MATERNAL INDUCTION OF DIAPAUSE IN THE LARVA OF *LUCILIA CAESAR* L. (DIPTERA: CALLIPHORIDAE)

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INTRODUCTION

Numerous reviews of the literature on diapause in insects and mites have been produced in recent years, notably by Andrewartha (1952), Hinton (1954, 1957), Lees (1955, 1956), Harvey (1962), de Wilde (1962), and Beck (1963). In the majority of species so far studied diapause is induced only in those individuals directly exposed to the influential stimuli. However, there are a number of instances in which it has been shown that stimuli applied to the mother can affect the diapause tendencies of the progeny.

Cousin (1932), having subjected adults of *Lycilia sericata* Mg. to various abnormal conditions, suggested that external conditions acting on the adults may be a causal factor of diapause in the larvae. Supporting this idea was Simmonds's (1948) demonstration of a connexion between the age, diet and effects of temperature on the mother and the incidence of diapause in the larvae of *Spalangia drosophilae* Ashm. and *Cryptus inornatus* Pratt. Schneiderman & Horwitz (1958) found a maternally induced larval diapause while working with *Mormoniella vitripennis* (Walker). Although their results did not reveal any correlation between intrinsic factors (such as maternal age) and the incidence of diapause, they proved that the exposure of female wasps to low temperature during oögenesis induced diapause in their progeny. The results of Saunders (1962, 1965) with this species also established the effects of a maternal influence, but in contrast to those of the former authors his results showed that as the maternal generation became more senile a greater proportion of the progeny entered diapause.

Fukuda (1951, 1952) and Hasegawa (1951, 1952) demonstrated that a hormone produced by the suboesophageal ganglion of the female silkmoth, *Bombyx mori* L., was concerned in the production of diapause eggs. By transplantation experiments they showed that, when the ovaries of the female were exposed to the influence of an extract of the suboesophageal ganglion, egg development was of the diapause type and in its absence only non-diapause eggs were formed.

More recently, Depner (1961, 1962) suggested that the photoperiod experienced by the adult female Horn Fly, *Siphona irritans* (L.), or by the developing eggs within the female, was responsible for the predisposition of the larvae to enter diapause. This effect became more intense as the season progressed and it tended to overcome the diapause-inhibiting effects of higher rearing temperatures. Jackson (1963) also found an instance of maternal physiology influencing larval development in the mymarid parasite, *Caraphractus cinctus* Walker. When breeding from females which had themselves emerged from diapause individuals she discovered that the larvae of such females did not all respond to the diapause-inducing conditions of short photoperiod, a small

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proportion usually completing development. From her results she concluded that a maternal influence was responsible for the direct development of these individuals. Working with the parasitic wasp, *Coeloides brunneri* Vier., Ryan (1965) concluded that the parent female was sensitive to photoperiod and transmitted the determination for diapause in the larva through the egg.

A significant discovery within the genus *Lucilia* R–D was that of Cragg & Cole (1952). They found that the egg batches from wild females of *L. sericata* caught in late summer to early autumn produced a high proportion of diapausing larvae even when reared under laboratory conditions favouring normal development. It was concluded that diapause in this species also was of maternal origin. Presumably this maternal influence is related to seasonal changes and ensures that the majority of larvae produced at the end of the blowfly season enter diapause in spite of the possible occurrence of ground conditions favouring pupation. Fraser & Smith (1963) reached a similar conclusion while maintaining cultures of *L. caesar*. They found that there were considerable differences in diapause tendency between larvae from different females although the larvae had received similar treatments since oviposition. These authors postulated that a maternal factor operating prior to oviposition determines the proportion of larvae entering diapause.

The main object of the investigations described in the present paper was to confirm the hypothesis that there is a maternal influence on larval diapause in *L. caesar* which increases in effect as the natural breeding season advances. Simultaneous studies were carried out to determine the environmental factors responsible for the production of such an influence, and to determine the nature of the maternal influence.

METHODS
(1) *Adult blowflies*

The Glasgow University field-station at Rossdhu Estate, Dunbartonshire, is situated in a fairly open woodland area which contains abundant bird and small mammal life and to which sheep and cattle have access. This area was chosen as a permanent trapping site, a choice that was justified by the high numbers of adults taken during the early part of the first season of these investigations.

