 weeks.....	33	9-38	17.2
31	20° C for 14 weeks.....	30	9-111	17.1

to determine whether exposure to a low temperature, followed by normal developmental temperatures would bring about an earlier and somewhat simultaneous breaking of diapause, as in many other insect species. In this experiment diapausing larvae of the Berkeley stock, that had been reared on chicken mash, were divided into two groups. One of these was held at 10° C and the other at 20° C for 14 weeks, and then both were transferred to 25° C. Pupation at 25° C was recorded at three-day intervals. The information is presented in table 17. It is seen that, on an average, there was no difference in time of pupation between the two groups. The range of the number of days spent in diapause following treatment, however, in the group exposed to 10° C was less, which might indicate that diapause was broken more simultaneously in this group. This conclusion should be taken with a certain reservation, because only two larvae were responsible for the wider range that occurred in the group held at 20° C. Thus, out of 30 larvae, 28 pupated within 21 days, 1 in 53 days, and 1 in 111 days. Although further experimental evidence with larger numbers of larvae would be desirable, it may be concluded that exposure to 10° C for 14 weeks was about in the same range of effectiveness in breaking diapause in *Plodia* larvae, as was exposure to 20° C for an equal period.

Exposure to Temperatures Below Freezing. In order to determine the effect of below-freezing temperatures on breaking diapause, an experiment was performed in which diapausing larvae of the Berkeley stock were exposed to -5° C for varying periods of time. Following this exposure, the larvae were successively transferred at 24-hour intervals to 0°, 5°, 12°, 20°, and finally to 25° C, at which temperature they were held. Pupation of the individuals surviving was recorded weekly. The periods of exposure to -5°

are given in table 18. The results show that exposure to -5°C for various periods, including lethal ones, did not result in an earlier termination of diapause. Other observations made during the course of the investigation, in addition to those given in table 18, also tend to substantiate the above conclusion.

TABLE 18

THE EFFECT OF EXPOSURE TO -5°C FOR VARYING PERIODS, ON BREAKING DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK, THAT WERE REARED AT 20°C AND 58 PER CENT R.H.

Days of exposure to -5°C	Number of larvae surviving exposure to -5°C *	Cumulative pupation of larvae at 25°C in 3 periods of 5 weeks each*			Number of larvae still in diapause after 15 weeks	Number of larvae that died during first 15 weeks
		First 5 weeks	Second 5 weeks	Third 5 weeks		
0	12	2	3	4	4	4
2	12	3	5	7	3	2
4	12	8	9	9	3	0
6	12	5	5	7	3	2
10	11	5	5	6	2	4
20	0
0	12	4	6	8	3	1
2	12	4	5	8	2	2
4	12	2	3	5	6	1
6	12	7	8	8	3	1
10	12	2	5	6	3	3
20	3	0	0	0	0	3
30	0

* Out of a total of 12 larvae.

TABLE 19

THE EFFECT OF EXPOSURE TO -18°C FOR VARYING PERIODS ON BREAKING DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK, WHICH WERE REARED AT 20°C AND 58 PER CENT R.H.

Minutes of exposure to -18°C	Number of larvae surviving exposure to -18°C	Cumulative pupation of larvae at 25°C in 2 periods of 5 weeks each*		Number of larvae still in diapause after 10 weeks	Number of larvae that died during first 10 weeks
		First 5 weeks	Second 5 weeks		
0.....	12	10	10	2	0
1.....	12	7	8	2	2
5.....	12	10	10	0	2
20.....	12	6	10	2	0
60.....	12	2	2	0	10
90.....	0

* Out of a total of 12 larvae.

In a second experiment the influence of exposure to -18°C for various periods on breaking diapause in diapausing larvae was investigated. The experimental procedure in bringing the larvae to the holding temperature of 25°C was the same as followed in the previous experiment. The data, which are given in table 19, show that exposure to -18°C for from 1 to 60 minutes failed to break diapause. This conclusion must, however, be accepted with certain reservations, because diapause was not profound in the

majority of the larvae used in the experiment, as shown by the fact that most of the individuals in the check pupated within the first 5 weeks of this experiment.

