

# SEASONAL CHANGES IN THE MODE OF DIAPAUSE IN THE PUPAE OF *ABRAXAS MIRANDA* BUTLER (LEPIDOPTERA : GEOMETRIDAE)

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## INTRODUCTION

The geometrid moth, *Abraxas miranda*, displays a complicated seasonal history. According to observations made at Tsu, the moth is bivoltine, and the larvae of the first generation feed in early summer, becoming mature before the hottest season. The ensuing pupae enter aestivation, resume to develop after two or three months, and emerge as the moth in autumn. Their progeny show a great diversity in the manner of overwintering. Some of them pupate in autumn and hibernate as pupae; others give rise to pupae in winter and pass the rest of the season in this stage; and still others continue to feed as larvae during the cold months and metamorphose in the next spring. The moths emerge almost synchronously in the spring despite this diversity. The length of the pupal stage thus varies strikingly with varying season of pupation, being probably controlled by diapause. Here is the key point to analyse the intricate seasonal history of this evergreen-feeder, though the matter is obviously far from simple.

In many insects the seasonal regulation of the life cycle is achieved by two phases of events involved in diapause. One is the timing of its onset and the other the timing of its completion. As regard to the first point, it has already been made clear that *Abraxas miranda* responds to the length of day in such a particular fashion that it deserves to be called a 'short-day' insect, and the reader is referred to a previous work for the detail of this story (MASAKI, 1958). The object of the present article is to trace the mode of completion of diapause in the pupae occurring at different seasons throughout the annual cycle of this moth.

## MATERIAL AND METHODS

All experiments and observations described in this paper were carried out at Tsu. The source of material, the methods of rearing the insects, and all other procedures were the same as stated in previous papers (MASAKI, 1957, 1958). The detail of these will be mentioned where it is necessary.

## RESULTS

(i) *Seasonal variation in the length of pupal stage in the insectary*

At the outset of the investigation, the moth was reared successively under approximately natural conditions in an insectary in 1956-7 and the development of the pupae that had been raised at different seasons was observed throughout the year. The weekly mean of temperature was from 2 to 3°C. higher in the insectary than out-of-doors, but the seasonal cycle was only a little different from that observed in the field.

The larvae of the summer generation pupated from the beginning of June to the middle of July. The resulting pupae were grouped according to the date of pupation and the emergence of the moths was observed daily. The results are presented in figure 1. Under the natural conditions of the insectary, the length of pupal stage varied from about two to three months. It decreased gradually as the pupae were formed later and the moths emerged in the latter half of September from all age-groups of pupae. The mean temperature during the pupal stage was from about 22 to 25°C. in different groups.

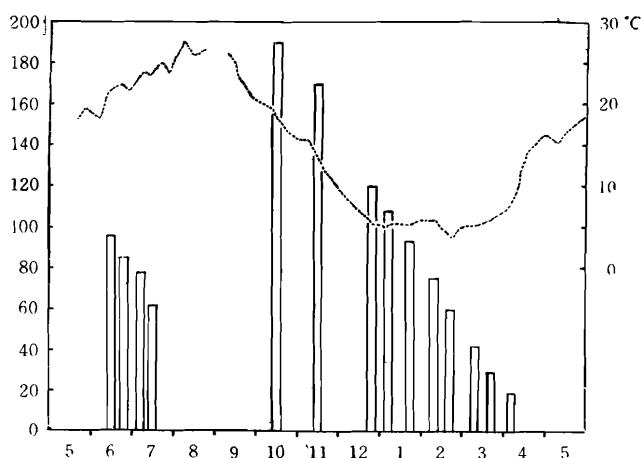


FIG. 1. The relation between the length of pupal stage and the date of pupation in *Abraxas miranda*. Ordinate, the length of pupal stage in days; abscissa, dates of pupation. Dotted line indicates the weekly mean of temperature in the insectary where the moth was bred throughout.

The larvae of the winter generation pupated from the end of October to the middle of April. The length of their pupal stage varied strikingly as shown in figure 1. The pupae occurring in October persisted as long as about 190 days; as the pupae had been raised later, they required a shorter time to develop, and those that had pupated in April emerged as moths in about 22 days. Because of this progressive shortening in the pupal stage, the moths emerged synchronously from the middle of April

to the beginning of May. The mean temperature during the pupal stage was from 7 to 16°C. in different age-groups.

(ii) *The length of pupal stage at different temperatures in the summer generation*

In the summer of 1957, the pupae that had been bred in the insectary were divided by the date of pupation, and one series of such groups was kept at 15°C. in a cool cabinet provided with an electric heating and chilling system. The other series was kept at 25°C. in a constant temperature cabinet, but the room temperature exceeded this value in the height of summer and so all the pupae could not be kept in precisely identical conditions.