During the years 1962 and 1963 blowflies were captured at regular intervals throughout the natural breeding season, fertile females being found from the beginning of June until the beginning of October. Usually samples were taken at weekly intervals, except during poor weather when more frequent sampling had to be employed because of the low numbers of females attracted to the bait. At first a standard chemical bait of ethyl mercaptan and hydrogen sulphide was employed (Cragg & Thurston, 1950). However, its success was closely linked with climatic conditions, blowflies being attracted only on warm, sunny days. Fresh horse-liver provided a highly successful substitute in all weather except high wind or heavy rainfall. The blowflies were captured as they approached or alighted on the bait and were immediately transferred to 3 in. × 1 in. glass tubes. This method ensured that the first egg batch obtained from a female was laid under laboratory conditions within a known time of capture.

Females captured in the field were maintained in the laboratory in individual lamp-glass cages (height 8 in., diameter of base 3 in.). Each cage was lightly stoppered with

cotton wool and set in a Petri dish containing moist filter paper. On arrival in the laboratory each female was supplied with sugar solution *ad lib.* Stock cultures were caged in standard glass tanks measuring 20 in. × 12 in. × 12 in., the open end being covered with a fine muslin sleeve. As above, the flies had free access to a sugar solution. Fresh liver covered with moist cotton was supplied daily for the first week and thereafter at 3-day intervals or when eggs were required. Eggs were allowed to hatch on the liver and in the case of stock cultures larvae from several egg batches, each laid by a different female, were allowed to intermingle.

The cages were housed in two constant temperature rooms, both at 22° C. and 60–70 % relative humidity. Illumination in the rooms was provided by 'warm-white' fluorescent tubes which, at cage level, produced a light intensity of approximately 100 foot-candles as measured by an E.E.L. photometer. In one room a time switch supplied a long photoperiod regime of 20 hr. of light alternating with 4 hr. of darkness (LPR); in the other a time switch gave a short photoperiod of 12 hr. of light alternating with 12 hr. of darkness (SPR).

The diapause tendency of the larvae from the first egg batch from each female was considered as being 'determined' in the field, if laid within 24 hr. of capture (Cragg & Cole, 1952). Only such batches were used when comparing the diapause tendency of early, middle and late season females. The incidence of diapause in the larvae from any subsequent egg batches laid by a female was also studied to see if it differed from that of the first batch and, if so, the nature and temporal pattern of the difference.

Control flies were unavailable during the first season of trapping, but in the second year stocks which had been bred in the laboratory from females captured in 1962 were used for comparative purposes. The controls were supplemented in September 1962 by the addition of a stock of *L. caesar* obtained from the Field Research Laboratory, Carlisle. This stock had been bred through many generations in the laboratory since the summer of 1961.

(2) *Offspring*

The larvae were transferred into 500 ml. rearing flasks as soon after eclosion as possible and cultured in the manner previously described (Ring, 1967).

Throughout these investigations two, or three where possible, culture flasks from each group of larvae were established using approximately fifty larvae per flask in each case. The flasks were kept in the constant temperature room in which the parent flies had been reared, except where otherwise stated. Since non-diapausing larvae pupate within 4–7 days of cessation of feeding, those individuals still in the larval stage of development after 14 days were arbitrarily regarded as being in diapause (Cragg & Cole, 1952; Fraser, 1957).

Results and discussions of investigations are presented under the following headings: (A) Induction of diapause via the mother, (B) Factors affecting the maternal generation, and (C) Nature of the maternal influence.

RESULTS AND DISCUSSION
(A) *Induction of diapause via the mother*

Throughout the breeding seasons of 1962 and 1963, 87 % of all captured females were identified as *L. caesar*, the remaining 13 % belonging to the closely related species *L. ampullacea* Villen. The diapause rate of the progeny from each sample of females of

Table 1. *Diapause incidence in progeny from first egg batches of Lucilia caesar females captured during the breeding season and maintained under long photoperiod conditions*