Exposure to High Temperatures. High temperatures were employed in an attempt to break diapause in the Indian-meal moth. Three experiments were conducted in which diapausing larvae, that had been held at 25° C,

TABLE 20
THE EFFECT OF EXPOSURE TO 50° C FOR VARYING PERIODS ON BREAKING DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK

Minutes of exposure to 50° C	Number of larvae surviving exposure to 50° C*	Cumulative pupation of larvae at 25° C in 2 periods of 5 weeks each*		Number of larvae still in diapause after 10 weeks	Number of larvae that died during first 10 weeks
		First 5 weeks	Second 5 weeks		
Experiment A					
0 (check).....	12	5	9	2	1
5.....	12	6	10	0	2
10.....	12	9	9	3	0
20.....	12	11	11	1	0
Experiment B					
0 (check).....	12	0	2	10	0
20.....	12	6	6	5	1
40.....	0
60.....	0
Experiment C					
0 (check).....	12	0	1	11	0
10.....	12	0	1	11	0
20.....	12	1	1	10	0
30.....	12	0	0	12	0
40.....	12	0	1	11	0
60.....	6	0	..	0	6

* Out of a total of 12 larvae.

were exposed to 50° C and 52 per cent R.H. for varying periods. The larvae were subsequently returned to 25° C and 53 per cent R.H., and pupation of those surviving the treatment was recorded weekly. The information obtained is presented as experiments A, B, and C, in table 20.

The results of experiment A show that exposure to 50° C for from 5 to 20 minutes resulted in an increase in pupation over the check, during the first five-week period. Further, the longer the exposure to 50° C the larger the number of larvae that pupated during the first five-week period. During the second five-week period, however, additional pupation took place only in the check and in the group exposed to 50° C for only 5 minutes. The results seem therefore to indicate that exposure to 50° C was effective in breaking diapause only when diapause was of low intensity.

In experiment B, exposures to 50° C for from 20 to 60 minutes were investigated, but the 40- and 60-minute exposures proved to be lethal. The

intensity of diapause in the larvae of this experiment was greater than in experiment A, as indicated by the fact that no larvae pupated in the check during the first five-week period. The results again show that exposure to 50° C for 20 minutes was effective in breaking diapause in some of the larvae.

In experiment C, larvae in intense diapause were exposed up to 60 minutes to 50° C. The results with this group, however, indicate that exposure to 50° C for up to 60 minutes was not effective in breaking diapause. It is worth noting that these larvae in intense diapause were also more heat-hardy than the larvae of experiment B, which had a less intense diapause.

TABLE 21
THE EFFECT OF WOUNDING ON BREAKING DIAPAUSE IN *PLODIA*
LARVAE OF THE BERKELEY STOCK

Number of larvae	Treatment	Number of larvae that survived	Cumulative pupation at 25° C, in two periods of 5 weeks each		Number of larvae still in diapause after 10 weeks	Number of larvae that died during first 10 weeks
			First 5 weeks	Second 5 weeks		
Experiment A						
42	Wounded lightly once.....	42	37	38	0	4
42	Control.....	42	31	31	3	8
Experiment B						
36	Wounded heavily once....	5	5	5	0	31
36	Wounded heavily three times.....	9	8	8	1	27
36	Control.....	36	5	10	26	0

The results of these three experiments seem to indicate that when diapause was of low intensity, exposure to 50° C had some effect on breaking diapause in some larvae. When, however, diapause was of high intensity, such exposure did not exert any effect. The whole subject is, therefore, in need of further investigation.

Wounding. Two experiments were designed in order to determine the effect of wounding on breaking diapause in *Plodia* larvae. Wounding was effected with a dissecting needle whose point was heated until it was red hot.

In the first experiment the larvae were lightly scorched on the right metathoracic leg. After wounding, the larvae were placed at 25° C and 53 per cent R.H., and pupation was recorded weekly. The results of this experiment are presented as experiment A in table 21. The information shows that wounding was not effective in breaking diapause. It should be noted, however, that the intensity of diapause was rather low, as shown by the number of individuals that pupated in the control during the first five weeks.

