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Seasonal plasticity in life history traits: growth and development in *Polygonia c-album* (Lepidoptera: Nymphalidae)

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The potentially multivoltine comma butterfly, *Polygonia c-album* L., hibernates in the adult stage. The adult seasonal morph is demonstrated to be a good indicator of whether an individual has entered reproductive diapause or is developing directly to sexual maturation. This fact, and the assumption that a short development time is not equally important to all categories of individuals, was used to test predictions on variation in life-history traits among categories (morphs and sexes) and environments (temperature and photoperiod) at the level of individuals and to some extent families and populations (the univoltine Stockholm population and the partially bivoltine Oxford population). Individuals developing to adults in a short time were expected to be smaller and lighter as a result of a basic trade-off between the two traits. Development times varied in accordance with predictions, but in most cases this was due to plastic growth and development in both the larval and pupal stages rather than through variation in size or weight, i.e. size was a highly canalized trait. This suggests a relationship between plasticity and canalization and a strong potential for plasticity to shield life-history traits from selection. Individuals regulated development times also within developmental pathways, in response to photoperiods indicating the progression of the season. These and other results suggest that development times are not normally minimized in temperate butterflies unless this is enforced by direct development and protandry. There is thus scope for a high degree of adaptive plasticity in growth- and developmental rates which may devalue the basic trade-offs assumed by life-history theory and account for inconsistencies with its predictions.

KEY WORDS:—Seasonality – plasticity – reaction norms – life histories – tradeoffs – canalization – sexual dimorphism – size.

CONTENTS

Introduction 301
Materials and methods. 303
Results 306
Main life cycle regulation 306
Weight and size 308
The search for trade-offs: morphs and sexes 308
The search for trade-offs: environments 313
The search for trade-offs: individuals 317
The search for trade-offs: families 318
The search for trade-offs: populations 319
Discussion 319
Acknowledgements 321
References 322

INTRODUCTION

Life-history theory is the attempt to explain differences in traits of reproduction, growth and development as adaptive in the sense that they have

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been shaped by natural selection for coadapted genotypes and phenotypes of high fitness in a given environment (cf. e.g. Stearns, 1976; Bell, 1980). The notion of 'trade-offs', i.e. "the costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another" (Stearns, 1989) is central to life-history theory. This is because life-history traits are often closely related to fitness. Without trade-offs, selection would drive such traits to their limits, eroding variation.

It has been observed, however, that negative correlations are not always seen between traits that are expected to be involved in a trade-off. Van Noordwijk & de Jong (1986) and others have shown how positive, rather than negative, phenotypic correlations among individuals can arise between life-history traits, e.g. because some individuals have more resources at hand to invest (in both traits) than others. Stearns (1989, 1991) discusses several associated problems, including the interface between "genetic" and "phenotype" trade-offs, and the important role of "intermediate structure", i.e. the physiological and developmental mechanisms connecting the genotypic to the phenotypic level (also cf. Roff, 1990). For instance, genotypes typically differ in reaction norms—the range of phenotypes expressed according to environment. Such gene by environment interactions (which form the basis for evolution of phenotypic plasticity) may result in "genetic" correlations changing sign between environments and hence in genetic trade-offs which are seen under one experimental condition but not under another. In other words, plasticity could shield genetic trade-offs from selection, if most of the variation in the traits involved is environmentally induced.

In the present study, I explore the potential trade-off between development rate and size/weight. It is a central assumption in life-history theory that a short development time should be negatively correlated with a large size, the former trait promoting rapid reproduction and the latter fecundity and competitive ability (e.g. "r- and K-selection"; MacArthur & Wilson, 1967). I test the hypotheses that a short development time is not equally important for all categories of the study species, the comma butterfly *Polygonia c-album* L., and that the reaction norms of individuals and populations therefore will represent different outcomes of trade-offs involving development time on one hand and some other trait associated with fitness on the other. I also test the assumption of basic life-history theory that this 'other trait' will often be adult size or weight.

Diapausing and directly developing insects often differ dramatically in life-history traits such as longevity, size and development rate among species (Denlinger, Chen & Tanaka, 1988) or individuals (especially evident at conditions when some individuals in a brood diapause and some develop directly, e.g. Wiklund, Persson & Wickman, 1983; Nylin, Wickman & Wiklund, 1989; Wiklund, Nylin & Forsberg, 1991), whereas seasonally occurring morphs (seasonal polyphenism) often are coupled with diapause (Shapiro, 1976). This means that species where this is the case offer fascinating possibilities for investigations on environmentally induced life-history variation, where the seasonal morph can be used as a convenient indication of the physiological state of the insect. *Polygonia c-album* was chosen as study organism because of the two distinct seasonal morphs which occur in this species. The dark morph generally enter a reproductive diapause and hibernate in the adult stage before mating and ovipositing in the spring. The other, light morph, rapidly mature sexually,

oviposit in the summer, and give rise to a new generation of butterflies (e.g. Frohawk, 1924; Nylin, 1989). A given female may give rise to a mixed brood of both morphs in the field or in the laboratory. In such broods individuals with relatively similar genotypes, experiencing similar environments, develop very differently. Directly developing individuals must develop very quickly in order to give rise to successful offspring (i.e. a brood which reaches the diapausing stage before winter) whereas their siblings destined for diapause instead have considerable surplus time.

