Effects of changing photoperiods in the life cycle regulation of the comma butterfly, *Polygonia c-album* (Nymphalidae)

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ABSTRACT. 1. Regulation of adult reproductive diapause and seasonal polyphenism was studied in two populations of the comma butterfly, *Polygonia c-album* (L.) (Nymphalidae), from Stockholm, Sweden, and Oxford, England.

2. In the univoltine Stockholm population short and long constant daylengths (in the range 12–22 h) at 20°C were ineffective in averting the production of the dark, generally diapausing, morph, but the non-diapausing light morph could be produced if daylengths were increased during larval development. The procedure was especially effective with increases from 12 to 22 h, but the tendency was the same with a more realistic increase, from 18 to 20 h.

3. In the partially bivoltine English population a critical constant daylength for morph and diapause induction was found between 12 and 18 h. Decreasing daylengths above the critical daylength early or late in larval development resulted in production of the diapausing morph.

4. These results suggest a system for environmental control where daylengths which increase throughout the larval period indicate an early date before summer solstice, meaning that there is sufficient time for a second generation of offspring to reach the hibernating adult stage before winter. The ecological significance of the results is discussed.

Key words. Photoperiodism, seasonality, polyphenism, diapause.

Introduction

Insects that live in seasonal environments must regulate their life cycles in response to environmental cues that indicate the time of year. It is now thought that photoperiod together with temperature are the seasonal cues that are most commonly used. Many species have been shown to react to critical constant photoperiods, often shifting with temperatures (Danilevski, 1965; Saunders, 1976; Beck, 1980). However, photoperiods are not constant in nature (cf. Fig. 4).

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Therefore, the question has often arisen as to what role adaptations regulated by the direction of change might play in photoperiodism (Corbet, 1955; Danilevski, 1965; Saunders, 1976; Beck, 1980). Several authors have reported effects of changing daylengths, involving diapause induction, maintenance and termination as well as morph determination, in many insect groups, e.g. Odonata (Corbet, 1955), Orthoptera (Norris, 1965; Tanaka, 1978), Coleoptera (Blake, 1960, 1963; Siew, 1966; Thiele, 1969), Lepidoptera (Danilevski, 1965; Wellso & Adkisson, 1966), Heteroptera (Vepsäläinen, 1971, 1974; Solbreck, 1979; Numata & Hidaka, 1983), Neuroptera (Tauber

& Tauber, 1970, 1973, 1976) and Diptera (Vinogradova, 1978).

The responses are of different types and can often be described as a sequence of developmental stages sensitive to critical photoperiods. Clear cases of sensitivity to changes in photoperiod *per se* (*sensu* Tauber *et al.*, 1986), by which is understood an ability to measure the direction of change of photoperiod itself, not only if it is above or below a threshold value during a particular developmental stage, are rare. The examples given by Tauber *et al.* (1986) involve effects of changes entirely above or below critical daylengths, which has been demonstrated at least in *Chrysopa carnea* Stephens (Tauber & Tauber, 1970), *Hylemyia antiqua* MG. (Vinogradova, 1978) and *Riptortus clavatus* Thunberg (Numata & Hidaka, 1983). The ecological significance of these results remain unclear (Tauber *et al.*, 1986).
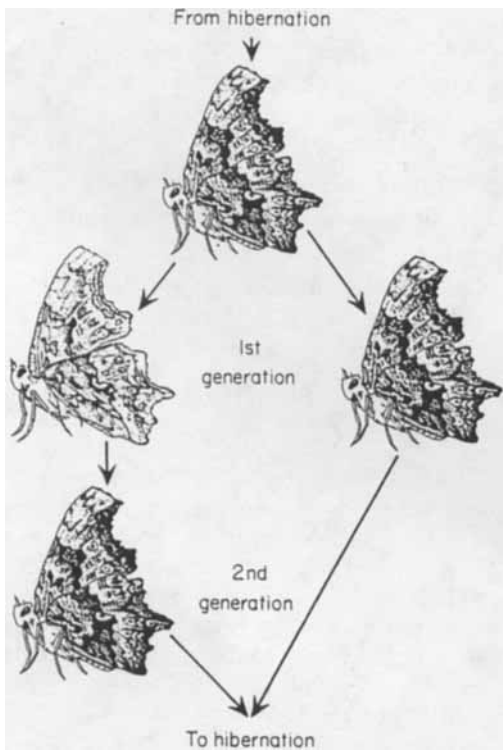

FIG. 1. The life cycle of *Polygonia c-album* in areas (e.g. England) where the species is partially bivoltine. Hibernation is in the adult stage. Females that oviposit in the spring may give rise to mixed broods of the dark (generally hibernating) and the light (non-diapausing) morph.

