Table 1 Median date of diapause termination (larval–pupal ecdysis) by *Meleoma signoretti* after transfer from out doors to various photoperiodic regimes

Date of transfer	Photoperiod (LD) 10:14	12:12	14:10	16:8	Natural
Nov. 22	— (0)	— (0)	Feb. 1 (10)	Feb. 1 (10)	Apr. 26 (2)
Dec. 22	— (0)	— (0)	Jan. 13 (11)	Jan. 31 (9)	Apr. 28 (5)
Jan. 22	— (0)	— (0)	Feb. 9 (10)	Feb. 9 (8)	May 1 (8)
Feb. 22	— (0)	— (0)	Mar. 5 (11)	Mar 7 (12)	Apr. 20 (7)
Mar. 22	Mar. 30 (12)	Mar. 30 (12)	Mar. 30 (12)	Mar. 30 (12)	Mar. 31 (12)

Temperature: stationary photoperiods 24 ± 1 °C; natural daylength 23 ± 4 °C. No. of surviving individuals, from the original 12 to 14, in parentheses.

photoperiod for diapause termination in the laboratory is between light–dark (LD) 12 : 12 and LD 14 : 10. This range in photoperiods corresponds with the daylength (sunrise to sunset, plus twilight) in March, at the time diapause ends in nature.

The higher incidence of pupation in late season samples (Table 1) suggests that low temperatures enhance survival during diapause, especially at the end of winter when metabolic reserves are probably low. The approximately one-month delay in pupation in the November, December, January and February samples (Table 1), for natural daylength (in relation to the March sample) suggests that, although low temperatures are not necessary for ending diapause, they hasten diapause termination at the end of winter.

Table 2 Number of days (mean ± s.d.) to terminate diapause (initiate oviposition) by *Chrysopa downesi* after transfer from outdoors to various photoperiodic regimes

Date of transfer	Photoperiod (LD) 11:13	12:12	13:11	14:10	15:9	Natural*
Dec. 22	‡	78±12	22±5	17±5	14±2	92±10
Feb. 7	81±12	46±25	10±3	—	8±3	32±5
Mar. 1	40±34†	7±1	7±2	—	—	6±1
Mar. 21	4±2	4±1	3±1	—	—	4±1

Temperature: stationary photoperiods 24±1 °C; natural daylength 23±4 °C. Number of pairs in each condition 8 to 10; incidence of oviposition in each condition 80 to 100%.

*Median dates of diapause termination in the December 22 to March 21 samples are April 5, March 20, March 8 and March 25 respectively.

†Diapause had broken in two animals in this sample.

‡Death occurred before diapause termination.

In contrast to those with *M. signoretti*, the tests (Table 2) with *C. downesi* show that: first, diapausing adults transferred into the laboratory after the winter solstice exhibit a quantitative response to daylengths that lie between LD 11 : 13 and LD 15 : 9, that is in the December 22 and February 7 samples the rate at which diapause comes to an end is directly related to the actual duration of daylength. Second, diapause maintenance after the winter solstice is related to the actual duration of the short winter days. Third, diapause is gradually brought to an end by the lengthening late winter days, that is, as the days lengthen there is an increase in the rate of diapause development, and diapause ends near the time of the vernal equinox (between March 1 and March 21), and fourth, diminution of both diapause intensity and sensitivity to photoperiod, which occurs slowly at the beginning of winter and quickly at the end of winter, is directly related to actual daylength.

Thus the data indicate that *C. downesi* and *M. signoretti* have evolved grossly different photoperiodic reactions that serve to synchronise the end of their diapause with the beginning of spring. In the case of *C. downesi* and other *Chrysopa* species for which we have considerable phenological data, the type of response is consistent with the phylogenetic relationships of the species[16]. For example, comparisons between populations of *C. downesi* and the closely related *C. carnea* from the north-eastern USA, show that both respond quantitatively to actual daylengths during diapause maintenance but each exhibits the response at a different time of the year—autumn for *C. carnea* and early and late winter for *C. downesi*. As a result, these sympatric species, which readily hybridise in the laboratory and which hibernate in overlapping habitats, end diapause and begin postdiapause reproductive activity at least a month apart. This seasonal difference in the timing of reproduction helps prevent the univoltine *C. downesi* from hybridising with its close relative *C. carnea*. Therefore, the characteristic response of *C. downesi* to daylength during the winter not only serves to time the end of diapause with the advent of favourable spring conditions, but it also functions as an effective reproductive barrier which maintains this species as a separate entity in the regions of north-eastern USA and eastern Canada.

