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## Life history plasticity: influence of photoperiod on growth and development in the common blue butterfly

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The daylength experienced by a larva provides information about the progression of the season, so that plasticity in growth and development with photoperiod might serve as an adaptation allowing efficient timing relative to the favorable part of the season. In an experiment with *Polyommatus icarus* it was found that shorter daylengths, indicating less time available until the season ends, resulted in faster development from hatching to adult eclosion. From hatching and into the earlier part of the final instar, larval mass increased approximately exponentially with time, but the rate of growth during this phase was not affected by photoperiod. Both the later part of the final instar and pupal development proceeded more rapidly in shorter daylengths. The decrease in total development time did not reduce female final size, measured as pupal mass, whereas males became somewhat smaller. Males developed slightly faster than females (protandry) and were heavier than females in the longer daylengths but lighter in the shorter daylengths. The observed lack of a trade-off between development time and adult size in females is discussed in the light of life history theory of optimal age and size at maturity.

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Insects in seasonal environments often have alternative developmental pathways, allowing a flexible allocation of time to growth and reproduction in favorable parts of the season and dormancy in unfavorable parts (Danks 1994). The pathway taken by a developing individual is typically determined by environmental cues, perhaps the most important one being the daylength experienced by the individual (Beck 1980). Although the induction of developmental pathways is the most striking, and most studied, example of plasticity in insect life histories, seasonality might also favor plasticity in the timing of development within a given pathway. Because of factors like variation in the time of oviposition, individuals of a given generation will start their development at different points in time, and thus vary in the amount of time available in the favorable part of the season. One might then expect that an individual experiencing daylengths indicating less time

available would speed up its development. This type of quantitative response to photoperiod has been demonstrated for nymphal development time in crickets (Masaki 1978) and for larval and pupal development times in butterflies (Nylin et al. 1989, Nylin 1992). Here I investigate the effect of photoperiod on growth and development in directly developing individuals of the common blue, *Polyommatus icarus*.

In spite of the considerable flexibility demonstrated by many insect life-cycles, larval growth rates are usually thought of as being determined mainly by temperature and food quality and availability. An insect with less time available for growth would then, all else being equal, follow a given growth trajectory for a shorter time, and thus become a smaller adult. This kind of reasoning lies behind life history analyses of latitudinal variation in development time and adult size (Roff 1980), the relationship between protandry and sexual

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size dimorphism (Singer 1982), and the relationship between time of emergence and adult size (Rowe and Ludwig 1991). However, an individual might be able to react to time pressure by either increasing larval growth rate (greater foraging effort) or by speeding up the non-growing phases of development (e.g., faster pupal development), and thus partially or wholly avoid a reduction in adult size (Abrams et al. 1996), as has been observed for butterflies (Nylin et al. 1989, Nylin 1992). In this study I attempt to measure the responses of *P. icarus* to time pressure in some detail, to be able to distinguish, e.g., between changes in larval growth rate and changes in the duration of larval growth.

A recurring theme in the literature on phenotypic plasticity is the question of whether observed reaction norms are optimal or if their evolution is constrained by lack of genetic variation (e.g., Scheiner 1993). For optimal life histories, the response of development time and adult size to time pressure would depend on the balance between the costs of faster growth and development and the benefits of larger adult size. Since such costs and benefits are generally poorly known empirically, one is usually left with the option of making a rough qualitative evaluation of whether an observed reaction norm agrees with predictions from life history theory. On the other hand, if one tentatively grants that observed life history responses are fairly close to optimal, one has the possibility of evaluating the reasonableness of the fitness functions assumed in life history models.

As an example, it is often assumed in life history models that adult size has a strong effect on reproduction (Roff 1992, Stearns 1992), as when female reproduction is taken to be proportional to body mass (e.g., Rowe and Ludwig 1991). This would mean that an individual with more time available has an incentive to use that time for additional growth. Based on the observed responses in *P. icarus* and other butterflies (Nylin et al. 1989, Nylin 1992), I will discuss whether the very weak or absent changes in adult body size with time pressure are compatible with the commonly made assumptions about the advantages of large size.