In the present study I investigated the effects of photoperiod and, in particular, changes in photoperiod during larval development in two populations of the comma butterfly, *Polygonia c-album* (L.) from Sweden and England. In insects, seasonally occurring morphs (seasonal polyphenism) are often coupled with diapause (Shapiro, 1976). Two distinct seasonal morphs occur in *P.c-album* (Frohawk, 1924; Ford, 1945). One morph, the 'spring' or 'dark' type, has the undersides of the wings coloured in dark brown, black and green. Individuals of this morph generally enter a reproductive diapause and hibernate in the adult stage before mating and ovipositing in the spring (Fig. 1). The other, 'summer' or 'light' morph, has wings with light brown or ochreous undersides. Individuals of this morph rapidly mature sexually, oviposit in the summer, and give rise to a new generation of butterflies. A given female of the dark morph in the spring may give rise to a mixed brood of both morphs. The ratio between the morphs, and consequently adult reproductive diapause, has long been thought to be under some kind of environmental control. Different explanations have involved temperature (Ford, 1945), food quality (Harper & Waller, 1950) and light (Bailey, 1984). I show that both populations respond to changes in photoperiod and discuss the ecological significance of these results and of other evidence for such responses in insects.

Materials and Methods

All material originated from females that were captured in the Stockholm area in Sweden (59.5°N) and in Oxford, England (52°N). The females oviposited on the principal hostplant *Urtica dioica* (L.) in the laboratory (in a short-day regime; 4–6 h light), whereupon the eggs were transferred to environmental cabinets. The larvae were reared in transparent plastic jars kept amply supplied with *U.dioica*. Temperatures were held constant (at 20°C when not stated otherwise) during development from egg to adult, and photoperiods were constant or changed during the larval stage according to each experiment described below and in the results sections. To avoid effects of selection for direct development, a maximum of two generations of larvae were bred from captured animals. They are labelled below as F_1 and F_2. At

the time of adult eclosion it was noted to which seasonal morph the animal belonged. The two morphs could easily be distinguished from each other and intermediates were not observed.

The adult morphs were used as indications of the probable developmental status (diapausing or directly developing) of each individual. There is ample evidence of a high correlation between the two in Palearctic *Polygonia*. In the field, in areas were both morphs occur, animals seen in the spring and autumn almost invariably are of the dark morph, whereas the light pigmented morph is almost exclusively seen in the summer in *P.c-album* (e.g. Frohawk, 1924; Ford, 1945; Langer, 1958; Dal, 1978; Henriksen & Kreutzer, 1982; Thomas, 1986; Anonymous, 1987), *P.egea* Cramer (Niculescu, 1965; Dal, 1978) and *P.c-aureum* L. (Hidaka & Aida, 1963) although exceptional individuals may occur (Frohawk, 1924; Ford, 1945). In the laboratory, females of the light morph seldom fails to mature sexually and oviposit within a week, whereas females of the dark morph normally do not mate or oviposit for several weeks after emergence in *P.c-album* (Nylin, this study) as in the closely related *P.c-aureum* (Hidaka & Aida, 1963) although, exceptionally, the dark morph may not diapause (Oliver, 1935; Nylin, this study). Finally, diapause regulation in the genus *Polygonia* is well known physiologically because of the work done on *P.c-aureum*. In this species production of the lightly pigmented summer form is induced by long days during the larval stage (Hidaka & Aida, 1963; Fukuda & Endo, 1966). Hidaka & Aida (1963) reported a 100% correlation between the adult morph and the state of ovarian development and concluded that the diapause seems to be inseparably bound to the seasonal form of the adult.