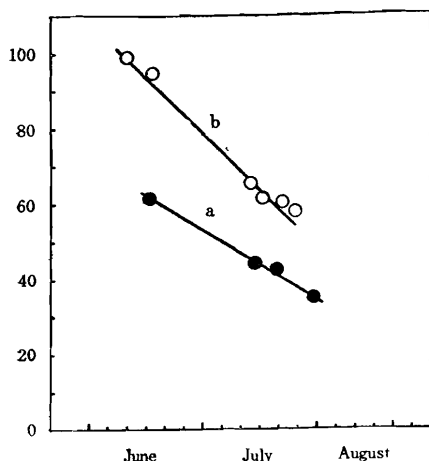


FIG. 2. The length of aestivating pupal stage at 15°C. (a) and about 25°C. (b). Ordinate, the length of pupal stage in days; abscissa, dates of pupation. The points represent means of each 28-63 pupae.

In figure 2 presented is the relation between the length of pupal stage and the date of pupation at the two temperatures. The same tendency can be seen in both series: diapause was reduced in length as the pupae were formed later in the summer. This decrease in the length or intensity of diapause was presumably responsible for the progressive shortening of the pupal stage that has been observed in the insectary. In addition to this, low temperature in autumn apparently accelerated the emergence of the moth, thus shortening the pupal stage in the later season. Such an effect of low temperature has been pointed out elsewhere and is further confirmed by the present results. Throughout the experiments the pupae completed development in a considerably shorter time at 15°C. than at the higher temperature. By subtracting the duration

of nondiapause development from that of aestivating pupae, it is inferred that aestivation diapause lasted about 10-37 days at 15°C. and 45-85 days at 25°C.

(iii) *The effect of high temperature before or after low-temperature treatment upon the completion of aestivation diapause*

As stated above the duration of aestivation diapause was much shortened by a low temperature, and extreme individuals developed in a very short time at 15°C. so that it was even doubtful if a real diapause was involved. It was therefore suspected that, at least in such pupae, aestivation was a state of heat torpor which did not take place at all at the low temperature. In order to confirm this point, the following experiments were undertaken.

TABLE 1. *The effect of high temperature after low-temperature treatment upon the completion of aestivation diapause in the pupae of Abraxas miranda.*

Days kept at 15°C.	Diapause-free		Diapausing	
	Days required to emerge at 22-28°C. Mean (range)	Number of moths that emerged	Days required to emerge at 22-28°C. Mean (range)	Number of moths that emerged
0	—	0	83.3 (80-90)	31
4	—	0	82.2 (76-86)	27
18	12.4 (11-14)	10	70.0 (62-81)	23
35	8.7 (4-15)	31	—	0
49	0.3 (-10-7)*	40	—	0
Till emergence			50.1 (40-64)	46

\* Moths began to emerge before being transferred to 22-28°C.

Batches of the aestivating pupae that had been raised in May-June were at first exposed to 15°C. for different periods, then transferred to the room temperature of 22-28°C. and the emergence of the moth was observed daily. The results are summarized in table 1. As judged from the number of diapause-free pupae after being transferred to the room temperature, diapause seems to be completed between 18th and 35th day at 15°C. This does not disagree with the results obtained by subtracting the length of pupal stage of the nondiapausing insect from that of the aestivating one. Furthermore, when pupae had been previously kept at the low temperature for an adequate period, they could complete metamorphosis in a short time even in the height of summer.

TABLE 2. *The effect of high temperature before low-temperature treatment upon the completion of aestivation diapause in the pupae of Abraxas miranda.*

Days kept at 22-28°C.	Days required to emerge at 15°C. Mean (range)	Number of moths that emerged	Total length of pupal stage. Mean
0	55.1 (48—68)	67	55.1
18	43.5 (35—66)	47	61.5
32	35.6 (32—48)	42	67.6
49	34.3 (32—39)	32	83.3
63	25.9 (22—30)	20	88.9
81	25.7 (21—30)	14	106.7
Till emergence	—	34	95.7

In the next series, aestivating pupae were first kept at the room temperature ranging from 22 to 28°C. for different periods and then removed to 15°C., at which they were kept until they emerged as the moth. This was designed in order to detect the the progression of diapause development at the room temperature in summer. If diapause development proceeded at a low but still perceptible rate throughout aestivation, the moths would emerge in a shorter time after being transferred to 15°C. in proportion to the length of previous exposure to the room temperature. The results set out in table 2 seem to suggest that aestivation diapause was gradually completed during the summer, though the speed was not uniform throughout.

The results of both series of tests may lead to the conclusion that aestivation in the pupae of *Abraxas miranda* is not a state of heat torpor but a definite physiological process, which is preferably called diapause.