In the second experiment wounding was effected as above, but was much more severe. Two groups of larvae were wounded. In one group of 36 diapausing larvae, scorching was applied once to the right metathoracic leg. In the other group, each larva was wounded in three parts of the body,

namely the right metathoracic leg, the pleuron of the third abdominal segment, and the dorsum of the last abdominal segment. The experimental method, following wounding, was the same as given in experiment A. The information obtained is shown under experiment B in table 21. It is seen that the severe wounding resulted in a high mortality. However, in the few larvae that survived, diapause was broken. Within five weeks, the majority or all of the larvae that survived the heavy wounding pupated, as opposed to only a relatively small number in the case of the control.

Although further experimental evidence on this subject is desirable, the information obtained from the above experiments indicates that wounding so severe as to cause high mortality, tended to break diapause in those larvae that survived the treatment.

Repeated Respinning of Hibernaculum. Theron (1943) reported that he succeeded in breaking diapause in codling moth larvae by removing them from their hibernacula, and forcing them to respin in fresh corrugated paper. The majority of his larvae pupated after the third or fourth respinning. In the present investigation diapausing larvae of *Plodia interpunctella*, that had spun their hibernacula in corrugated paper, were placed at 25° C and 53 per cent R.H. in the dark. At weekly intervals their hibernacula were torn and partially or wholly removed. The larvae had the tendency to respin the destroyed hibernaculum on the spot, or to leave the old gallery and spin anew in another gallery of the corrugated paper. Some larvae were more active in respinning than others. A few would not respin immediately, but wandered about in the jar for a week or more before settling again in the corrugated paper. The results of such repeated respinning on breaking diapause are presented in table 22. It is seen that repeated respinning had a tendency to break diapause in *Plodia* larvae. During the first five-week and second five-week periods, about three times as many individuals pupated in the respinning group as in the control. After 15 weeks, only one larva in the respinning group was still in diapause, while in the control 13 larvae remained in diapause.

TEMPERATURE ACCLIMATIZATION AND COLD-HARDINESS

The various aspects of the lethal action of low temperature on insects and other animals have been the subject of much study by various workers, and have recently been discussed by Andrewartha and Birch (1954).

Insects living in temperate regions usually have a stage in their life cycle which is more resistant to low temperatures than the other stages. This also is generally the stage in which winter diapause occurs, and the stage in which the species passes the winter. In the case of *Plodia interpunctella*, it has been demonstrated that this stage is the mature larva.

Mellanby (1939) has shown the importance of temperature acclimatization in modifying the "chill-coma temperature" in a number of insects of medical importance, and the "cold-death point" in the oriental cockroach. He concluded that acclimatization with regard to cold-hardiness is fairly rapid, and that 20 to 24 hours are enough for such an acclimatization, although he pointed out that the temperature where death occurs after long chilling,

(as opposed to freezing), may be altered by previously keeping the insects at different temperatures.

Although the cold-hardiness of the Indian-meal moth has been reported upon by other workers, including Cotton and Wagner (1941), a few experiments were conducted during the present investigation to determine the influence of temperature acclimatization on the cold-hardiness. Specifically studied were the action upon mature larvae and the possible differences in cold-hardiness between diapausing and nondiapausing mature larvae. In all cases, after exposure to low temperatures, the larvae were successively

TABLE 22
THE EFFECT OF REPEATED RESPINNING OF HIBERNACULUM ON BREAKING DIAPAUSE IN *PLODIA* LARVAE OF THE BERKELEY STOCK

Treatment	Cumulative pupation at 25° C in three periods of 5 weeks each*			Number of larvae still in diapause after 15 weeks*	Mortality during first 15 weeks*
	First 5 weeks	Second 5 weeks	Third 5 weeks		
Respinning weekly.....	14	27	33	1	2
Control.....	5	10	23	13	0

* Out of a total of 36 larvae.

transferred, at 24-hour intervals, to 0°, 5°, 12°, 20°, and 25° C. Mortality counts were made 24 hours after the larvae were brought to 25° C.