A number of experiments were carried out during the summers of 1985 to 1988:

(a) As a check on the correlation between the morphs and adult reproductive diapause each summer a number of F_1 adults (>5 pairs of each morph) were kept in cages with *U.dioica* for a period of 1–2 months, and the occurrence of matings or eggs were noted. In 1986, adults of both morphs were also kept together in cages, dark males with lightly coloured females and vice versa, and finally several pairs of the light morph were kept separately each year in 1986–88.

(b) The offspring of Swedish females that were caught at first sighting in the spring of 1985 (early May) were used. As soon as they hatched, a group of larvae were transferred to outdoor flight chambers where *U.dioica* was cultured in pots. This was done on three occasions beginning with the first eggs laid, on 13 May.

(c) The F_1 offspring of Swedish females, caught in early May of 1985, were kept in six combinations of two temperatures and three constant photoperiods (12L/12D, 17L/7D and 22L/2D). The temperatures used were 15°C, which is similar to daily mean field temperatures during June in the Stockholm area (15.3°C) and 20°C, which is a typical daytime maximum temperature for June, according to statistics from the Swedish Meteorological and Hydrological Institute. In addition, some of the larvae were divided into four groups which were transferred between photoperiods. The F_2-generation, offspring of the directly developing individuals of the F_1-generation, were transferred from 12 h to 22 h 8 days after hatching. In 1986 the same procedure was repeated with the F_1-offspring of females captured in early May, and a few larvae were kept in a constant daylength of 22 h.

(d) The F_2-offspring of one female was divided into four categories which experienced constant or changing photoperiods. In this experiment the changes were more similar to those in nature, between 18 h and 20 h.

(e) The F_1-offspring of one English female captured in April of 1987 was split into eight groups (later combined into seven), that were kept in constant or changing daylengths (12–20 h).

Results

(a) *Light and dark morph F_1 in cages*

No matings between adults of the dark morph, or ovipositing by darkly coloured females, were observed in 1985–88 ($N>25$ pairs). In contrast, matings and eggs were seen each year in the cages with lightly coloured insects. In a more detailed experiment the result was the expected (if there is a high correlation between morph and diapause): many (>100) eggs were laid within a week in the cage with only the light morph (five pairs) as well as in the cage with dark males and lightly coloured females (four pairs), but none in the cages with only the dark morph (five pairs) or

with light males and dark females (three pairs). The dark females in the two last cages were dissected after 2 months and found to contain no mature eggs. In addition, five pairs of lightly coloured insects were kept in separate cages. None failed to produce at least some eggs. The same was true when this was repeated in 1987 with seven pairs of English *P.c-album* and in 1988 with seven Swedish pairs. The two morphs were otherwise not usually kept together, but when this was done on one occasion in 1987 two matings between dark males and light females were observed.

(b) *Swedish F_1 in outdoor conditions*

There was a slight, but consistent, difference between the sexes of *P.c-album* concerning the proportion of individuals developing into the light morph in experiments b–e (the frequency was lower in males). Since this only marginally affects the larger differences between environmental conditions these results will be discussed elsewhere and all animals reared in one group have here been pooled.

A total of forty-seven adults eclosed, the first on 8 July. Without exception they were of the dark morph. Since the parental females were captured very early in spring, and the first eggs laid by them after capture were used in this experiment, this result suggests that *P.c-album* was univoltine in 1985 in the Stockholm area. The early summer of this year was not unusually cool. The mean temperature during May (from 13 May) was 12.7°C and during June 14.7°C, compared to 11.0°C and 15.3°C, respectively, for a 30-year period in the Stockholm area according to meteorological records (SMHI). Thus, there is reason to conclude that this population of *P.c-album* is generally univoltine. Additional evidence comes from the fact that the light morph of *P.c-album* is only rarely seen in northern Europe (always in summer; Langer, 1958; Dal, 1978) and is not represented in the collection of Swedish *P.c-album* at the Swedish Natural History Museum.