## Materials and methods

### Study organism

*Polyommatus icarus* (Rottemburg, 1775) (Lycaenidae: Polyommataini), is a widely occurring palaeartic lycaenid butterfly. Except in the northernmost part of its range, it has more than one generation per season. The last brood produced in a season enters diapause and overwinters in the form of half-grown (third instar) larvae. The larvae are oligophagous, utilizing a range of host plants in the family Fabaceae. As is the case with many other lycaenids, larvae of *P. icarus* associate

mutualistically with ants. The association is facultative (classified as moderately myrmecophilous in Fiedler 1991), and larvae develop normally in the absence of ants (Fiedler and Hölldobler 1992).

The animals in this study are randomly selected, non-inbred grandoffspring of four *P. icarus* females, caught in the summer of 1991 on the island of Öland, on the eastern coast of southern Sweden (lat. 56.5°N). In this region, *P. icarus* is bivoltine, with adults of the first (overwintering) generation appearing in late May or early June and flying into July; the second (directly developing) generation appears in late July or early August and continues flying into September.

### Experimental arrangement

My intention was to expose *P. icarus* larvae to day-lengths spanning the range encountered by early to late second generation individuals. Six environmental cabinets with a 24-h L/D cycle and light periods (h:m) of 19:00, 18:40, 18:20, 18:00, 17:40, and 17:20 were used. Although a straightforward translation to calendar dates is not possible, this would roughly correspond to the range from the end of June to the end of July. At 56.5°N and on 1 July, daylength and daylength plus twice the civil twilight are 17:43 and 20:02; the corresponding figures for 1 August are 16:16 and 17:58 (Beck 1980).

In each cabinet, 25 recently hatched larvae were introduced. The larvae were placed individually in plastic jars containing fresh cuttings of *Medicago sativa* L. (Fabaceae). The jars were checked regularly, and new plants added when needed. In order to even out temperature differences within cabinets, the jars were shifted around every second day. The temperature in the cabinets was checked daily and kept at 23°C.

For each individual, I tried to estimate the following development times: the time from hatching to reaching a mass of 30 mg (well into the final instar), to pupation, and to adult eclosion. The larvae were weighed at the start of the experiment. When a larva was seen emerging from the egg, this was noted (12 cases). For those that had started to feed, the time of hatching was estimated using a growth curve (see below; the average estimated age at the start of the experiment of these larvae was 0.75 d). After 13 d the larvae were again weighed, and if the mass was less than 30 mg, reweighed on the following day(s) until a mass greater than 30 mg was obtained (except for diapausing larvae). For larvae with observations of final instar masses bracketing 30 mg (61 cases), the time at 30 mg was interpolated assuming exponential growth; these data were also used to compute an average relative growth rate in the final instar. For remaining final instar larvae, the time at 30 mg was estimated assuming exponential growth with this average relative growth rate. Since the

growth rate in the final instar could vary with photoperiod, the time at 30 mg was also estimated using cabinet average growth rates. These data are not reported, because the difference between the two estimates was quite small and had a negligible effect on the results.

When the larvae approached pupation, the jars were checked daily, the day of pupation noted, and the pupae weighed on the day after pupation. This mass was taken to be a measure of adult size. Around the time of eclosion, pupae were checked twice daily, and the time of eclosion and sex of the individual noted.

In order to determine a growth curve, five additional individuals were raised in the cabinet with 19 h light, with great care expended to avoid differences in temperature and host plant quality. These individuals were weighed daily, except in the vicinity of pupation, until they eclosed.

### Statistical methods

In addition to photoperiod, the larvae in a cabinet shared other potentially varying factors, primarily temperature fluctuations. There is thus a danger of spurious significances if individual values are used in regressions on photoperiod. To avoid this, effects of photoperiod and sex were tested for using analyses of covariance on cabinet averages, with duration of light as covariate and sex as factor. However, for pupal mass an analysis of covariance using individual values was also performed.

### Results

The growth pattern of directly developing *P. icarus* larvae consists of four instars. As seen in Fig. 1, larval mass increases exponentially with time in each instar, i.e. linearly on log scale. The relative rate of increase is approximately the same in the different instars. Mass increases with about a factor of ten in the first instar, and with a factor of six in the remaining three instars. In the fourth instar, exponential growth continues up to around 60 mg, after which the growth rate gradually levels off. Including six d from the laying of an egg to larval hatching, the total development time from egg to adult is about 39 d for 19 h light and 23°C. This is considerably less than the corresponding development time in the wild, which can be estimated to two months.