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Effect of light on egg-laying rate and mating speed in phototactic strains of *Drosophila*

IN *Drosophila*, phototactic behaviour can be quantitatively described using Hirsch–Hadler classification mazes[1]. Flies entering the maze make a series of 15 consecutive light–dark choices and receive phototactic scores ranging from 1.0 (highly photonegative) to 16.0 (highly photopositive). A photoneutral population has an expected mean photoscore of 8.5. The phototaxis maze has provided a useful tool for the characterisation of phototactic behaviour in natural populations of *Drosophila* and for the creation of photopositive and photonegative strains of flies by artificial selection. Natural populations of *D. melanogaster* and *D. pseudoobscura* are photoneutral in general, but respond rapidly to selection for positive or negative phototactic behaviour[2,4,7,8]. Genetic analysis of phototaxis in *Drosophila* suggests that this behaviour is a polygenic trait with low heritability[3,4,6]. Suspension of artificial selection results in rapid reversion to photoneutrality which illustrates the principle of genetic homeostasis and suggests that changes

in fitness accompany selection for photopositive and photonegative behaviour[8].

Two components of fitness—rate of egg deposition and mating speed—were measured in an unselected population and in a photopositive and photonegative population of *D. melanogaster*. The investigation was carried out under two sets of environmental conditions: continuous darkness and continuous light. Ten pairs of flies from each population were maintained separately for 1 week in continuous light and ten pairs from each population were maintained for 1 week in continuous darkness. Five replications were performed for each population in each condition. Egg-laying surfaces containing fresh cornmeal–molasses medium were replaced daily and the number of eggs deposited during the preceding 24 h was recorded.

Table 1 Average number of eggs laid by phototactic strains of *D. melanogaster* during 1 week of constant light and constant darkness

Population	Light (mean ±s.e.)	Dark (mean ±s.e.)	*t*
Unselected (7.9±0.12)	1,111.2±27.61	1,110.1±34.76	0.25
Strain 0 (+) (13.93±0.14)	748.2±33.11	526.6±25.26	5.32*
Strain 0 (−) (2.91±0.11)	560.4±36.17	1,672.7±126.9	15.22†

* $P = 0.005$.
† $P = 0.0001$.

Results are shown in Table 1. The unselected strain was fairly photoneutral and the number of eggs deposited during 1 week did not differ in light or darkness. On the other hand, strain 0 (+) was highly photopositive and is seen to lay more eggs in continuous light than in a continuously dark environment. The opposite is true of flies from strain 0 (−), many more eggs being deposited when the flies were kept in continuous darkness.

To determine whether reduced insemination in light or dark was responsible for the reduction in oviposition, the effect of light and darkness on mating speed was investigated among flies from each population. Groups of twenty virgin males and twenty virgin females from each population were stored separately at 24±1 °C for 3 d. Males and females from the same population were then placed together in total darkness or light. After 5, 15, 30 and 60 min females were removed and placed individually in vials. At least five replications were made of each test. The presence of larvae in the vial indicated that the female had mated.

The proportion of flies mating at each time is shown in Fig. 1. In the unselected population, flies mated faster in the light. After 2 h (not shown) virtually 100% of the females had mated. Flies from strain 0 (+) mated even faster in the light than did the unselected flies. At all four times, however, a greater proportion of flies from strain 0 (−) had mated in darkness than in the light. Early mating was definitely inhibited by the unpreferred environment but within 1 or 2 h females from all strains had mated both in light and in darkness. Therefore absence of insemination is not likely to be the cause of the alteration of oviposition rates in phototactic strains when placed in an unpreferred environment.

Table 2 Average number of eggs laid by phototactic strains of *D. psuedoobscura* during a week of constant light and constant darkness

Population	Light (mean ±s.e.)	Dark (mean ±s.e.)	*t*
Unselected (8.6±0.19)	834.6±112.94	880.6±69.44	0.34
Strain 25 (14.93±0.08)	1,641.0±66.18	868.0±115.14	5.82†
Strain 27 (2.54±0.10)	1,346.6±81.94	2,026.2±152.35	3.92*

* $P = 0.005$.
† $P = 0.0005$.