(iv) *The effect of cold exposure on the completion of aestivation diapause*

In order to estimate the duration of aestivation diapause at a temperature lower than 15°C. two series of experiments were carried out. In the first series, batches of aestivating pupae were exposed to 5-10°C. for different periods and then returned to the laboratory where the weekly mean of temperature varied from 21 to 28°C. during the experiment. The emergence of the moth was observed daily, and the results are summarized in table 3. The table shows that the aestivating pupae required a considerable length of cold exposure for completing diapause. During the first ten days at 5-10°C. aestivation diapause persisted in all pupae,

and none developed promptly after they were removed to the room temperature. Thereafter the proportion of the pupae free of diapause increased with increasing length of the cold treatment. Most of the pupae had finished diapause by 66th day and subsequently begun post-diapause morphogenesis at the low temperature. They metamorphosed at the room temperature in much shorter time than did the nondiapause pupae. The mean length of diapause at 5-10°C. can be estimated at about 40 days.

TABLE 3. *The effect of cold exposure on the completion of aestivation diapause in the pupae of Abraxas miranda.* (1)

Days kept at 5-10°C.	Diapause-free		Diapausing	
	Days required to emerge at 22-28°C. Mean (range)	Number of moths that emerged	Days required to emerge at 22-28°C. Mean(range)	Number of moths that emerged
0	—	0	99.1(94—117)	31
10	—	0	89.4(83—99)	33
20	13.5 (13—14)	2	84.4(72—98)	39
30	12.5 (11—14)	12	84.7(73—93)	22
66	9.0 (5—12)	30	55.7(49—60)	3

TABLE 4. *The effect of cold exposure on the completion of aestivation diapause in the pupae of Abraxas miranda.* (2)

Days kept at 5-10°C.	Diapause-free		Diapausing	
	Days required to emerge at 15°C. Mean (range)	Number of moths that emerged	Days required to emerge at 15°C. Mean (range)	Number of moths that emerged
0	—	0	55.1 (48—68)	67
14	25.4 (22—31)	11	38.5 (32—68)	35
35	23.4 (15—31)	49	—	0
42	22.1 (19—32)	47	—	0
49	20.3 (15—28)	51	—	0
56	20.4 (13—28)	50	47	1
64	14.0 (10—32)	38	48	1
0*	24.5 (22—31)	83	—	—

\* Nondiapausing pupae obtained by an artificial photoperiod of 8 hours during the larval stage.

In the other series of experiments, pupae were kept at 15°C. after being exposed to 5-10°C. for various periods. A batch of nondiapause pupae that had been obtained by an artificial day-length of 8 hours was kept together at 15°C. for comparison. As shown at the bottom of table 4 these pupae took about three to four weeks at this temperature for transforming into the adult.

About a third of the aestivating pupae completed diapause in two weeks at 5-10°C. and all did after 35 days. This is considerably shorter as compared with the results obtained at 25°C. after the cold exposure. Since the experiments were carried out in different years, annual fluctuation in the intensity of diapause might be responsible for this difference. It is also possible that the temperature after

chilling would influence the initiation of post-diapause morphogenesis as observed in *Cephus cinctus* (CHURCH, 1954).

(v) *The length of the pupal stage at different temperatures in the winter generation*

In the winters of 1956-7 and 1957-8, newly formed pupae were removed from the insectary at three-day intervals and distributed into three series, which were kept at 15, 20 and 25°C., respectively, and the emergence of moths was observed. Similar results were obtained in both seasons, and those of the last year are illustrated in figure 3. The figure shows that as the larvae pupated later the resulting pupae gave rise to the adult in a shorter time. This trend is particularly remarkable at the lower temperatures. The pupae arising in October persisted for very long periods, ranging from 113 to 175 days at 25°C. and from 91 to 185 days at 20°C. Similar pupae developed within a much shorter time, from 27 to 46 days, at 25°C. The length of pupal stage decreased rapidly in the first half of winter, and at the end of December it was 25.6 days at 25°C. and 48.3 days at 15°C. Though the decreasing tendency became less conspicuous, it still continued after this month, and in April newly formed pupae gave rise to the adult in the shortest time, 16 days at 25°C. and 33 days at 15°C. These values exceed the length of nondiapausing development by only a few days.