Over the range of photoperiods in the experiment, most individuals developed directly (Table 1). However, in the three cabinets with shortest daylengths, a few individuals stopped growing and entered diapause development.

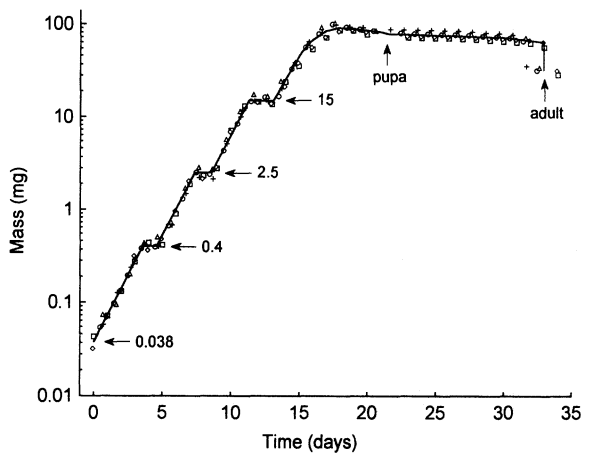


Fig. 1. Growth curve of *P. icarus* in 19 h light and 23°C, from hatching to eclosion. The horizontal arrows indicate approximate masses (mg) at hatching and at the three larval molts. The five symbols represent daily measurements of five individuals; the curve has been sketched to fit these points.

### Development time

For both males and females, the total development time (hatching to eclosion) was longer in treatments with longer daylengths (Table 2 and Fig. 2), corresponding to earlier times in the season. Thus, individuals with less time remaining in the season developed more quickly. Over the range of photoperiods, the magnitude of the effect was about 3.3 d (Fig. 2). Splitting development into three parts, there was no effect of photoperiod on the duration of the exponential growth phase up to 30 mg mass, but both the time from 30 mg to pupation and pupal development time increased with light duration (Table 2 and Fig. 3). Thus, the response to photoperiod was concentrated to the later, primarily non-growing phases of development.

Comparing development times of males and females, a slight protandry was found, with males developing in about 0.75 d less time than females (Fig. 2). Splitting development into three parts revealed that the faster development of males was concentrated to the phase from 30 mg mass to pupation (Table 2 and Fig. 3). The absence of a significant light by sex interaction for any of the development times (Table 2), indicates that the degree of protandry did not vary with photoperiod.

Table 1. The incidence of direct development vs diapause in the different photoperiods (h:m light) and at 23°C.

Light	Females	Males	Diapause*	Dead
17:20	13	6	2	4
17:40	9	11	3	2
18:00	11	10	2	2
18:20	15	9	0	1
18:40	11	13	0	1
19:00	16	9	0	0

\* Sex was not determined for diapausing larvae.

Table 2. Statistical test of effects of duration of light and sex on (cabinet) average development times and pupal masses: *P*-values in analyses of covariance with duration of light as covariate and sex as factor.\*

Response variable	Light	Sex	Light × Sex
Time to pupation	0.001	0.014	0.504
Time to eclosion	0.001	0.013	0.542
Time to 30 mg	0.156	0.453	0.697
Time 30 mg to pupation	0.001	0.006	0.783
Time pupation to eclosion	0.001	0.392	0.973
Pupal mass	0.016	0.733	0.049

\* *df* for Light, Sex, Light × Sex, and Error are, respectively, 1, 1, and 8 in all cases.

### Pupal mass

For pupal mass, the picture is somewhat more complicated. The analysis of covariance in Table 2 showed a significant light by sex interaction, which means that male and female pupal mass responded differently to photoperiod. Using cabinet averages, the male pupal mass was significantly correlated with daylength ( $r = 0.92$ ,  $N = 6$ ,  $P = 0.008$ ), but not the female pupal mass ( $r = 0.22$ ,  $N = 6$ ,  $P = 0.68$ ).