(c) *Swedish F_1 and F_2 in daylengths of 12–22 h*

The results from the first in the series of laboratory experiments are shown in Table 1. It can

TABLE 1. Proportion of the lightly pigmented, non-diapausing, morph of *Polygonia c-album* produced in different combinations of temperatures and constant or changing photoperiods, in offspring of females from the Swedish population.

Exp. category		Temperature (°C)	Photoperiod (h)		Light morph (%)	N
			Early	Late		
F_1	1985	15		12	0	25
		15		17	0	25
		15		22	0	19
		20		12	0	200
		20		17	0	191
		20		22	0	70
		20	12	→ 22*	0	4
		20	12	→ 22†	78	9
		20	22	→ 12*	0	9
		20	22	→ 12†	0	10
F_2	1985	20	12	→ 22†	36	248
F_1	1986	♀1 20	12	→ 22†	100	23
		♀2 20	12	→ 22†	100	46
		♀3 20	12	→ 22†	74	35
		20		22	20	10

* Moved to new photoperiod at the time of hatching from the egg.
† Moved at time of hatching + 8 days (about the time of moulting from second to third larval instar).

be seen that in all constant daylengths only the dark morph was produced. Hence, a critical daylength for the induction of the light morph and direct development was not found at the experimental temperatures. The dark morph was also produced when larvae experienced decreasing daylengths and when they were transferred from 12 h to 22 h at the time of hatching. In contrast, when larvae were transferred from a 12 h daylength to 22 h 8 days after hatching (at about the time of moulting from the second to the third larval instar) a majority of the directly developing light morph was produced (the deviation from the expected (only dark morph) result is significant; Fisher's exact test, $P=0.00226$). Thus, diapause may be averted by an increase in photoperiod during larval development. The egg stage does not seem to be sensitive. Since individuals of the light morph gave rise to offspring after having been transferred to a short-day regime at eclosion in this and the following experiments the adult stage likewise does not seem to be sensitive to photoperiod.

When the offspring of these light morph insects experienced the same increase in daylength 36% developed into the light morph (Table 1).

A very high proportion of the light morph (100% in the offspring of two of the parental females) was produced when the same increase in daylength was applied to a new F_1-generation of offspring in 1986 (Table 1). The proportion developing into the light morph was lower in the offspring of one of the parental females (Fisher's exact test $P = 0.00027$), indicating that genetic differences (or maternal effects; cf. Hidaka & Takahashi, 1967) may influence the frequency of diapause. This is also indicated by the large variation between years and broods, e.g. in 1986 a minor proportion of the light morph was also produced in a constant daylength of 22 h (Table 1).

(d) *Swedish F_2 in daylengths of 18–20 h*

To control for any effects of genetic of maternal differences the two following investigations were conducted as split-clutch experiments, using the offspring of a single parental pair.

In the previously described experiments, the change in daylength experienced by the larvae (+10 h) was larger than under natural conditions, where a difference of about +2 h between early and late larval instars would be

more realistic (cf. Fig. 5). Fig. 2 shows the results of such a test, using as parents offspring from the previous experiment. A minor proportion of the individuals also developed directly in constant daylengths in this experiment, but a majority of the light morph was produced only when daylengths increased, from 18 h to 20 h (not significant, Fisher's exact test). This was not the case when larvae were moved back again to 18 h after 7 days, so that after an initial increase in daylength they experienced decreasing daylengths towards the end of larval development.
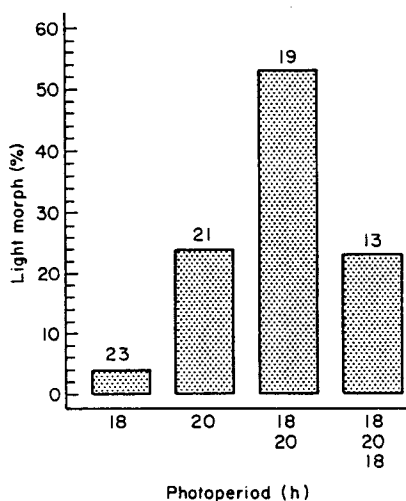

FIG. 2. The proportion of the light morph of *Polygonia c-album* produced in 20°C and constant or changing photoperiods in the offspring of a single parental pair of the Swedish population. Figures on top of bars show the number of individuals in each category. The sequence of photoperiods experienced by the larvae are given below each bar (from top to bottom).