Date of capture	Field test stocks									Laboratory control stocks		
	1962				1963				1962, 1963 Mean diapause rate (%)			
	No. of females	Diapause larvae	Non-diapause	% diapause	No. of females	Diapause larvae	Non-diapause	% diapause		Diapause larvae	Non-diapause	% diapause
2–8 June	8	0	545	0	20	0	1159	0	0	—	—	—
9–15 June	9	0	420	0	21	16	1638	1	1	—	—	—
16–22 June	10	5	473	1	6	26	187	12	5	6	77	7
23–29 June	13	155	520	23	0	—	—	—	23	—	—	—
30 June–6 July	6	205	101	67	1	21	26	45	64	23	75	23
7–13 July	2	50	31	62	9	357	51	88	83	23	148	13
14–20 July	10	581	3	99	14	725	236	75	85	21	71	23
21–27 July	11	653	12	98	6	292	28	91	96	10	64	14
28 July–3 Aug.	2	95	0	100	10	517	95	84	87	0	43	0
4–10 Aug.	0	—	—	—	0	—	—	—	—	0	106	0
11–17 Aug.	0	—	—	—	4	239	0	100	100	0	46	0
18–24 Aug.	5	189	2	99	0	—	—	—	99	0	62	0
25–31 Aug.	12	786	0	100	10	431	5	99	100	101	93	52
1–7 Sept.	0	—	—	—	7	337	7	98	98	—	—	—
8–14 Sept.	4	274	3	99	0	—	—	—	99	—	—	—
15–21 Sept.	4	299	0	100	6	—	—	—	100	—	—	—
22–28 Sept.	0	—	—	—	0	281	0	100	100	—	—	—
29 Sept.–5 Oct.	6	439	0	100	2	110	0	100	100	—	—	—

L. caesar is given in Table 1 and the combined data for both seasons are plotted in Fig. 1.

The first ovigerous females were captured during the first week of June and for the greater part of the month the diapause incidence remained at a very low level. Towards the end of June the proportion of females producing higher diapause incidence among their progeny began to increase. The records for July showed considerable scatter in diapause performance but with the majority of results appearing within the upper part of the range, between 60 and 100 % diapause. In order to demonstrate the range of
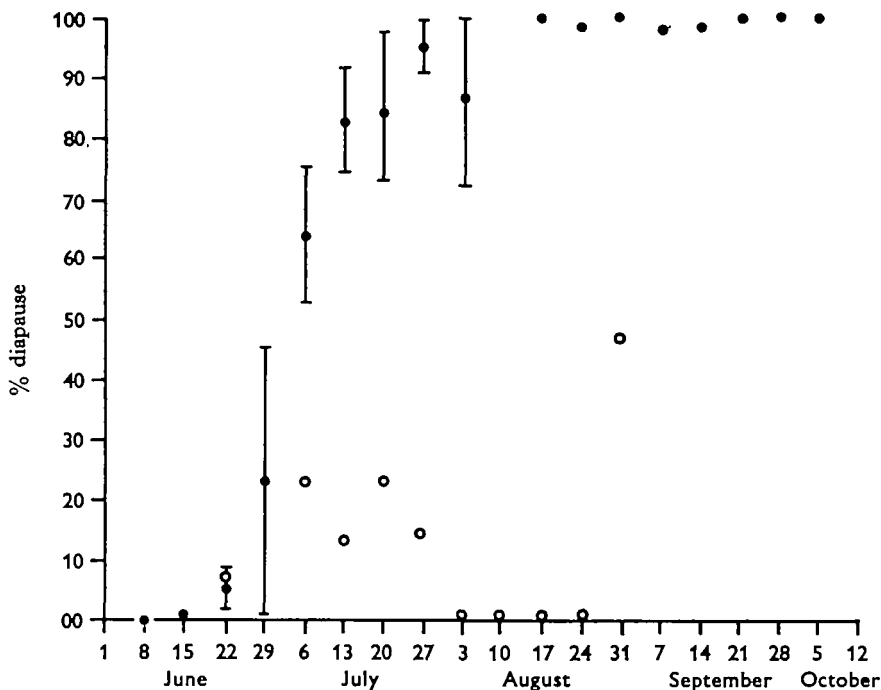
Fig. 1. The seasonal pattern of diapause incidence in the progeny from the first egg batches of *L. caesar* females captured throughout breeding seasons 1962 and 1963. Solid black circles represent diapause incidence in the progeny of field-captured females. Open circles represent diapause incidence in the progeny of laboratory-reared females.

variation in diapause rate in the offspring of each female, the standard error (s.e.) in percentage diapause is shown in Fig. 1 for samples of females captured during that part of the season when there is a sudden increase from low to high diapause incidence. It is obvious from the July results that different females, although experiencing similar environmental conditions in the field, reacted to these conditions in different ways as manifested by the diapause rate of their offspring. This month, therefore, is a transition period between the relatively low diapause rate in June and the very high rate among the offspring of all females captured after the beginning of August. From the beginning of August until the end of the natural breeding season in early October the diapause rate remained at a constantly high level and never fell below an average of 98 %.