Not using the individual pupal masses in statistical testing is a conservative approach. Since a lack of response in female size is of some interest, it is important to examine this question with a more sensitive test. Fig. 4 shows an analysis of covariance on individual values. There appears to be a shift in sexual size

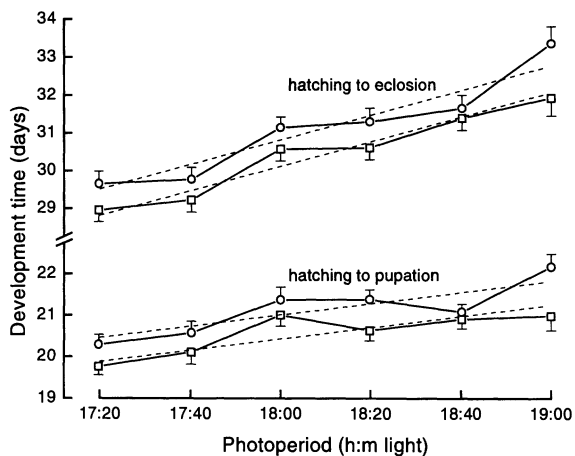


Fig. 2. Development times from hatching to pupation (lower curves) and to eclosion (upper curves) in different photoperiods. The squares and circles respectively denote male and female averages, and the bars show standard errors. The dashed regression lines represent the analysis of covariance of cabinet averages (Table 2). For time to pupation the central intercepts (at 18:10 light) are 20.56 (males) and 21.14 (females), and the common slope is 0.81. Corresponding values for time to eclosion are 30.44 (males), 31.14 (females), and 1.95 (common slope).

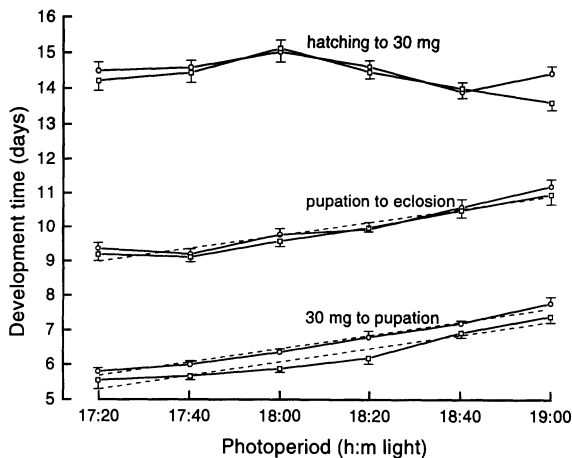


Fig. 3. Development time split into three periods. The squares and circles respectively denote male and female averages, and the bars show standard errors. The dashed regression lines represent the analysis of covariance of cabinet averages (Table 2).

dimorphism, with males being heavier than females in the early season treatments and lighter than females in the late season treatments. As could be expected, the significance of the light by sex interaction and of the male response to photoperiod is strengthened in comparison with the analysis of cabinet averages. Nevertheless, there is still no indication of a response in females (Fig. 4).

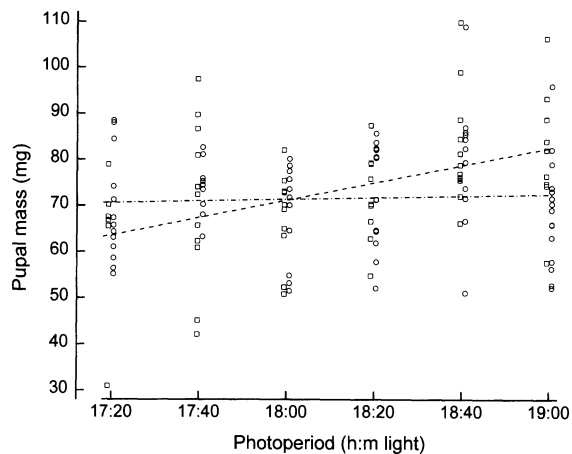


Fig. 4. Pupal mass in different photoperiods. The squares and circles respectively denote male and female values. For clarity, male and female data points have been shifted slightly to the left and to the right. The regression lines for males (dash) and females (dash-dot), representing an analysis of covariance of individual pupal masses, differ significantly in slope ( $P = 0.009$ ). For males the central intercept (at 18:10 light) is 73.01 and the slope is 11.30; females have central intercept 71.50 and slope 1.04. The male slope is significantly positive ( $P < 0.001$ ), whereas the female slope does not differ significantly from zero ( $P = 0.65$ ).

