Effects of Photoperiod and Parental Age on the Maternal Induction of Larval Diapause in the Blowfly, *Calliphora vicina*

ROBINEAU-DESVOIDY (Diptera: Calliphoridae)

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The blowfly, *Calliphora vicina* entered larval diapause after cessation of feeding in the third instar under the influence of photoperiodic conditions and age of the maternal generation. Adults reared under short-day conditions (12L-12D) produced diapause-destined progeny, whereas those reared under long-day conditions (18L-6D) produced nondiapause-destined progeny at 20°C. After transfer from long-day to short-day conditions, the adults began to produce diapause-destined progeny. Even under constant long-day conditions, aged adults produced some diapause-destined progeny. Furthermore, the variation in the duration of larval development in diapause larvae was larger when the parents were old.

Key words: *Calliphora vicina*, larval diapause, maternal induction, photoperiod, aging

INTRODUCTION

The blowfly, *Calliphora vicina*, is widely distributed in temperate and subarctic zones of the Holarctic. Complicated control of larval and adult diapause by photoperiod and temperature ensures the survival of *C. vicina* in various climatic conditions. In the southern part of its distribution, *C. vicina* develops without diapause during the warm winter. Under moderate climate, this species overwinters as diapause adults. Under cool climate in the northern areas and those at higher altitudes, however, diapause in third instar larvae after cessation of feeding is important for winter survival (see Vinogradova, 1984, 1991 for review). The larval diapause in *C. vicina* is controlled by both photoperiod in the adult stage of the previous generation and temperature during larval development of the current generation. Short-day conditions during the previous generation in combination with low temperatures for the current generation induce larval diapause (Vinogradova and Zinovjeva, 1972; Saunders et al., 1986; Saunders, 1987).

Like many other flies, adults of *C. vicina* have an extended longevity and lengthy reproductive period of three months or longer (Vinogradova, 1976). Therefore females emerging in spring possibly lay eggs throughout the summer. However, in spring and early summer, production of nondiapause progeny is adaptive, although in late summer production of diapause progeny is preferable. Therefore, it seems ecologically significant for adults of *C. vicina* to have the potential to reprogram maternal determination of larval develop-

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ment during the course of their reproductive period. Vinogradova and Zinovjeva (1972) and Vinogradova (1976) showed that adults of C. vicina can reprogram maternal induction of larval diapause in response to the change from long-day to short-day conditions. However, they did not show the results of the control group that had been continuously kept under long-day conditions. Chernysh (1977) reported preliminary results that older adults produce more diapause-destined progeny, even though they were kept continuously under long-day conditions. We must discriminate between the effect of photoperiod and that of adult age. Furthermore, larval diapause in C. vicina is not an all-or-none response and maternal conditions also control its duration (Saunders, 1987). In the present study, therefore, we re-examine the reprogramming of the maternal induction of larval diapause by photoperiodic changes and adult age, recording not only the incidence of diapause but also the duration of larval development.

MATERIALS AND METHODS

A laboratory culture of C. vicina that originated from the Murmansk suburbs (68°57′ N, 33°10′ E), North Russia, was used. This population is characterized by relatively stable larval diapause as compared with southern populations (Vinogradova, 1988; Chernysh and Simonenko, 1988). Adults, at a density of 2–3 individuals/l, were maintained in 30 l gauze-covered cages under 20L–4D at 20 ± 1°C. A continuous diet of beet sugar, dry milk and fresh beef was supplied and water-soaked cotton pads were placed in the cages. Pieces of meat were also used for egg collection. Those pieces of meat containing eggs were placed in 250 or 500 ml glass jars on slightly moistened sawdust covered by filter paper, and maintained under 12L–12D at 12 ± 1°C. Fresh meat was added when the previous portion was consumed until the end of the feeding period. After feeding, larvae migrated into the sawdust where they pupariated.

After adult emergence, five females and five males were reared in each cage (700 ml) at 20°C. The cage was made of a glass tube placed on a plastic dish with compartments for water-soaked cotton, dry milk, sugar and fresh meat, and the top was covered by gauze. Adult flies were divided into three groups, each of which included ten cages. In the first group, flies were continuously kept under long-day conditions (18L–6D). In the second group, they were transferred from long-day to short-day (12L–12D) conditions 7 days after adult emergence, because about 7 days are necessary for the maturation of the first egg batches at this temperature. In the third group, flies were continuously kept under short-day conditions. Oviposited eggs were collected from the cages on days 9, 11, 18, 24 and 31, mixed and placed in glass jars with meat and sawdust. These were also kept under 12L–12D at 12°C. Under these conditions larvae entered diapause during the third instar, after cessation of feeding depending on the photoperiodic conditions during the adult period of the maternal generation (Vinogradova, 1984). To check the duration of larval development, puparia were collected daily or every few days, in accordance with the dynamics of pupariation.

RESULTS

From the pupariation profiles of 15 groups of larvae, we considered the insects pupariating earlier than 60 days after oviposition as nondiapause (open columns in Fig. 1) and those pupariating later as diapause (shaded columns in Fig. 1). The eggs laid on days 9,
11 or 18 by the adults kept under long-day conditions primarily became nondiapausing larvae. When adults were transferred from long-day to short-day conditions on day 7, however, the proportion of diapausing progeny increased drastically between days 11 and 18 (Fig. 1). Thus, the females reprogrammed the maternal determination of larval diapause in response to the change in photoperiodic conditions. Although 22% of the eggs laid on day 9 by adults kept under short-day conditions became nondiapausing larvae, most or all eggs laid on days 11, 18, 24 or 31 entered larval diapause. Even under constant long-day
conditions, the adults began to produce diapause progeny on day 24, and the proportion of diapause progeny was still higher on day 31 (Fig. 1).