These results may lead to the conclusion that the length of pupal stage is primarily determined during the larval stage, and secondarily influenced by temperature after pupation. That is, the intensity or length of diapause in the

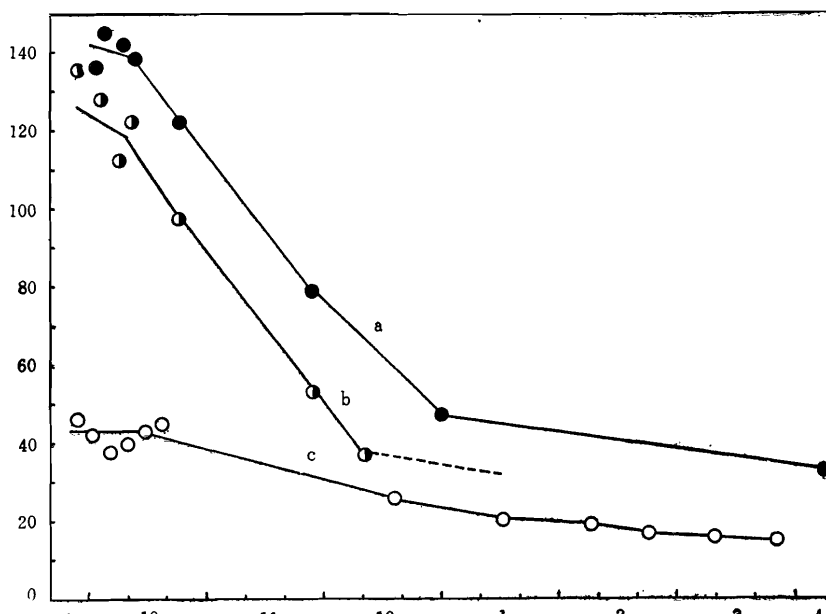


FIG. 3. The length of pupal stage at 15 (a), 20 (b) and 25°C. (c) in the winter generation of *Abraxas miranda* in relation to the date of pupation. Ordinate, length of the pupal stage in days; abscissa, date of pupation. The points represent means of each 16-88 pupae.

winter generation seems to be controlled by the environmental conditions during the larval stage.

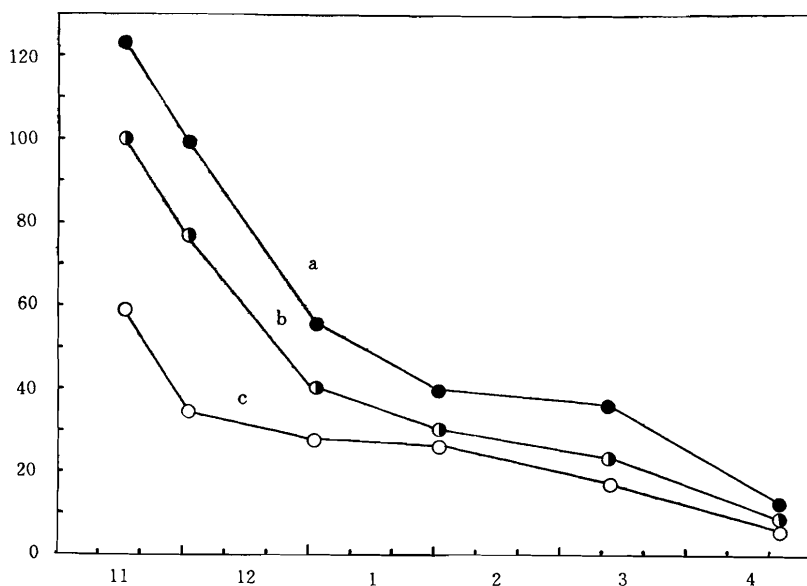


FIG. 4. The effect of incubation at 15 (a), 20 (b) and 25°C. (c) at different times during hibernation (abscissa) upon the development (ordinate, time in days) of the pupae of *Abraxas miranda* that had been raised in October. The points represent means of each 15-28 pupae.

(vi) *The length of diapause under hibernating conditions*

As mentioned above, the pupae formed in autumn undergo a long diapause when they are kept at a low temperature. Therefore, these pupae are presumably in diapause for a very long period when they hibernate in the field. In order to confirm this, diapausing pupae that had been bred as larvae in September and October, 1956, were kept hibernating in a cellar and transferred to various temperatures at different times. The mean temperature in the cellar decreased from 17.3°C in the first week of November to 6.5°C. in the second week of February, and then rose again to 15°C. in the last week of April. As shown in figure 4, the pupae developed in a progressively shorter time as they were incubated later in the season. Judging from the length of the pupal stage after incubation, a small amount of diapause still remained in the pupae at the beginning of March, but all of the hibernating pupae had apparently begun differentiation into the adult by the middle of April, for they emerged in a considerably shorter time after incubation than is necessary for nondiapause development. Consequently, it seems that diapause development was completed in the latter half of March or the first half of April in advance of the emergence of moths occurring a month or so later. As indicated by the seasonal prevalence of the moth, the matter might be only a little different in the field, where diapause in the pupae occurring in autumn probably lasts for about four to five months.