## Discussion

In the region where the animals in this study derive from, adults of the first (overwintering) generation are present over a period of about one month, which means that the offspring of the first generation will start their development over a comparable range of dates. Some of these offspring might enter larval diapause (Table 1) and overwinter, thus following a univoltine pattern, but those that develop directly and make up the second generation need sufficient time in the season to produce a brood that reaches larval diapause before conditions for growth become unfavorable. It seems reasonable that late second generation females suffer a cost, both because larvae hatching from late eggs might fail to reach diapause before the season ends and because host plant quality might deteriorate (e.g., less inflorescences and young leaves; cf. Pierce 1985, Fiedler 1990), leading to lower-quality offspring. Late second generation males face the additional problem of a lower chance of mating (Wiklund and Fagerström 1977).

If late second generation individuals suffer a cost, an alternative is to instead enter diapause development. For *P. icarus* in parts of Britain the second generation is only partial (Frohawk 1924), and the same may be true for Swedish populations. Partial second generations have been observed in other butterfly populations (e.g., Wickman et al. 1990, Wiklund et al. 1991). The diapausing individuals in this study occurred in the shorter daylength treatments (Table 1), but the proportion diapausing was low also in the shortest daylength. Diapause induction often depends on temperature as well as photoperiod (Beck 1980), and this is the case for *P. icarus*; at a given photoperiod the tendency to enter diapause is greater at lower temperatures (A. Axén, pers. comm.). Thus, running the experiment at lower temperatures would have increased the diapausing proportion.

These arguments indicate that it is advantageous for late, directly developing individuals to speed up their development, and this was also observed (Fig. 2). However, daylength did not affect all phases of development equally. There was no effect on the growth rate during the phase of exponential growth up to 30 mg mass, which includes the first three instars and a good portion of the final instar and consumes about half the time from hatching to eclosion (Fig. 1), but both the time from 30 mg to pupation and pupal development time decreased in shorter daylengths (Fig. 3). The lack of response of larval growth rate could be because growth rate is at a physiological maximum given the temperature and food availability, but there are other, slightly different interpretations. At least the first two instars could have the option of switching developmental pathway (diapause), which might reduce variation in the optimal growth rate prior to the switching point. Alternatively, increased foraging activity might expose a

larva to an accelerating risk of attacks by predators and parasitoids, whereas a moderate decrease in the amount of time spent as prepupa or pupa has smaller fitness effects. For lycaenid larvae, the risk of enemy attack can depend on ant attendance (Pierce and Mead 1981). Fiedler and Hölldobler (1992) compared the development of *P. icarus* with and without ants, but found no significant effects on growth rate.

As is commonly observed in butterflies and other insects in seasonal environments (Wiklund and Fagerström 1977) males eclosed somewhat earlier than females (Fig. 2). Males achieved this protandry by spending somewhat less time in the phase from 30 mg mass to pupation (Fig. 3), but neither the time to 30 mg nor the pupal development time differed significantly between the sexes (Table 2). Thus, the manner in which faster development is achieved depends on whether it is proximately caused by the sex of the individual or the daylength experienced. Protandry as a result of shorter male larval development time, but not shorter pupal development time, has been observed in other butterfly species (Nylin et al. 1989, Nylin 1992).

From the longest to the shortest daylength in the experiment, the average amount of time spent in the stage from 30 mg mass to pupation decreased by approximately two d (Fig. 3). In spite of this relatively substantial effect, female pupal mass did not decrease, whereas male pupae became smaller (Fig. 4). It might seem surprising that females in the longer daylengths did not use the extra time to grow larger, but this kind of observation is not atypical for butterflies. Reduction in larval development time without any reduction in pupal mass has been observed as a response to photoperiod (Nylin et al. 1989) and to choice of developmental pathway (Wiklund et al. 1991, Nylin 1992).

An organism's optimal age and size at maturity is a frequently studied problem in life history theory (Roff 1992, Stearns 1992). The simplest approach is to assume that the organism, in a given environment, follows some specified growth curve, and optimal maturation occurs when the mortality cost of additional growth balances the benefit of increased size. Plastic responses to time pressure offer a way of checking an assumption of a fixed growth curve. The situation in *P. icarus* is more complicated than this, since females could decrease development time without becoming smaller.