(e) *English F_1 in daylengths of 12–20 h*

Fig. 3 shows the results of the experiment where the offspring of one English female were reared in eight (combined into seven) different environmental conditions. It can be seen that a high proportion of the light morph was produced in constant daylengths of 18 h and 20 h, but not in 12 h (the differences are significant, χ^2, $P<0.001$). Hence, a critical constant daylength for the induction of the light morph and direct development seems to exist between 12 h and 18 h.
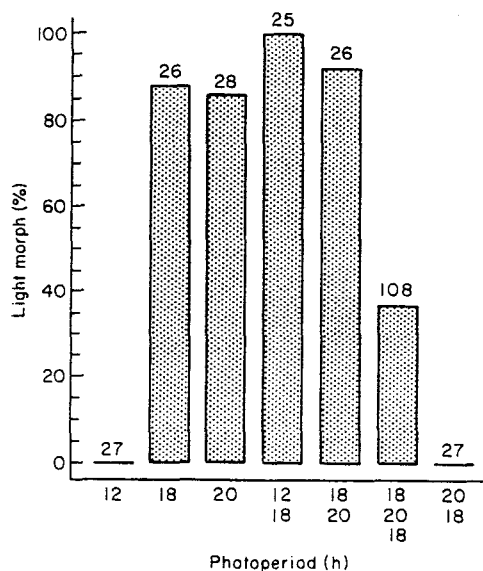
FIG. 3. The proportion of the light morph of *Polygonia c-album* produced in 20°C and constant or changing photoperiods in the offspring of a single parental pair of the English population. Figures on top of bars show the number of individuals in each category. The sequence of photoperiods experienced by the larvae are given below each bar (from top to bottom).

A slightly higher proportion (not significant, χ^2) was produced when daylengths were increased, from 12 h to 18 h and from 18 h to 20 h (Fig. 3). Since the former change was 100% effective in producing the light morph, the effects of a short daylength early in development was evidently nullified by the later long-day regime, meaning either that the photoperiod during the later stages is the decisive factor (but see below) or that the increase in daylength itself is responsible for averting diapause.

Decreases in daylength above the critical daylength were effective in inducing the diapausing morph. When daylengths were decreased after 8 days, from 20 h to 18 h, only the dark morph was produced (Fig. 3), which also shows that the early larval stages are sensitive to photoperiod and important in the photoperiodic regulation of diapause. In two categories daylengths were decreased to 18 h towards the end of larval development after an initial increase from 18 h to 20 h, and this was done after 5 and 7 days in the long daylength, respectively. Since there was no obvious (or significant, χ^2) difference between the results from these two categories they have

been pooled in Fig. 3. The proportion developing into the light morph was smaller in these categories than when only the transfer from 18 h to 20 h was performed (χ^2, $P<0.001$). Hence, decreases in daylength above the critical daylength are also effective if they occur in the late larval stages and also if daylengths have been initially increased.

Discussion

P.c-album is partially bivoltine in England, the directly developing light morph constituting 30–40% of the offspring from the hibernating dark morph in the spring (Frohawk, 1924). Frohawk (1924) and Ford (1945) both stated that it is the first eggs laid in the spring that will develop into the light morph. This is to be expected, since in a partially bivoltine population the individual offspring that hatch earliest are most likely to have enough time for the completion of two generations during the same season.

Concerning the Stockholm population the results suggest that it is generally univoltine in the field. Nevertheless, it was found that an increase in daylength can still induce the development of the non-diapausing light morph. Thus, the ability to develop without diapause is retained by the population and possibly can have selective value in nature in exceptional years. In English insects, there seem to be a critical constant daylength for the induction of the light morph (this result has to be taken with some caution, since the English stock originated from a single female). Nevertheless, a decrease in daylength above the critical daylength, either in the beginning of or towards the end of larval development, will result in a production of mostly the generally diapausing dark morph, even if daylengths are initially increased. A similar tendency was found in the Swedish population.