The data presented in tables 23, 24, and 25, which are substantiated by the results of additional experiments not presented, show that nondiapausing larvae acclimatized at 5° C survived longer exposures to -5° C, and were able to pupate normally when nonacclimatized larvae could not (table 23). Larvae acclimatized at 10° C for 15 and 28 days, were more resistant to -5° C than those acclimatized for only three days (table 24), and larvae held for 16 and 44 days at 10° C were more resistant to -18° C than larvae held

TABLE 23
THE EFFECT OF ACCLIMATIZATION FOR VARIOUS PERIODS AT 5° C AND 70 PER CENT R.H. OF NONDIAPAUSING *PLODIA* LARVAE OF THE FRESNO STOCK ON THEIR SURVIVAL WHEN EXPOSED TO -5° C*

Days of exposure to -5° C	Days of acclimatization at 5° C that preceded exposure to -5° C					
	0		1		5	
	Number surviving out of 12	Number pupating out of 12	Number surviving out of 12	Number pupating out of 12	Number surviving out of 12	Number pupating out of 12
0.....	12	12	12	12	12	12
2.....	9	9	12	12	12	12
4.....	6	0	12	4	11	7
6.....	0	0	3	0	12	3
10.....	0	0	0	0	0	0
20.....	0	0	0	0	0	0

* The larvae were reared on chicken mash, at 20° C and 58 per cent R.H.

TABLE 24
THE INFLUENCE OF ACCLIMATIZATION FOR VARIOUS PERIODS AT 10°C AND 68 PER CENT R.H. OF NONDIAPAUSING *PLODIA* LARVAE OF THE FRESNO STOCK, ON SURVIVING EXPOSURES TO -5°C*

Days of exposure to -5° C	Number of larvae surviving out of 12		
	Days of acclimatization at 10° C prior to exposure to -5° C†		
	3	15	28
3.....	8	10	8
6.....	7	10	9
9.....	0	2	10
12.....	0	1	4
15.....	0	0	2

* The larvae were reared on chicken mash at 20° C and 58 per cent R.H.

† All larvae were further acclimatized for 1 day at 5°, then for 1 day at 0° C, before they were exposed to -5° C.

TABLE 25
THE EFFECT OF ACCLIMATIZATION FOR VARIOUS PERIODS AT 10°C AND 68 PER CENT R.H. OF NONDIAPAUSING *PLODIA* LARVAE OF THE FRESNO STOCK, ON SURVIVING EXPOSURES TO -18°C*

Hours of exposure to -18° C	Number of larvae surviving out of 12		
	Days of acclimatization at 10° C prior to exposure to -18° C†		
	2	16	44
2.....	3	8	12
4.....	0	8	12
6.....	0	7	12
8.....	0	4	12
10.....	0	5	12

* The larvae were reared on chicken mash at 20° C and 58 per cent R.H.

† All larvae were further acclimatized for 1 day at 5°, 0°, and -5° C, before they were exposed to -18° C.

at 10° C for only two days (table 25). In all cases the cold-hardiness of the larvae increased with the length of the acclimatization period. This indicates that adaptation of *Plodia* larvae to cold through acclimatization may not be as rapid as in other insect species which have been studied. Further, the acclimatization period appears to exert an influence beyond a 24-hour period.

Table 26 shows the cold-hardiness of diapausing and nondiapausing larvae, with and without temperature acclimatization. It is seen that the diapausing larvae were more cold-hardy, because they survived and pupated after longer exposures to -5° C than did the nondiapausing larvae. This difference in cold-hardiness due to diapause, was smaller when acclimatization to 5° C and 0° C preceded exposure to -5° C.

TABLE 26
 DIFFERENCE IN COLD-HARDINESS TO VARYING EXPOSURES TO -5°C,
 BETWEEN DIAPAUSING AND NONDIAPAUSING *PLODIA* LARVAE
 THAT WERE REARED AT 20°C AND 58 PER CENT R.H.

Days of exposure to -5°C	Larvae surviving, out of 12				Larvae pupating, out of 12			
	Exposed to -5°C directly		Exposed to -5°C after acclimatization for 1 day at 5° and 1 day at 0° C		Exposed to -5°C directly		Exposed to -5°C after acclimatization for 1 day at 5° and 1 day at 0° C	
	Diapaus- ing	Nondia- pausing	Diapaus- ing	Nondia- pausing	Diapaus- ing	Nondia- pausing	Diapaus- ing	Nondia- pausing
0.....	12	12	12	12	9	12	10	12
2.....	12	9	12	12	12	9	11	12
4.....	12	6	12	10	12	0	10	10
6.....	12	0	12	11	10	0	11	2
10.....	11	0	12	0	8	0	8	0
20.....	0	0	3	0	0	0	0	0
30.....	0	0	0	0	0	0	0	0