The variation in the duration of larval development in diapause insects also fluctuated as adults aged (Fig. 2). The coefficient of variation was significantly larger in the progeny laid on day 31 than in those laid on day 24 in each photoperiod group \[ p < 0.01 \] by two-tailed variance ratio test (ZAR, 1984, p.125–126). Thus, age of adults had some effects on the duration of larval diapause in the next generation.

**DISCUSSION**

Maternal photoperiodic effects on the induction of larval diapause have been reported in some insects (DANKS, 1987; MOUSSEAU and DINGLE, 1991) including three species of Calliphoridae, i.e., *Lucilia sericata* (Cragg and Cole, 1952; Saunders et al., 1986), *Lucilia caesar* (Fraser and Smith, 1963; RING, 1967) and *C. vicina* (Vinogradova and Zinovjeva, 1972; Saunders et al., 1986; Saunders, 1987). The present results confirm the maternal photoperiodic control of larval diapause in the Murmansk strain of *C. vicina*. In the same geographic population, however, Vinogradova (1988) showed that the incidence of diapause varies between 55 and 100% when the parents are reared under long-day conditions ranging between 16L–8D and 24L–0D. How can we explain these conflicting results, even when the rearing temperature was the same? Vinogradova (1988) used the average percentage of diapause in several egg batches laid over 45 days for each photoperiod. Even in our experiment, adults began to produce diapause-destined progeny on day 24 under long-day conditions, and the incidence of diapause was still higher in the progeny laid on day 31. On the other hand, the incidence of diapause under long-day conditions fluctuates between 0 and 90% in successive laboratory generations in the Gorkiy strain of *C. vicina* (Vinogradova and Bogdanova, 1980). Therefore, the effect of aging or the spontaneous fluctuation in the incidence of diapause, or both, may have caused the high incidence of diapause under long-day conditions in the experiment by Vinogradova (1988).
Maternal Induction of Diapause

Maternal age affects diapause in offspring in many insects, and in most cases the proportion of diapause increases with maternal age (MOUSSEAU and DINGLE, 1991). In L. caesar, maternal aging produces an increase in the incidence of larval diapause under long-day conditions in the progeny (RING, 1967). In C. vicina also, old adults produced a notable proportion of diapause-destined progeny even though they were kept continuously under long-day conditions. We can speculate that the induction of diapause by maternal aging is an adaptation at high latitudes where temperature drops abruptly during the season when the daylength is still relatively long, although we have not yet shown the critical daylength for the induction of diapause in this strain.

Furthermore, the adults that had once produced nondiapause-destined progeny began to produce diapause-destined progeny after being transferred to short-day conditions. Thus, adults of this species can reprogram the maternal determination of larval diapause in response to the change in photoperiodic conditions. Because of the long reproductive period of C. vicina, this reprogramming has some ecological significance, especially in the northern part of its distribution where warm seasons are relatively short. In the Scottish strain of C. vicina, adults under 12L–12D at 18–26°C that lay eggs on or before day 9 give rise to a low incidence of diapause, whereas those laid on day 10 and later give rise to a high incidence (SAUNDERS, 1987). From these results, SAUNDERS (1987) concluded that there is a temperature-compensated mechanism for accumulating short-day cycles. In the Murmansk strain, as well, maternal induction of diapause was not complete on day 9 under 12L–12D at 20°C, although the incidence of diapause (78%) was much higher than on day 9 (0%), but a little less than on day 10 (86%), under the same conditions in the Scottish strain (SAUNDERS, 1987). Furthermore, when 11 short-day cycles were experienced after the photoperiodic transfer (day 18), the incidence of diapause (74%) was similar to the value on day 9 under continuous short-day conditions. Therefore, the number of short-day cycles necessary for diapause determination in this species is about 10 in both populations and in both programming and reprogramming of the progeny development.

We show here another effect of maternal aging. The variation in the duration of larval development in diapause larvae was larger when the parents were old. This means that adults lose the ability to induce the proper intensity of diapause in their progeny by aging. Furthermore, there exists the possibility that the diapause-destined progeny in old parents under long-day conditions resulted from aging only and had no ecological significance, although we speculate this was adaptive, as described above. More than 50% of the studies up to the present that have reported maternal control of diapause have dealt with egg diapause (DANKS, 1987; MOUSSEAU and DINGLE, 1991), and the mechanisms by which mothers control diapause of their eggs have been extensively studied in the silkworm, Bombyx mori (YAMASHITA and HASEGAWA, 1984). In contrast, we know almost nothing of the mechanism by which mothers control diapause in later stages (ROCKEY et al., 1989; MOUSSEAU and DINGLE, 1991). However, complex and delicate mechanisms must exist for this control, because physiological mechanisms in the body of mothers cannot directly control development in the later stages of their progeny. During adult aging, insects gradually lose the efficiency of various physiological mechanisms (ROCKSTEIN and MIQUEL, 1973). The maternal control mechanisms may well lose their ability to function during the aging processes, and therefore, old adults cannot control the intensity of diapause in their progeny.
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