Comparison between the incidence of diapause in control stocks and that shown by

the offspring of field-captured females clearly reveals that during the period when diapause from field-captured females is increasing the diapause rate of the laboratory controls remains at a relatively low level. Laboratory conditions, therefore, were not responsible for the sudden transition from low to high diapause incidence which occurs in the progeny of field captured females soon after the summer solstice. Cragg & Cole (1952) have shown that the carriage of captured blowflies from the field to the laboratory has no effect on the subsequent diapause performance of the larvae. Furthermore, since all adults and larvae were tested under the same laboratory conditions throughout the season, the differences in diapause incidence among the offspring of different females must have been brought about by a pre-ovipositional influence.

(B) *Factors affecting the maternal generation*

Cragg & Cole (1952) suggested that diapause in *L. sericata* was of maternal origin and clearly related to some seasonal change; in view of the importance of photoperiod and temperature to other organisms these factors were considered in the case of adult *L. caesar*. A survey of changes in environmental factors during the critical period of July revealed a possible correlation between decreasing photoperiod and the increasing number of diapausing individuals. At the summer solstice at 56° N the daylength (arbitrarily defined here as midway between calendar and civil daylength) is 18 hr. 40 min. as calculated from the values given in the abridged *Nautical Almanac* (1959). By the end of July it has fallen to 17 hr. at which time almost all the field progeny were found to enter diapause. Although most insects respond to absolute photoperiod a few appear to be sensitive to changing daylength (Lees, 1955; Corbet, 1956; Blake, 1960, 1963; Norris, 1965), and therefore the latter possibility was investigated experimentally with *L. caesar*.

Effects of changing photoperiods

In this experiment two photoperiod cabinets were employed, the first controlled by a time switch with a solar dial set to give daily decrements in the daylength and the second controlled to give a daylength maintained at a constant level. Illumination was provided by two 15 W. fluorescent tubes with a light intensity of 150–200 foot-candles at cage level. To prevent a build-up in temperature the lights were separated from the rest of the cabinet by double plate-glass walls, and the cabinet was so constructed that compressed air, after circulating through the part containing the stock cage, was made to flow over the light fittings. Despite these precautions, however, the temperature in the cabinets always rose 5° C. above the ambient (22° C.) during the 'day'. The relative humidity was maintained at approximately 70 % by passing the compressed air through water before entry into the cabinets.

Each cabinet was stocked with laboratory reared flies from the same parent source, and egg batches were obtained in the normal way. Two larval cultures at a time from each cabinet were set up, one being kept in the original photoperiod regime under which the parents had been reared and the other being transferred to the alternative photoperiod regime. This served to identify any direct action of photoperiod on the larvae themselves.

In the first test the effect of daily decrements (2–3 min.), equivalent to those prevailing in the field immediately after the summer solstice, was compared with that of a

constant photoperiod of 20 hr. The solar dial was set to give the maximum daylength of 20½ hr. and the experiment was continued until the photoperiod had decreased to 19 hr.

The results from seven egg batches collected throughout the test period showed that the diapause incidence under conditions of progressively decreasing photoperiod remained at zero throughout the experiment. Similarly, under control conditions there was complete absence of diapause during the same period.

A second test was then set up to study the effect of decreasing the photoperiod by regular decrements from 18–14 hr. The time switch of the control cabinet was set to give a constant daylength of 18 hr. Decrements of 10 min. per day were chosen so that the test could be conducted and concluded within a reasonable period of time. As is discussed later in this paper, a stock maintained in the laboratory for over 6 weeks shows the tendency for a maternal ageing effect to influence the diapause rate.