DISCUSSION OF RESULTS

It was mentioned earlier that Michelbacher (1953), commenting on the data presented in the papers by Hamlin *et al.* (1931), and Simmons *et al.* (1931), expressed the opinion that the Indian-meal moth hibernates as a mature larva in diapause. The present investigation has confirmed his opinion. In the Berkeley strain, facultative diapause was observed repeatedly and induced artificially. A difference in the tendency to diapause between different strains of *Plodia interpunctella* was also observed. Thus, individuals of the Fresno strain failed to diapause when exposed to environmental conditions that caused up to 28 per cent diapause in larvae of the Berkeley strain. Furthermore, conditions that caused all of the larvae of the Berkeley strain to enter a profound diapause, induced but a rather weak diapause in only one eighth of the larvae of the Fresno strain. This marked difference in the tendency to diapause between these two strains might have been even greater had a different basis for distinguishing diapausing from nondiapausing larvae been employed.⁸

Within the same strain, namely the Berkeley stock, the intensity of diapause, expressed in terms of diapause duration at 25° C, varied widely between individuals of the same group. This occurred even though the eggs were from the same parents and the larvae were reared under identical conditions. The average intensity of diapause varied also between groups of larvae exposed to different environmental conditions.

Temperature and photoperiod proved to be the important factors in inducing or preventing diapause in larvae of the Indian-meal moth. Within the range of normal developmental temperatures for this species, a constant temperature of 30° C during the incubation period, and a temperature of 20° C during larval growth, induced a profound diapause in the majority

⁸ In the present investigation mature larvae that did not pupate within three weeks, when held at 25° C and 53 per cent R.H., were considered to be in diapause.

of the larvae, while a temperature of 20° C during both incubation and larval growth prevented diapause. Diapause was also prevented by a temperature of 25° C during larval growth, even if incubation had taken place at 30° C. It seems, therefore, that for diapause to occur in *Plodia interpunctella*, a rather high temperature during incubation, and a lower temperature during larval growth were required. If temperature was low during incubation, or high during larval growth, and particularly during late larval growth, diapause did not occur.

The presence of light during larval development, and especially during the latter part of larval growth, tended to reduce diapause, while darkness tended to induce it. This effect of light, however, was noticed only when temperature during incubation and larval development allowed diapause to occur. Thus, when eggs were incubated at 30° C and the larvae reared at 20° C in the dark, a profound diapause was induced in the majority or all of the larvae. The major factor involved in inducing diapause was, however, high temperature during incubation.

To the author's knowledge, *Plodia interpunctella* represents the first instance in which high temperatures during incubation were definitely demonstrated to be responsible for inducing diapause in mature larvae. It would be particularly interesting to study this matter in other Lepidoptera associated with the Indian-meal moth, such as species of *Ephestia*, in some of which diapause is known to occur.

During the present investigation it was demonstrated that within California strains of *Plodia interpunctella* differ considerably in their tendency to diapause. From the results it is reasonable to expect that strains from northern areas with cold winters probably have a stronger tendency to diapause than does the Berkeley strain discussed in this paper. Because of the possible existence of such strains, it is risky to make generalizations and predictions on the information obtained from any given strain.

It might be worth speculating on the voltinism of the Indian-meal moth under California conditions. On the basis of the data given by Hamlin *et al.* (1931), and Simmons *et al.* (1931), and the information obtained during the present investigation, the seasonal life-history would be approximately as follows: In spring, the overwintered larvae will pupate, the adults emerge, and a sequence of generations will start, the number depending mainly on the quality and quantity of food available, and on the prevailing temperature. Spring generations will not diapause, because temperatures during incubation are not high enough to induce such a condition. During the summer, temperatures during incubation are sufficiently high, but diapause will not take place, because high temperatures will continue during late larval growth, and will prevent it. As the season progresses and the annual march of temperature goes downward, a point is reached when the eggs are incubated at a temperature sufficiently high, and the larvae grow at a temperature low enough for diapause to occur. At that time the majority of larvae will enter diapause. These larvae will overwinter in diapause, and will pupate in the spring or earlier, depending on the intensity of their diapause and on the winter temperatures. The larvae that did not enter diapause will develop into adults which will lay eggs late in the season. These eggs, which are laid when temperature during incubation is not high enough to induce

diapause, will give rise to nondiapausing larvae. These larvae will grow slowly because of low fall and winter temperature, and will usually overwinter as immature larvae, occasionally feeding and growing when temperature conditions permit. In areas where winter temperatures do not reach lethal levels, the larvae that survive will complete their growth and pupate in the spring, and will start the same sequence of generations as the overwintered diapausing larvae. Thus, in winter, two kinds of larvae are encountered: Diapausing mature larvae, and nondiapausing immature larvae which find the winter temperature high enough for their survival.