The effect of light or dark on egg deposition was examined in a photopositive population (strain 25) and a photonegative population (strain 27) of *D. pseudoobscura* obtained from Professor Th. Dobzhansky. A recently collected population of *D. pseudoobscura* was provided by Dr F. Ayala. Egg deposition was measured in these three populations by the same method described for *D. melanogaster* (Table 2). Again, the presence or absence of light had no effect on the number of eggs laid by the unselected flies. Continuous light or darkness affected the photopositive and photonegative populations of *D. pseudoobscura* in the same way as observed for *D. melanogaster*.

It is difficult to know whether the preferred environmental condition (light or its absence) stimulates oviposition or if the unpreferred condition inhibits egg laying, or both. Regardless of the cause, it is obvious that the *Drosophila* species investigated here have a greater relative fitness in environments that they are genetically influenced to select.

Both *D. melanogaster* and *D. pseudoobscura* are light-independent with respect to mating behaviour[9]. Our results show that selection for phototactic behaviour may modify this light-independence in one direction or the other, at least for early matings. Photopositive and photonegative strains of *D. pseudoobscura* have been shown to mate with similar frequency in light, while in darkness, photonegative flies mate slightly more rapidly[10].

Equally important to overall reproductive fitness is the

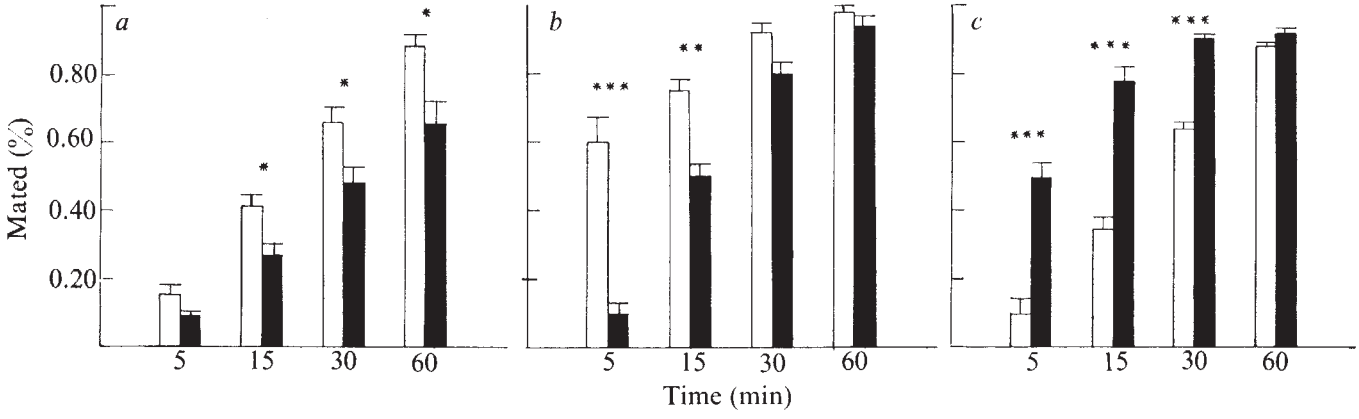

Fig. 1 Average percentage of females mated after 5, 15, 30 and 60 min in light (open bars) and darkness (solid bars). *a*, Unselected; *b*, strain 0 (+); *c*, strain 0 (−). * $P=0.05$; ** $P=0.01$; *** $P=0.005$.

deposition of eggs after insemination. Individuals mating more slowly and depositing fewer eggs will leave fewer offspring relative to those individuals that mate and oviposit quickly. Light is an important environmental variable affecting natural populations. The presence of genetic variation for phototactic behaviour may be extremely important for adaptation of *Drosophila* populations to new or changing environments. In the experiments reported here, the light-dependent fitness of flies is directly related to their genotype for phototactic behaviour. Mayr[11] has proposed that behavioural changes precede morphological changes during evolution. The results presented here strongly support his idea.