Table 2. *Diapause incidence in the progeny of females*
exposed to decreasing photoperiods

Decreasing photoperiod (10 min. decrements)		Constant photoperiod	
Photoperiod (hr)	Diapause rate (%)	Photoperiod (hr.)	Diapause rate (%)
18	0	18	0
17¼	0	18	1
16¼	15	18	0
15¼	14	18	0
14½	96	18	1
14	90	18	0

The results again showed that the actual decrease in length of the photoperiod is not in itself responsible for diapause induction in *L. caesar* (see Table 2). The diapause rate remained at a relatively low level from photoperiods of 18–15½ hr. By the time the photoperiod had reached 14½ hr., however, the diapause rate had increased to 96 %, indicating that the threshold level of the females' photoperiodic response had been passed. The diapause rate in the control groups, on the other hand, remained very low throughout the test period.

Effects of constant photoperiods

Since the preliminary tests indicated that *L. caesar* females do not respond to decreasing photoperiod *per se*, the effects of a constant long photoperiod (20 hr.) and a constant short photoperiod (12 hr.) were investigated. A sample of wild females captured in the field during the breeding season and whose first egg batches provided the data supplied in Table 1, were used in this experiment. The females were maintained in individual cages in one or other of the constant temperature rooms and the diapause performance of the larvae from their successive egg batches was recorded. All larvae were reared under otherwise standard conditions.

The data for each photoperiod regime are summarized in Figs. 2 and 3. It should be noted that the diapause rate of many batches is in the region of 90–100 %; all the females that produced these batches were captured during the period between the end of July and beginning of October, when diapause incidence in the field is very high.

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The percentage diapause of larvae which developed from the first and subsequent egg batches of twenty females maintained under LPR is shown on the ordinate of Fig. 2, the number of batches laid by each female being traced along the abscissa. When diapause is low in the first batch then it remains at a low level in successive batches, five females showing a complete absence of diapause among the larvae developing from all their egg batches. Where diapause is initially high, however, then it gradually diminishes in successive batches under these photoperiod conditions. There were two
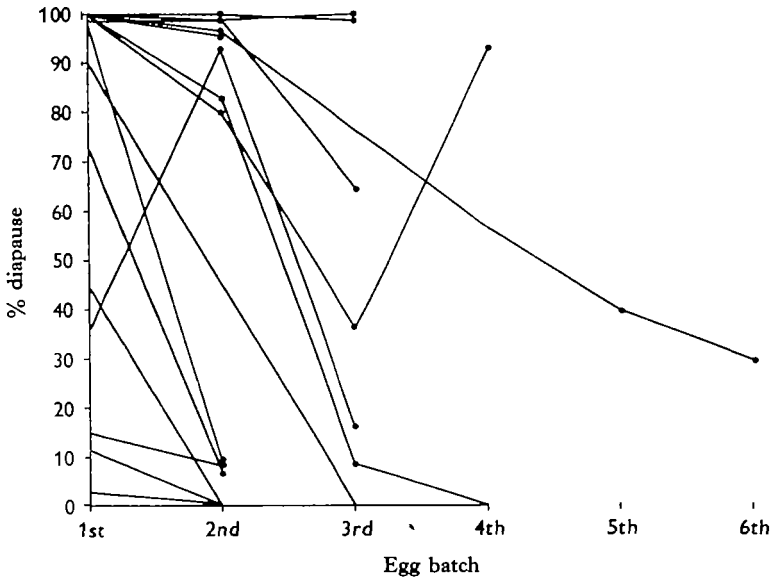
Fig 2. Diapause tendency of the progeny from successive egg batches of twenty *L. caesar* females maintained under constant long photoperiod (20 hr).
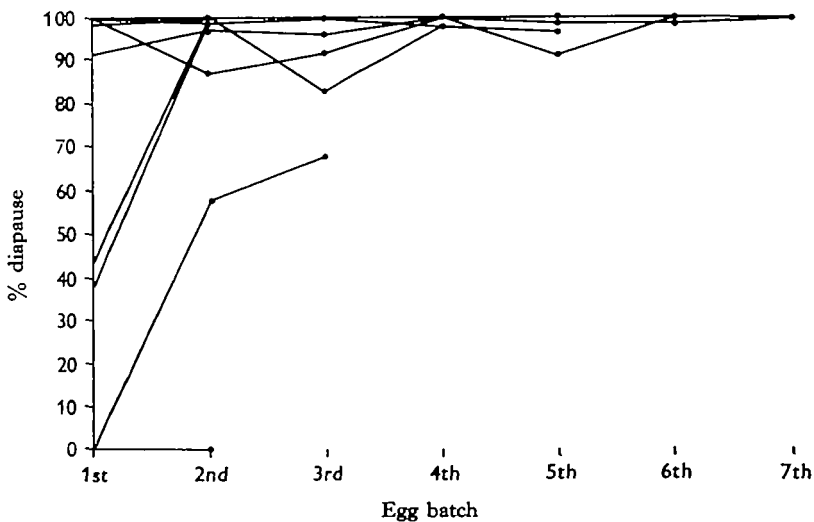