When considering optimal growth, an interesting question is whether there are general relationships between juvenile size and the ability to assimilate energy (Reiss 1989). Observed growth curves in butterflies show that larval size can increase roughly exponentially with time (e.g., Fig. 1, Blau 1981, Nylin et al. 1989, Wickman et al. 1990). Thus, over a very large range of sizes, a butterfly larva can increase its mass by approximately the same percentage from one day of foraging. These kinds of observations make it unlikely that the

levelling off of growth prior to pupation (Fig. 1) is due to a reduced energy assimilation ability that is some general (e.g., allometric) function of size.

However, an undiminished capacity for proportional growth also for larvae nearing their final size makes it difficult to explain a lack of response of pupal mass to time pressure. If larval mortality is size independent and female lifetime fecundity is an allometric function of size, life history modelling shows that extra time between hatching and eclosion should be used for further (exponential) growth (Abrams et al. 1996), resulting in pronounced responses in adult size to time pressure. Thus, if observed weak or absent responses in pupal mass are to be close to optimal, some of the above assumptions must be invalid, and it is of interest to evaluate them in the light of current knowledge of butterfly biology.

First, it may be that a larva rapidly loses its capacity for further proportional growth when its size becomes comparable to the structures it is feeding on (leaves, flowers, etc.). Relationships between larval size, growth performance, and host plant have been little studied, but the pattern seems to be that larvae become larger on host plants allowing more rapid growth for all instars (Schroeder 1986, Ohsaki and Sato 1994), rather than because of size-dependent variation in growth efficiency. Perhaps more conclusive evidence against a rapid decline in growth efficiency at a particular larval size is provided by related species of different adult sizes using the same host plant. Wickman et al. (1990) showed that at the size where one species stops growing, larvae of other species continue growing at an undiminished rate.

A second possibility is that above a certain size foraging rapidly becomes more dangerous. Field observations on butterfly larval mortality give no support for this (e.g., Courtney and Duggan 1983, Feeny et al. 1985, Pierce and Estal 1986, Scriber and Lederhouse 1992, Kristensen 1994); final instars tend to survive equally well as or sometimes better than earlier instars. However, causes of mortality can vary with size (Dempster 1984, Feeny et al. 1985, Kristensen 1994), and it is conceivable that predation by, for instance, vertebrates would increase rapidly if larvae grew beyond their normal size.

Finally, the increase in reproductive value with adult size might show a diminishing return pattern, so that additional growth becomes less valuable as a larva grows larger. In ectotherms, female fecundity often seems to depend allometrically on body size (Roff 1992), with fecundity increasing proportionally faster than body mass. Laboratory data on lifetime fecundity in butterflies agrees with this (e.g., Blau 1981, Jones et al. 1982, Karlsson and Wickman 1990) and there is thus no evidence of diminishing returns. However, size variation in the above studies is only partially due to (genetic) differences in growth and maturation strate-

gies in a given environment; responses to rearing temperature and random differences in host plant quality also play a role. Artificial selection for large size seems not to result in similar fecundity gains (Gilbert 1984, 1986).

Size-dependent larval mortality or diminishing returns in reproduction with larger adult size are then the most likely factors that could make optimal size fairly insensitive to time pressure. More generally, it is clear that at present we know relatively little about what typically determines optimal body size in butterflies, for instance whether constraints on larval growth or variation in adult performance with size are more important.