It has been observed in the preceding section that the pupae underwent a shorter period of diapause as they had grown as larvae later in winter. It will be interesting to compare this with the present results. The comparison may give an impression as if diapause development proceeded at the same rate irrespective of whether the insects hibernated as larvae or pupae.

(vii) *The comparison of the thermal reactions of the pupae occurring at different seasons*

In figure 5 which is based on the data described above, the length of pupal stage at different seasons is plotted against temperature. Although only a few temperatures were available, it clearly illustrates that the thermal reaction of the pupae of *Abraxas miranda* varies strikingly from season to season. Within the moderate range of temperature between 15 and 25°C., diapause development in the summer pupae is promoted by lowering temperature. Contrary to this, in the autumn pupae it is accelerated by rising temperature. Two different patterns of diapause development can be realized from these different thermal reactions. In short, aestivation diapause shows a negative temperature coefficient for its

completion, while hibernation diapause a positive one. Aestivation diapause is, however, not shortened further but rather a little prolonged by a temperature lower than 15°C., for it was estimated to take on the average about 20 or 40 days at 5-10°C. and about 25 days at 15°C. On the other hand, hibernation diapause is no more prolonged by a temperature lower than 15°C.; it took about 120 days for its completion at a mean temperature of about 10°C. in the cellar. This is almost comparable to the results obtained at 15°C. The spring pupae grew promptly and their diapause was almost negligible. There was, nevertheless, a graded series between long-term autumn pupae and short-term spring pupae in regard to the duration of diapause, and the pupae retained a positive thermal coefficient for completing diapause throughout the winter generation.

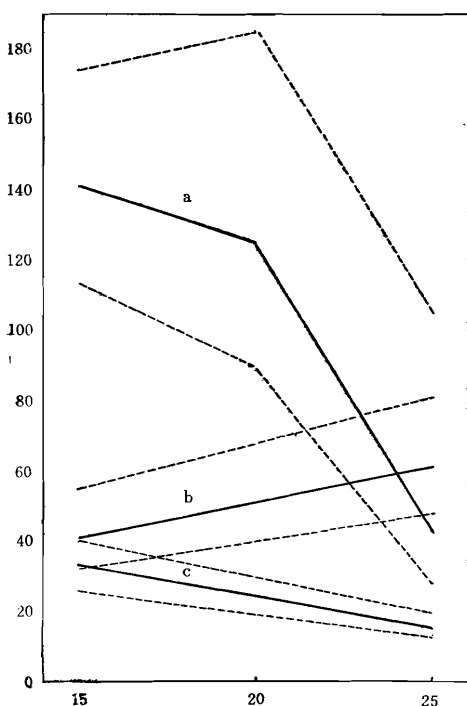


FIG. 5. Thermal reactions of the pupae of *Abraxas miranda* that had been formed in different seasons. a, autumn pupae; b, summer pupae; c, spring pupae. Full line indicates means and dotted line minimum or maximum values. Ordinate, the length of pupal stage in days; abscissa, temperature during the pupal stage.

Reference to figure 5 shows further that the curves exhibiting thermal reactions of the pupae in summer, autumn and spring, respectively, cross or very close to each other at certain temperatures. When considerable (individual) variations in the duration of pupal



stage of each type is taken into consideration, the distinction of the pupal types seems to be even impractical at such temperatures. At a certain high temperature the hibernating pupae of autumn could hardly be distinguished in duration from aestivating pupae and at a low temperature some aestivating pupae developed so fast that their diapause seemed to last less than a few days. This does not, however, necessarily mean that in such cases a similar physiogenesis took place in the pupae of physiologically different nature that would respond differently to certain other temperatures.

(viii) *The effect of temperature and photoperiod during the larval stage upon the type of diapause development*

It has been known that the occurrence and duration of diapause in the pupae of *Abraxas miranda* are influenced by photoperiod and temperature during the larval stage (MASAKI, 1958). In the light of the present investigation, it seems certain that different thermal reactions are involved in diapause of varying duration which is induced under different regimes of temperature and photoperiod. This was experimentally tested.