Fig. 3. Diapause tendency of the progeny from successive egg batches of sixteen *L. caesar* females maintained under constant short photoperiod (12 hr.).

exceptional cases where the diapause rate of the progeny of females captured later in the breeding season remained at a very high level, even after their third egg batch and 20–30 days experience of the LPR. A possible explanation of this is given later.

Fig. 3 demonstrates that a high rate of diapause is induced and maintained in the successive batches of 14 out of 16 females reared under short photoperiod conditions. Again, however, there were some individuals that did not conform to the general pattern, two females showing a complete absence of diapause in their first and second batches in the SPR. These females were captured in mid-June and their first batch was produced on the day of capture, and, in each case, the second batch after only five days in the short photoperiod. It is possible that 5 days' exposure to the short photoperiod cycle is not long enough to induce diapause in the offspring of a wild female brought into the laboratory from the naturally long photoperiod conditions of mid-June.

The females which produced an intermediate diapause rate (10–90 %) in their first egg batch showed the most dramatic response to photoperiod changes. In the LPR the diapause incidence had dropped to a very low level by the third egg batch (produced within 8 days of capture), while in the SPR it had increased to almost 100 % by the second egg batch (produced within 8–10 days of capture).

Temperature

Temperature records (data supplied by the Meteorological Office, Glasgow) for the region described show that at the beginning of June when diapause incidence is negligible the mean temperature is about 12·5° C. This temperature is reached once again in mid-September, at the time when all captured females are producing virtually 100 % diapause among their progeny. In fact, the mean daily temperature reaches a peak of about 16° C. in early August at the time when 100 % diapause is reached in the field. It appears unlikely, therefore, that temperature plays a predominant role in determining the 'direction' of the maternal influence in the field. It is more likely that photoperiod is the main environmental agency controlling diapause induction in *L. caesar* and that temperature plays a modifying role by altering the threshold of response to photoperiod.

Senility

While breeding from stock cultures in the LPR it was observed that after 6–10 weeks maintenance in the laboratory the larval diapause incidence in a culture tended to increase (Fig. 4). This would suggest that diapause tendency among the progeny increases with the age of the mother. Such a mechanism may not come into operation until very late in the life of an individual female which would explain why other workers on diapause in *Lucilia* spp. have failed to find any correlation between diapause tendency and maternal age. For instance, neither Cragg & Cole (1952) nor Fraser & Smith (1963), who denied the presence of such an effect, maintained their cultures for long enough periods.

Maternal ageing effects may explain why some females, captured in the field in autumn do not show any reduction of larval diapause incidence in their successive batches when maintained under long photoperiod conditions (Fig. 2). It is difficult to determine the age of field-captured flies, but it is probable that autumn captures