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## References

- Abrams, P. A., Leimar, O., Nylin, S. and Wiklund, C. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. – *Am. Nat.* 147: 381–395.
- Beck, S. D. 1980. *Insect photoperiodism*. – Academic Press, New York.
- Blau, W. S. 1981. Life history variation in the black swallowtail butterfly. – *Oecologia* 48: 116–122.
- Courtney, S. P. and Duggan, A. E. 1983. The population biology of the Orange Tip butterfly *Anthocaris cardamines* in Britain. – *Ecol. Entomol.* 8: 271–281.
- Danks, H. V. 1994. Diversity and integration of life-cycle control in insects. – In: Danks, H. V. (ed.), *Insect life-cycle polymorphism*. Kluwer, Dordrecht, pp. 5–40.
- Dempster, J. P. 1984. The natural enemies of butterflies. – In: Vane-Wright, R. I. and Ackery, P. R. (eds), *The biology of butterflies*. Academic Press, London, pp. 97–104.
- Feeny, P., Blau, W. S. and Kareiva, P. M. 1985. Larval growth and survivorship of the black swallowtail butterfly in central New York. – *Ecol. Monogr.* 55: 167–187.
- Fiedler, K. 1990. Effects of larval diet on myrmecophilous qualities of *Polyommatus icarus* caterpillars (Lepidoptera: Lycaenidae). – *Oecologia* 83: 284–287.
- 1991. European and North West African Lycaenidae (Lepidoptera) and their association with ants. – *J. Res. Lepidop.* 28: 239–257.
- and Hölldobler, B. 1992. Ants and *Polyommatus icarus* immatures (Lycaenidae) – sex-related developmental benefits and costs of ant attendance. – *Oecologia* 91: 468–473.
- Frohawke, F. W. 1924. *Natural history of British butterflies*, Vol II. – Hutchinson & Co., London.
- Gilbert, N. 1984. Control of fecundity in *Pieris rapae*. III. Synthesis. – *J. Anim. Ecol.* 53: 599–609.
- 1986. Control of fecundity in *Pieris rapae*. IV. Patterns of variation and their ecological consequences. – *J. Anim. Ecol.* 55: 317–329.
- Jones, R. E., Hart, J. R. and Bull, G. D. 1982. Temperature, size and egg production in the cabbage butterfly, *Pieris rapae* L. – *Aust. J. Zool.* 30: 223–232.
- Karlsson, B. and Wickman, P.-O. 1990. Increase in reproductive effort as explained by body size and resource allocation in the speckled wood butterfly, *Pararge aegeria* (L.). – *Funct. Ecol.* 4: 609–617.
- Kristensen, C. O. 1994. Investigations on the natural mortality of eggs and larvae of the large white *Pieris brassicae* (L.) (Lep., Pieridae). – *J. Appl. Entomol.* 117: 92–98.

- Masaki, S. 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. – In: Dingle, H. (ed.), *Evolution of insect migration and diapause*. Springer, New York, pp. 72–100.
- Nylin, S. 1992. Seasonal plasticity in life history traits: growth and development in *Polygonia c-album* (Lepidoptera: Nymphalidae). – *Biol. J. Linn. Soc.* 47: 301–323.
- , Wickman, P.-O. and Wiklund, C. 1989. Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyridae). – *Biol. J. Linn. Soc.* 38: 155–171.
- Ohsaki, N. and Sato, Y. 1994. Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. – *Ecology* 75: 59–68.
- Pierce, N. E. 1985. Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein-rich food plants. – *Am. Nat.* 125: 888–895.
- and Mead, P. S. 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. – *Science* 211: 1185–1187.
- and Esté, S. 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. – *J. Anim. Ecol.* 55: 451–462.
- Reiss, M. J. 1989. *The allometry of growth and reproduction*. – Cambridge Univ. Press, Cambridge.
- Roff, D. A. 1980. Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. – *Oecologia* 45: 202–208.
- 1992. *The evolution of life histories: Theory and analysis*. – Chapman and Hall, New York.
- Rowe, L. and Ludwig, D. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. – *Ecology* 72: 413–427.
- Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. – *Annu. Rev. Ecol. Syst.* 24: 35–68.
- Schroeder, L. A. 1986. Changes in tree leaf quality and growth performance of lepidopteran larvae. – *Ecology* 67: 1628–1636.
- Scriber, J. M. and Lederhouse, R. C. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. – In: Hunter, M. R., Ohgushi, T. and Price, P. W. (eds), *Effects of resource distributions on animal plant interactions*. Academic Press, New York, pp. 429–466.
- Singer, M. C. 1982. Sexual selection for small size in male butterflies. – *Am. Nat.* 119: 440–443.
- Stearns, S. C. 1992. *The evolution of life histories*. – Oxford Univ. Press, Oxford.
- Wickman, P.-O., Wiklund, C. and Karlsson, B. 1990. Comparative phenology of four satyrine butterflies inhabiting dry grasslands in Sweden. – *Holarct. Ecol.* 13: 238–346.
- Wiklund, C., and Fagerström, T. 1977. Why do males emerge before females? – *Oecologia* 31: 153–158.
- , Nylin, S. and Forsberg, J. 1991. Sex related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly, *Pieris napi*. – *Oikos* 60: 241–250.