Several batches of larvae were reared under different artificial conditions of temperature and photoperiod, and on pupation each batch was divided into two groups, one being kept at 15°C. and the other at about 25°C. The length of the pupal stage was measured at these temperatures and the results are summarized in table 5. The number of moths that emerged are illustrated in figure 6, where the results obtained under the natural conditions of the insectary are also presented for comparison. In certain batches, pupae of different types of development occurred concurrently and the moths emerged irregularly over a very long period. But it can be seen in table 5 and also in figure 6 that the thermal reaction of the pupae was influenced by day-length and temperature during the larval stage. When the

TABLE 5. *The effect of photoperiod and temperature during the larval stage on the thermal reaction of the resulting pupae.*

Photoperiod and temperature in the larval stage	Temperature in the pupal stage	Diapause-free		Diapausing	
		Days required to emerge. Mean (range)	Number of moths that emerged	Days required to emerge. Mean (range)	Number of moths that emerged
Ohr, 25°C.	15°C.	20 (17-23)	3	45.7 (40-55)	17
	25	13.2 (11-15)	13	81.0 (46-103)	36
Ditto	15°C.	—	0	40.8 (25-52)	40
	25	13.0 (12-14)	4	70.3 (66-81)	50
Ohr, 15-20°C.	15°C.	29.8 (20-40)	10	151.3 (118-205)	7
	25	14.3 (13-16)	8	84.6 (61-97)	8
9hr, 24°C.	15°C.	32.3 (23-45)*	51	113.5 (110-117)	2
	25	13.2 (10-16)	29	68.0 (29-87)	12
12hr, 24°C.	15°C.	26.9 (24-34)	10	146.4 (124-154)	5
	25	13.7 (11-16)	18	56.7 (32-93)	28
13hr, 24°C.	15°C.	26.4 (20-33)	5	119.0 (51-173)	11
	25	12.7 (12-14)	9	39.9 (26-81)	21
15hr, 24°C.	15°C.	—	0	45.4 (37-55)	46
	25	—	0	65.5 (59-82)	36

\*The emergence of moths from these pupae showed a unimodal curve and the pupae undergoing diapause of very short duration could hardly be separated from nondiapausing ones.

larvae had been bred at a mean temperature of 24°C. in 15-hour photoperiod or in darkness, aestivation pupae occurred, that is, they completed diapause in a shorter time at 15°C. than at 25°C. On the other hand, under the conditions of 9-, 12- or 13-hour photoperiods at the same temperature, a considerable proportion of the resulting pupae averted diapause. The development of these pupae was of course accelerated by the high temperature. The rest of the pupae entered a prolonged diapause at the low temperature, but resumed to develop in a much shorter time at the high temperature. This is apparently a feature of winter diapause.

Thus pupae of different types of development could be obtained by artificial conditions of light and temperature. Their thermal reactions are clearly distinguished from each other as illustrated in figure 7 where the mean length of pupal stage in each type of emergence is plotted against temperature.

Comparing these curves with those in figure 5, there leaves little doubt that the three thermal reactions of the pupae observed in these experiments correspond to those exhibited by the summer, autumn and spring pupae, respectively. There is, however, a contradiction between the results of these tests and the insectary breeding as to the occurrence of hibernation diapause. A considerable proportion of the pupae averted diapause under the artificial photoperiods which are comparable to the autumn day-length, while almost all pupae entered hibernation diapause in autumn in the field as well as in the insectary. Some factor responsible for the universal occurrence of hibernation diapause have been overlooked. This may be a joint action of particular day-length and temperature.

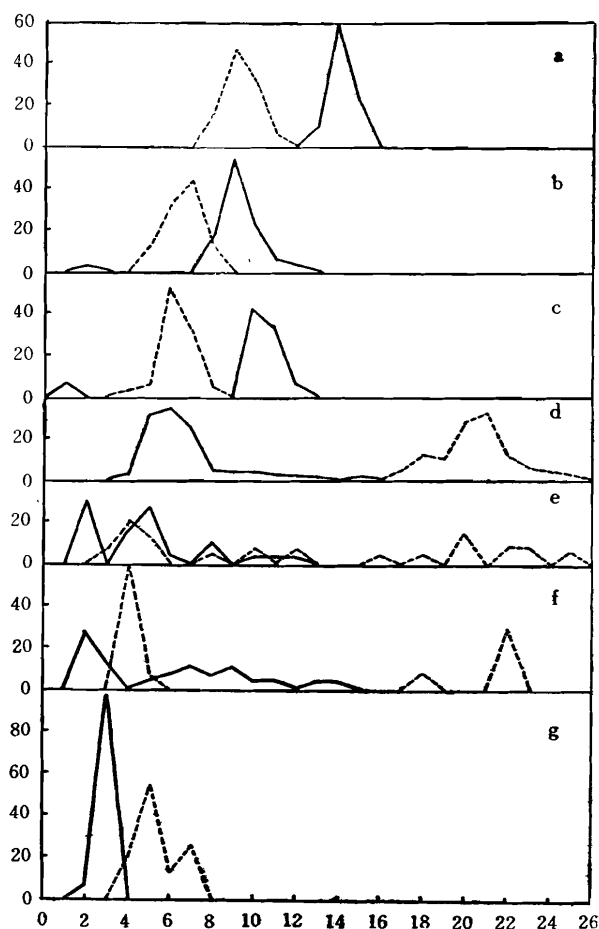


FIG. 6. The emergence of moths at 15 (dotted line) and 25°C. (full line) from the pupae that had been reared as larvae under: a, natural conditions in May-June; b, 15-hour daily light and 24°C.; c, darkness and 25°C.; d, natural conditions in September-October; e, 13-hour light and 24°C.; f, 12-hour light and 24°C.; g, natural conditions from October to March. Ordinate, number of moths; abscissa, time in weeks.