contain a high proportion of old individuals. It is noteworthy that although *L. caesar* females from culture cages in which the original stock has not been replenished have continued to produce egg batches for up to 11 weeks, an individual fecund female has never been reared in isolation for more than 6 weeks.
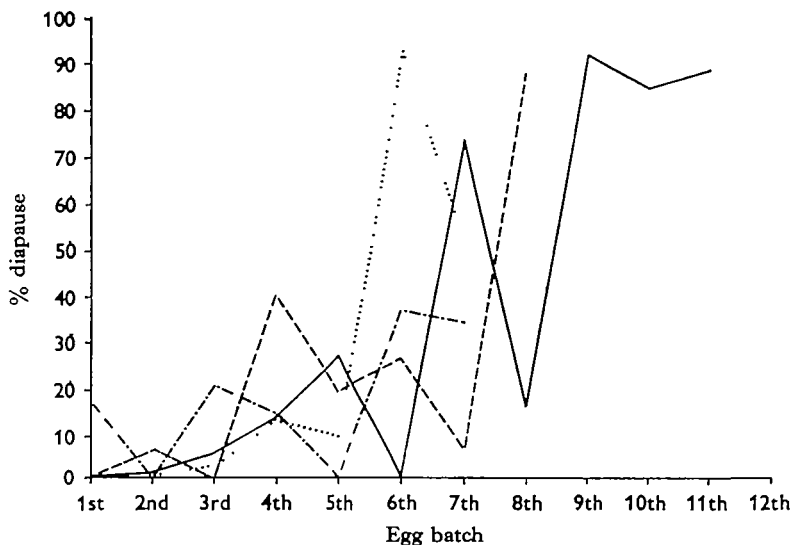

Fig. 4. Effect of increasing maternal age on the larval diapause incidence in four *L. caesar* stocks maintained under long photoperiod conditions. Egg batches were taken from each stock at weekly intervals.

(C) *The nature of the maternal influence*

The immediate cause of diapause in insects is generally recognized as an endocrine deficiency of the prothoracic gland or of the corpora allata (de Wilde, 1962). There remain, however, a few authors who maintain that arrest of growth and development is brought about by the the presence of a diapause hormone. Hinton (1954) postulates that diapause is initiated when the brain ceases to inhibit the release of the diapause hormone. This is certainly the case in the silkworm, *Bombyx mori*, where growth is arrested in the early stages of embryogenesis. Here failure to develop is evoked not by the absence of a growth-promoting factor but by the presence of a hormone, or a balance of hormones (Morohoshi, 1959), in the mother's blood at a time when the future condition of the egg is being determined.

The presence of a maternally-produced inhibitory substance explains satisfactorily how a maternal influence could operate when developmental arrest occurs in the early stages of the embryo. However, nothing is known about how an environmental stimulus acting on the parent can have a delayed action in producing diapause in the offspring after several moults. The view that the central nervous system of the developing insect carries and eventually transmits the 'message' obtained from environmental stimuli can only be supported if the interval between the sensitive stage and the responsive stage does not bridge the early stages of embryogenesis (Lees, 1955). There are now a number of instances known where this interval is apparently bridged (e.g. Schneiderman & Horwitz, 1958; Fraser & Smith, 1963; Saunders, 1965; Ryan, 1965), and the results of this paper also support this conclusion. An attempt was therefore

made to determine whether or not the maternal influence on larval diapause in *L. caesar* was humoral in nature.

By definition, any organ that produces a hormone liberates it into the blood stream which then carries it to the target organ or tissue. The haemolymph of the adult female was therefore regarded as a suitable source of the hypothetical diapause hormone. An attempt was made to transplant haemolymph from a female showing high diapause incidence among her offspring to one with low diapause incidence. A Rossdhu stock of *L. caesar*, the haemolymph donor, was maintained under SPR, while a Carlisle stock was maintained under LPR, and for the duration of the experiment the former retained a high diapause rate while the latter showed a relatively low rate. Sham-operated females injected with Ringer and antibiotics alone were kept as controls.

It was found that operated flies survived as long as non-operated ones. Experimental females injected with haemolymph (plus Ringer and antibiotics) appeared healthy but did not, unfortunately, lay any further egg batches. The injected controls, on the other hand, frequently laid additional egg batches with one female in particular laying seven subsequent batches. At the moment it is not possible to explain why females injected with haemolymph did not lay post-operational eggs even though their ovaries were in a mature condition.

The absence of positive results prevents any conclusions about a diapause hormone in the blood of female *L. caesar* exposed to short photoperiod conditions. The control results, however, indicate that the operational technique was not detrimental to the health of the flies and did not interfere to any extent with the laying of subsequent egg batches. It is hoped in future work to attempt, first of all, to identify the organ(s) responsible for secreting the hypothetical active principle. This could be carried out by a series of transplantation experiments in a manner similar to that of Fukuda (1951, 1952). If such a diapause hormone exists in *L. caesar*, then extracts from the secreting organ would furnish a purer and more concentrated form than could be found in the haemolymph.