These results may be the effects of a system for environmental control where daylengths increasing from an initial short day indicate an early date before summer solstice (21 June), when enough time may remain for a second generation of offspring, while decreasing daylengths indicate a date after summer solstice. The advantages of such a system of environmental control can easily be appreciated. With the exception of summer solstice, every absolute value of daylength will occur twice during each
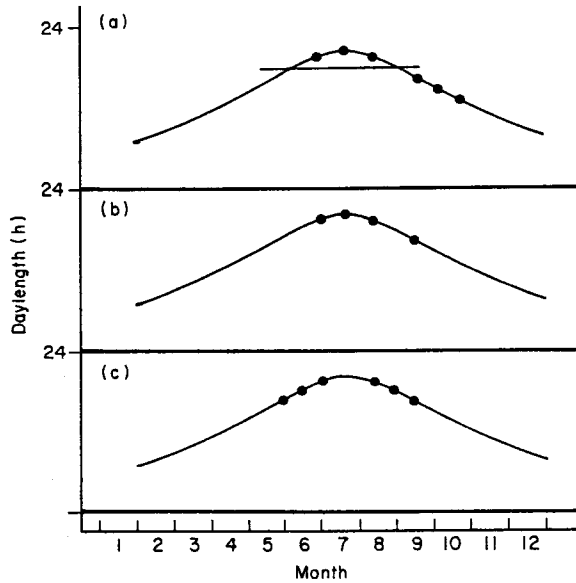
FIG. 4. Three hypothetical insect life cycles. The curves show changes in daylength over the year (in Sweden). The portions of the curves marked by dots indicate those photoperiods which may be experienced by the development stage which is sensitive to photoperiod. (a) The sensitive stage of the first generation occurs at summer solstice, but since the second generation is complete, direct development may be induced by any critical daylength which is passed between generations (one example is indicated by the horizontal line). (b) If the second generation is partial, only the earliest members of the first generation should ideally develop directly and contribute to it. Thus, confusing photoperiods before and after summer solstice should be avoided (see text). (c) This is also the case when the sensitive stages of the first and second generation occur at similar daylengths.

summer (Fig. 4), once before and once after summer solstice. Only a system for photoperiodic regulation which is sensitive to the direction of change in daylength will be able to distinguish between, for instance, early spring and late autumn photoperiods (cf. Corbet, 1955).

Sensitivity to the direction of change in daylength may, however, be more probable in some cases than in others. For instance, the common long-day requirement for direct development will often function to regulate an insect's life cycle, especially when there are two or more complete generations (Fig. 4a). In contrast, concerning diapause induction, I suggest two types of life cycles where the information provided by the photoperiod is equivocal: (1) In partially bivoltine populations, where the photoperiod-sensitive stages of the first generation occur close to summer solstice (Fig. 4b). Those stages may occur at similar daylengths before and after this date, but direct development should be induced

only in the early part of this generation. (2) In bi- or multivoltine populations, where one generation occurs before and one after summer solstice at similar absolute values of daylength (Fig. 4c), and in which diapause should only be induced in the late generation.

Different populations of *P.c-album* are exposed to one or both of these situations in different parts of the geographical range of the species. For instance, in the partially bivoltine English population the first generation of larvae occur chiefly in May–June, the second in July–August (Thomas, 1986; Fig. 5) at similar daylengths. Only for the early part of the first generation is there a selective advantage for non-diapausing development.

I will discuss four evolutionary solutions to the problem of equivocal environmental signals, considering only photoperiod as a seasonal cue: (1) Sensitivity to photoperiod is confined to the developmental stages that immediately precedes diapause or to the diapausing stage itself. Long

days during these stages would mean impending summer conditions and result in the induction of non-diapausing development (i.e. a typical 'long-day species'). (2) The reverse situation, where short days early in development indicates spring conditions (a 'short-day species'). (3) There are two or more sensitive stages with different critical daylengths or with a single critical daylength that has to be passed during development. Short days followed by long days would indicate spring conditions (a 'short-day/long-day species' *sensu* Tauber *et al.* (1986)). (4) The insect is sensitive to the direction of change in photoperiod *per se, sensu* Tauber *et al.* (1986).