## (ix) Conclusion

Although there is yet some question to be investigated further, the intricate mode of diapause in *Abraxas miranda* can tentatively be outlined as set out in table 6, which is based on the results described in this paper and also elsewhere (MASAKI, 1957, 1958).

It is certain that aestivation diapause, which is induced by the long day and rising temperature in early summer, is characterized by a negative temperature coefficient for its completion. On the other hand, hibernation diapause, which is probably induced by medium day-length and mild temperature in autumn, shows a positive temperature coefficient. It would seem that a special combination of day-length and temperature is necessary to induce all the pupae into long hibernation diapause. Seasonal changes of this combination may also be responsible for shortening diapause regularly in the pupae formed successively later in winter. In the insectary this decreasing trend was rapid between the beginning of November and the end of

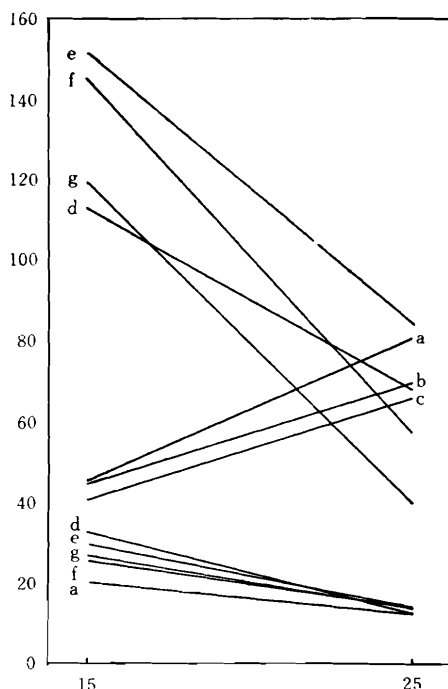


FIG. 7. The thermal reactions of the pupae that had been reared as larvae in darkness at 25°C. (a and b) or 15-20°C. (e), or at about 24°C. in 15 (c), 13 (g), 12 (f), and 9 (d) hours of photoperiod. Ordinate, the length of the pupal stage in days; abscissa, temperature during the pupal stage.

TABLE 6. Seasonal variation in the mode of diapause in the pupae of *Abraxas miranda*.

Generation	I		II		
Season of larval growth	Early summer		Autumn	Autumn - winter	Autumn - spring
Conditions during larval feeding	Long day moderate (rising) temperature		Medium day moderate (lowering) temperature	- short day - low temperature	- medium day - low temperature
Season of pupation	Summer		Autumn	Winter	Spring
Type of pupal development	Aestivation		Long hibernation	Short hibernation	Nondiapause
Length of pupal stage in nature	2-3 months		5-6 months	2-4 months	1 month
Length of pupal stage at:	15°C.	35-65 days	120-170 days	40-60 days	20-30 days
	25°C.	50-100 days	30-80 days	20-30 days	14-20 days
Thermal coefficient	-		+	+	+

December. During this period the length of day became shorter day by day until the winter solstice was reached on 22 of December. This is a condition which tends to suppress the occurrence of diapause. The larvae were at the same time influenced by winter cold which has also been known to reduce the length of diapause. These factors might exert their joint action upon the larvae so that the amount of diapause in the resulting pupae would be gradually diminished during winter, and this diapause-averting action would be complete before early spring. All these complicated seasonal changes in the character and intensity of diapause may perhaps be controlled by the neurosecretory system which receives "token" stimuli signalling the seasonal changes.

#### DISCUSSION

The temperature requirement of insects for completing diapause varies from species to species, which seems to be closely related to the climatic conditions of the habitat as extensively reviewed by LEES (1955). Insects inhabiting cold districts are, in general, able to complete diapause at freezing temperature, those living in temperate zones need relatively mild temperature, and those thriving in subtropical or tropical countries require almost similar ranges of temperature for diapause and morphogenesis, if they undergo diapause. In view of this ecological rule, it might be expected that similar diversity is found among species which inhabit the same climatic region but differ in seasonal cycle. The phenological differentiation of the temperature requirement for diapause development may be manifested most clearly by comparing hibernating and aestivating forms. It might further be expected that diapause is differentiated into two seasonal types even in the same species which enters diapause both in the summer and winter generations. This is what we have found in *Abraxas miranda*.