GENERAL DISCUSSION

It has now been firmly established that larval diapause in *Lucilia caesar* is influenced by the effect of photoperiod on the maternal generation. Preliminary investigations showed that female blowflies do not respond to the intrinsic rate of change in the photoperiod; it is the absolute length of the light and dark periods that is important.

As de Wilde (1962) points out, the effective length of the light phase under field conditions may be different from the actual calendar daylength. In the event of the threshold being in the region of 1 foot-candle (Lees, 1955), the period of civil twilight* may be added to the daylength between dawn and sunset to obtain effective natural photoperiod. Since the action of photoperiod is known to be closely linked with that of temperature it is possible that low morning temperatures render early illumination ineffective. At any rate it is probable that in *L. caesar* the effective daylength lies somewhere between calendar and civil daylength, the exact position depending on the intensity threshold and the effect of low temperatures on this threshold. At a tempera-ture of 27° C. the threshold photoperiod under laboratory conditions is in the region of

* Civil twilight is the period between the time the sun is on the horizon and when it is 6° below the horizon. At the latter point the light intensity is in the order of 0·4 foot-candles.

15 hr. Since temperature modifies the level of the critical photoperiod in other insects it is likely that at 20° C., the temperature prevalent in the field on a warm summer's day, the threshold for *L. caesar* females will be higher. At the beginning of June when the first females are laying eggs in the field and when the diapause incidence is very low, the photoperiod is in the region of 18 hr. 10 min. and the average temperature is about 12·4° C. This photoperiod occurs again about mid-July when the average temperature is about 15° C., and when the first females giving 100% diapausing larvae begin to appear. It seems probable, therefore, that the critical photoperiod for the majority of *L. caesar* females at field temperatures is slightly over 18 hr. By extrapolating from the work of other authors this figure appears to be a valid one for the latitude, 56° N.

Ring (1967) has shown that under laboratory conditions photoperiod has also a direct effect upon the larvae, but under field conditions this seems to be obscured to a greater or lesser extent by the maternal influence. Early in the breeding season diapause is absent from the offspring, but soon after the summer solstice the incidence increases rapidly to 100% even though the larvae are maintained under long photoperiod conditions. It appears that the maternal influence in the latter part of the breeding season is masking the diapause-preventing-effect of long photoperiod acting directly on the larvae. Conversely, if the larvae from females captured early in the season are reared under short photoperiod conditions there is no increase in diapause incidence relative to the control larvae kept under long photoperiod. It would thus seem that the maternal influence not only induces diapause in the later part of the season but also prevents diapause in the early part of the season. The direct action of photoperiod on the larvae only becomes apparent during the transition period of the breeding season. In these cases the maternal influence and the larval sensitivity towards photoperiod seem to be working in a complementary fashion. The maternal influence is presumably relatively weak with the result that the larvae are capable of responding independently to the attributes of their environment.

It is interesting to note that the diapause incidence tends to increase towards the end of the life of stock cultures maintained in the laboratory under LPR. This usually occurs after 6–10 weeks and it has been postulated that it is an effect of maternal ageing.

SUMMARY

1. The seasonal pattern of diapause incidence in *Lucilia caesar* L. shows that diapause in the 3rd-instar larvae of field-captured females increases rapidly during the month of July. By rearing and testing all larvae under standard laboratory conditions confirmation has been given to the hypothesis that this sudden increase, which occurs soon after the summer solstice, is due to a maternal influence.

2. It has been shown that photoperiod is the most important factor controlling this maternal influence, with temperature playing a modifying role in the photoperiodic response. Females do not respond to the intrinsic rate of change in the photoperiod, but to the absolute levels of the light/dark phases. Long photoperiods (20 hr.) tend to avert, and short ones (12 hr.) tend to induce, larval diapause. Thus *L. caesar* is another example of a 'long-day' species as described by Lees (1955).

3. Under laboratory conditions there is a time lag of 8–10 days before a change in

the absolute length of the photoperiod acting on the mother reflects its diapause influencing effect on the larvae.

4. Maternal ageing produces an increase in larval diapause incidence after 6–10 weeks.

5. It is not yet known whether or not the maternal influence is hormonal in character.

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