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Corpus allatum activity and wing determination in *Megoura viciae*

ALARY polymorphism in aphids is influenced by several environmental stimuli acting prenatally and/or postnatally[1]. In *Megoura viciae*, alatae are determined prenatally by exposing previously isolated apterae to a short crowding stimulus[2], and the physiological mechanism controlling this process would be expected also to show an immediate response to the stimulus. White[3] suggested that the prenatal physiological control of alary polymorphism is exercised by the activity of the maternal corpus allatum (CA) which would produce less juvenile hormone (JH) when aphids are crowded than when they are isolated. She assumed that CA volume and nuclear diameter were directly proportional to JH synthesis and secretion and she reported that in *Brevicoryne brassicae* the CA nuclear diameter is greater in isolated aphids than in crowded aphids[3]. She also found that CA volume was greater in alatae, which have only apterous progeny, than in apterae which have alate and apterous progeny[4]. The application of JH analogues to alatiform larvae resulted in the apparent suppression of alate characters[5,6]. Experiments with aphids, however, have shown that synthetic JH only initiates the production of supernumary larvae[7] and that it has no apterising effect[8]. In locusts volume cannot be correlated with JH concentration in either CA or haemolymph[9]. These studies have raised serious doubts about the role of JH in the control of alary polymorphism and the experiments reported here were carried out to determine the effect of crowding on the volume and ultrastructure of CA in apterous *M. viciae* in which alary polymorphism is controlled by a maternal physiological mechanism.

Isolated adult apterae, reared on 'tic' beans at 15±2 °C and a photoperiod of 16.5 h were prepared as alatae producers and apterae producers by confining them in specimen tubes either singly or in groups of 10 for 24 h (ref. 2). Aphids were fixed, embedded and stained for light and electron microscopy and the methods used are summarised in Table 1. Sagittal sections of whole aphids were cut serially and CA volume was estimated from planimetric measurements of consecutive sections in a series.

The mean CA volume in apterae producers (22,804 μm^3; s.d. 5,660 μm^3; $n = 10$) is not significantly different from that of alatae producers (19,028 μm^3; s.d. 4,888 μm^3; $n = 12$) ($P > 0.05$). Sagittal sections of the heads of three isolated and three crowded apterae were cut with glass knives. Thin sections were examined through an electron microscope (AEI model 6B) and the CA was identified with the aid of semithin sections (0.05 μm). Nuclei are irregularly shaped in both isolated and crowded apterae, they occur near the periphery of the gland, are often elongated and the nuclear membrane is highly invaginated. We therefore consider that nuclear dimensions cannot be used as a criterion of CA activity and that the contradictory descriptions of nuclear shape in active CA of other insect species[10–13] make it impossible to use shape as an index for JH synthesis and secretion in *M. viciae*. Although mitochondria are usually larger in active CA than in inactive CA[11,13], there is no significant difference between the mean sizes of fifty mitochondria from each of the six aphids examined ($P > 0.05$). Smooth endoplasmic reticulum, membranous whorls and cytoplasmic vesicules, which are characteristic of inactive CA in some insect species[14,15], occur in both isolated and crowded apterae, and the cytoplasm also contains numerous neurosecretory axons.

The results indicate that the synthetic and secretory activity in CA of apterae-producing and alatae-producing aphids are the same, since the volume, mitochondrial size and cytoplasmic membrane composition are similar in both groups of aphids. Nuclear dimensions cannot be used as an index of CA activity, since nuclei have an irregular shape in adult apterae, and changes in the ultrastructure of the endoplasmic reticulum (which is the best individual index of CA activity) occur as much within a larval, pupal or imaginal instar as they do between instars[14,15]. We therefore consider that differences in volumetric and nuclear dimensions between alatae producers and apterae producers and between alatiform and apteriform larvae can no longer be regarded as indicative of differences in CA activity[3,4,16]. We can find no evidence to support either White's[3] assertion that the maternal CA is involved in the prenatal control of alary polymorphism or Elliott's[16] suggestion that the CA is involved in the control of both ovarian growth and larval development in aphids. This does not mean that alary polymorphism is unaffected by JH concentration in the haemolymph since this may be controlled by the presence of specific metabolic enzymes[17] and protein carriers[18] which have been reported in other insect species.

Table 1 Summary of methods used in fixing, embedding and staining *M. viciae* for light and electron microscopy

	Fixative	Embedding material	Section thickness	Stain
Whole aphid	Aq. Bouin + 0.5% TCA[19]	Celloidin and Paraplast	7 μm	Paraldehyde Fuchsin[19]
Heads	Formaldehyde-glutaraldehyde[20]	Araldite	0.5 μm	Toluidine blue
			60–120 nm	Uranyl acetate + lead citrate