Andrewartha and Birch (1954) reviewing the subject of diapause, stated the following:

“When diapause happens to be induced by temperature or food, the same stimulus, low temperature or poor food will also cause the animal to grow more slowly, and it is therefore impossible to discover the causal relationship between slow growth and diapause.”

It has been shown, during the present investigation, that the situation in regard to diapause in *Plodia interpunctella* is different. In this insect high temperature during incubation is the stimulus inducing diapause. For this reason, the Indian-meal moth may be a useful tool in investigations involving the relationship that exists between slow growth and the occurrence of diapause.

Points Needing Further Investigation

Many interesting questions developed during the course of the present investigation. The answer to these must await further research. Following are some of the points that warrant additional study:

1. The influence of a wider range of high and low temperatures during incubation, and furthermore during each particular stage of embryonic development, on inducing diapause in *Plodia* larvae. This would be the next logical point to investigate.

2. A detailed study to determine the ranges and optima of temperatures favorable for morphogenesis and for the diapause-ending processes of this species.

3. The effect of temperature on inducing diapause in strains of *Plodia interpunctella* from other parts of the world having a climate similar to that of California.

4. The occurrence and type of diapause in strains of the Indian-meal moth which live out-of-doors in regions having cold winters, such as Utah and British Columbia.

5. The comparative susceptibility to insecticides of diapausing and nondiapausing *Plodia* larvae.

The evidence obtained during the present investigation illustrates how complex and intricate are the environmental factors inducing diapause. As many authors have pointed out, extensive studies are still needed before the phenomenon of insect diapause is fully understood. This will require the work of both insect ecologists and physiologists.

SUMMARY

The Indian-meal moth, *Plodia interpunctella* (Hübner), is an important pest of stored food products, especially dried fruit and nuts in California, and many other parts of the world. Many authors believe that this species, which in certain areas may complete several generations per year, will grow and breed continuously when held under conditions favorable for growth. Some experimental data, however, obtained in California, suggested that late in the season, the insect may enter a facultative diapause as a mature larva. The present investigation has shown that this actually occurs.

For diapause to take place the following conditions were required: a) a temperature of 25° C or higher during incubation of the eggs, and b) a temperature of 20° C or lower especially during the latter part of larval growth. Under temperature conditions favorable to diapause, continuous darkness, particularly during late larval growth, increased the tendency of the larvae to diapause.

Investigations were conducted with two different strains of *Plodia interpunctella* obtained in California, and it was found that the two strains exhibited a marked difference in the tendency to diapause. Regardless of the strain, a wide variation in the intensity of diapause was observed. The duration of diapause depended upon the intensity of diapause and on temperature. The lower the diapause intensity and the higher the temperature, the shorter the duration of diapause. The intensity of diapause and, therefore, the duration of diapause varied between groups that were reared under different conditions. More important was the fact that under the same conditions, it varied greatly between individuals from the same parents.

Low temperatures were not required for the normal termination of diapause, although a mildly low temperature of 10° C for a sufficient period, was about as favorable for breaking diapause as was a temperature of 20° C. Wounding of the larvae, and repeated respinning, had some effect on breaking diapause. Exposures to -5°, -18°, and +50° C for varying periods had little or no effect on breaking diapause.

On an average, diapausing larvae grew slower than nondiapausing individuals. However, some of the slowest growing specimens were nondiapausing larvae.

The investigation indicated that throughout much of California diapause occurs in the fall, probably because temperature during incubation of the eggs is sufficiently high to induce diapause, and later, during larval growth, sufficiently low to allow diapause to occur.

Temperature acclimatization increased the cold-hardiness of both diapausing and nondiapausing individuals. However, diapausing larvae were more cold-hardy than nondiapausing larvae of the same strain.

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