It is clear from the present study that two kinds of diapause, which differ physiologically as well as ecologically from one another, occur in the seasonal cycle of *Abraxas miranda*. They are induced by different conditions of light and temperature, and can be called aestivation and hibernation diapause, respectively, from the phenological point of view. The cabbage moth, *Barathra brassicae* affords another example of this kind (MASAKI, 1956). In these bivoltine forms and also in the univoltine saturniids, *Dictyoploca japonica*, *Rhodinia fugax* and *Antheraea yamamai*, the aestivating pupae can readily terminate diapause at a temperature suitable for morphogenesis (UMEYA, 1950; YAMAZAKI *et al.*, 1956; YASHIKA, 1954). It appears that diapause development in these moths proceeds most rapidly at the mild temperature prevailing in autumn. Such a thermal requirement is undoubtedly a prerequisite for the autumn emergence of those moths and may be considered as a feature of aestivation diapause in our temperate regions. In this point, aestivation diapause makes a clear-cut contrast to hibernation diapause which is normally completed at much lower temperatures. This distinction is, however, by no means absolute. One may find a continuous series of transient forms in the so-called winter moths. Some members of this peculiar group of the Geometridae emerge from diapause in late autumn, others in mid-winter and still others in late winter or early spring, as judged from their seasonal prevalence (INOUE, 1956). This is probably correlated with their thermal requirements for

diapause, and it seems probable that, the lower the temperature they require, the later in the season they would emerge.

In contrast to many known cases of winter diapause, the completion of diapause in the hibernating pupae of *Abraxas miranda* is remarkably promoted by rising temperature up to near the higher threshold for morphogenesis and is greatly delayed by a temperature lower than 15°C. It would seem that this unusual response is connected with certain other physiological characters or ecological demands of this insect. The pupae are able to grow at a temperature as low as 5-10°C. after having completed diapause (tables 3 and 4). Because of this very low threshold for morphogenesis, they would metamorphose even in winter if they could complete diapause most rapidly at a low temperature, say 5-10°C. as in many cases of winter diapause. The hibernating pupae avoid such an untimely growth by their own special reaction to temperature, and emerge as the moth in the next spring. The pupae occurring successively later during winter undergo diapause of shorter duration, but they respond to temperature in a more or less similar way so that their metamorphosis is retarded in winter and accelerated in spring. As a result the moths are on the wing synchronously in the spring.

In order to keep this regulation mechanism as a successful one, the hibernating pupae must be ensured against risks of getting free of diapause before winter. In the field they are seldom found before October when temperature is low enough to minimize the speed of diapause development. This proper timing is obviously owing to the occurrence of aestivation diapause in the preceding generation. Otherwise the pupae would occur much earlier and would begin to develop before winter, for they complete diapause rapidly at higher temperatures. Besides its own role in escaping the hottest season and timing the moth flight for autumn, aestivation diapause is thus responsible for synchronizing the spring flight of the moths. It is assumed that every phase of the seasonal cycle and every feature of the habit have evolved in close connexion to each other in this evergreen-feeder, *Abraxas miranda*.

#### SUMMARY

The pupae of *Abraxas miranda* enter diapause of different physiological characters in summer and winter, respectively.

*Aestivation diapause* (i) is induced by the long day-length and rising temperature in early summer, (ii) lasts from two to three months under the natural conditions in an insectary, and (iii) is much shortened by a low temperature but prolonged by a high one.

*Hibernation diapause* (i) is presumably induced by a combined action of the medium day-length and mild temperature in autumn, (ii) lasts for about five months under the natural conditions in the insectary, and (iii) is remarkably prolonged by a low temperature, but lasts shorter than aestivation diapause at a high temperature. (iv) It is progressively reduced in intensity among the pupae formed successively later in winter, probably under the influence of shortening day-length and lowering temperature during the larval stage, but (v) it shows a positive temperature coefficient for its completion throughout.

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#### 要 約

ユウマダラエダシャクは2化性であるが世代によって休眠の様式が異っている。夏の休眠は高温長日によって誘導され、自然界においては2—3ヶ月続く。休眠完了の過程は負の温度係数を示し、低温によって著しく加速され高温によって遅延する。他方冬の休眠は中間日長と特定の温度条件によって誘導され秋に生じた蛹においては4—5ヶ月続く。休眠完了の過程は正の温度係数を示し、高温下においては夏の休眠よりも短くなるが低温下では著しく遅延する。しかし冬型休眠の長さは蛹化月日がおそくなるにしたがって短縮され、早春には遂に不休眠蛹が現われる。このような著しい休眠の intensity の変化にもかかわらず冬世代全体を通じて休眠完了の過程は正の温度係数を示す。