(1–2) Concerning *P.c-album*, the second of these possibilities is not supported by the results. A long-day requirement could be the background to the observed critical daylength in the English population. Note, however, that it is the earliest part of the first generation, which experiences relatively shorter daylengths than the later part (Fig. 5), that should develop directly – not the opposite. Hence, a long-day requirement by itself, found in many butterflies including *P.c-aureum* (Hidaka & Aida, 1963), would
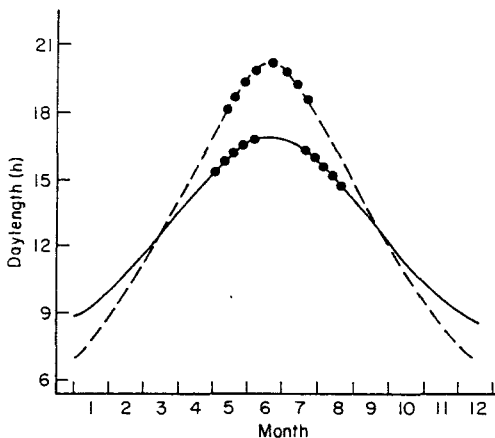

FIG. 5. The changes in daylength (including civil twilight) over the year in Sweden (upper curve) and England (lower curve). The portions of the curves marked by dots indicate those photoperiods which may be experienced by larvae in the two populations of *Polygonia c-album*. The Swedish population is univoltine and the approximate seasonal occurrence of the larval stage is shown. The English population is partially bivoltine and the larval stages of both generations are shown (based on Thomas, 1986). The larval stage of each individual lasts about 1–1.5 months and thus may occupy only a portion of the time indicated in the figure.

not be a functional solution. (3) Regarding the 'short-day/long-day' possibility, short daylengths early in development is evidently not a requirement in the English population. The Swedish population could be described as having a 'short-day/long-day' requirement for direct development, although there is no evidence for critical daylengths. (4) Finally, at least the English population is sensitive to changes in photoperiod *per se*.

If Swedish *P.c-album* also has such sensitivity, as seems probable on the basis of the results (in the absence of a critical constant daylength this cannot easily be proven), I suggest that both studied populations could be described as being of the 'short-day/long-day' type (cf. Norris, 1965; Thiele, 1969), but with a sensitivity to the direction of changes in photoperiod during the larval stage which greatly modifies or overrules any other photoperiodic effects. The fact that long constant daylengths induce direct development in a majority of the English individuals is perhaps best considered as an artefact, since such conditions do not exist in nature.

The Stockholm population is normally univoltine. This may be because, as the experiment with the outdoor breeding of larvae shows, the adult offspring of the spring generation normally do not eclose before the second week of July (larvae from later eggs several weeks later) and so all larvae pupate after summer solstice. Thus, they will experience decreasing daylengths towards the end of larval development. In contrast, part of the English population normally pupate before summer solstice (Fig. 5). Larvae also appear later in Sweden, which means that they will not experience very short days during early development. Finally, effects of temperature has not been extensively investigated in the present study but may of course affect the life cycle regulation and the differences in voltinism between the Swedish and English populations in the field.

Investigations of a comparative, ecological nature in the field of photoperiodism would be valuable, so that an attempt can be made to unify the concepts of critical constant daylengths and the different kinds of sensitivity to changes in daylengths and to develop ecological explanations for the differences in type of life cycle regulation. Any such explanations would probably be dependent on the insect group, its typical sensitive and diapausing stages and the patterns

of voltinism. For instance, in butterflies the larval instars that precedes diapause is the typical sensitive stage and most species studied seem to be of the 'long-day' type (e.g. Danilevski, 1965; Clark & Platt, 1969; Claret, 1972). The hibernating stage is often conservative for a given monophyletic group of butterfly species and the larva or pupa are the stages most commonly found. I would expect sensitivity to changing daylengths and other untypical adaptations to be found most probably associated with more unusual life cycles such as that of members of the tribe Nymphalini to which *P.c-album* belongs. Since they hibernate as adults the larval stages in the first generation occur early, close to summer solstice (cf. Fig. 5), while the second generation is partial in large parts of the Holarctic.

Acknowledgments

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