As a consequence of this reasoning, I predicted that: (1) Shorter development times and smaller sizes will be expressed by individuals developing into the non-diapausing light morph in mixed broods. In addition, predictions regarding variation in development time and size among sexes, environments, individuals, families and populations were tested to some extent. (2) Males may be more time-constrained than females as a result of selection for protandry (Wiklund & Fagerström, 1977; Fagerström & Wiklund, 1982). It can be predicted that males will display shorter development times than females, and there could be a corresponding female-biased size dimorphism (Singer, 1982). This should be true among directly developing insects but not among diapausing insects. In the latter category sexual differences in pre-diapause development time would not result in protandry, since hibernation synchronizes the population. (3) Low temperature should result in longer development times and may result in larger size, as is often found in insects and in many butterflies (e.g. Nylin *et al.*, 1989). (4) If individuals are able to detect and respond quantitatively to photoperiodic information, development times will decrease as photoperiods indicate progressively later dates in the season and less time available before winter (e.g. Nylin *et al.*, 1989). A decrease in size could be a consequence. (5) At least within each category of individuals and environments (a given sex and morph at a given temperature and photoperiod) there will be a trade-off between short development time and size/weight among individuals. (6) If there is genetic polymorphism within the potentially multivoltine populations, with genotypes varying in their tendency to diapause, they could also show genetically correlated variation in development time and size (cf. Mosseau & Roff, 1989). If so, families with a high tendency to diapause will display long development times and large size, and vice versa. (7) When populations are compared, partially bivoltine populations—where only individuals capable of producing a second generation will gain the high pay-off in fitness in favourable years—should as a rule be more time-constrained than univoltine populations. Theory on latitudinal size patterns (e.g. Masaki, 1967, 1978; Roff, 1980, 1983; Mosseau & Roff, 1989; Nylin & Svärd, 1991) would predict smaller size in a partially bivoltine population (such as the Oxford population of *P. c-album*) compared with a univoltine population well to the south of the northern extreme range of the species (such as the Stockholm population), as a result of shorter development times.

MATERIALS AND METHODS

Choice of study organism

There is evidence indicating that adult morph and reproductive diapause are highly, although not absolutely, correlated in *Polygonia c-album* (Frohawk, 1924;

Nylin, 1989, and references therein; this paper) and *P. c-aureum* L. (Hidaka & Aida, 1963; Fukuda & Endo, 1966; Masaki & Kumagai, 1988; Masaki, Endo & Kumagai, 1989). This suggests that the developmental pathway is already determined by the time adults emerge (Nylin, 1989).

Stock used

When not otherwise stated, insects used were offspring of dark morph females of *P. c-album* caught in the Stockholm area (59'5°N), where the species is normally univoltine (Nylin, 1988, 1989). Stock from Oxford, England (52°N; a partially bivoltine population; Frohawk, 1924; Thomas, 1986), was used in some cases. Since this stock originated from a single female, results are included mostly to show similarities between populations rather than differences. A minority of individuals develop directly in the Oxford population (30–40%; Frohawk, 1924) and it is thus in the northern part of the bivoltine zone of the species. The range of the species extends northwards to about 67°N in Scandinavia and the Stockholm population seems to be more or less in the centre of the univoltine zone.

General methods

In all experiments, larvae were reared in environmental cabinets. They were reared individually in plastic jars where the principal foodplant *Urtica dioica* L. was cultured in ample supply.

Regulation of diapause and polyphenism

The strength of the correlation between adult morph and reproductive diapause among females and the effects of constant and changing photoperiods in diapause regulation was tested using a split-brood design, i.e. the offspring of one female was divided among three photoperiodic conditions at 21°C: 16 hours light (16 h), 18 h and a transfer from 16 h to 18 h at about the time of molting from second to third larval instar (8 days after hatching). As they emerged, adult females were transferred to flight cages where they had access to a solution of sugar in water at all times and the principal foodplant *U. dioica* was presented at intervals. Ovipositing females were scored as direct developers (not being in reproductive diapause). The remainder were killed by freezing after 10–14 days in the flight cages and dissected. Insects then found to contain eggs were also scored as direct developers. Experiments 4–6 were made with larvae transferred to longer photoperiods at different ages (4, 6 and 8 days), and experiments 7–9 were made at three temperatures (17, 20 and 23°C) partly to investigate the effects of day of transfer and temperature, respectively, in diapause and morph regulation.

Life-history traits studied

To investigate the relationships between pupal weight and adult size (a life-history variable which may be more directly associated with fitness than pupal weight), forewing length of all individuals was measured in experiment 2a (of Table 1) and in two simultaneous additional rearings (b–c; also in 12 h followed by 22 h after 8 days, using offspring from single females) where only the light morph was produced.

Data were collected on larval development time, pupal weights (measured the

TABLE 1. Development time (from hatchling to adult) ±SE for the sexes and morphs of *Polygonia c-album* from Stockholm and Oxford

					Category			
					Light morph		Dark morph	
E	Pop.	T	L	D	Males	Females	Males	Females
1	Oxford	20	18/20/18	7/7	28.5±0.7 (6)	29.9±0.8 (11)	31.7±0.5 (18)	32.4±0.5 (11)
2a	Stkhlm	20	12/22	8	32.0±0.3 (13)	32.5±0.5 (13)	35.4±0.5 (7)	35.0±2.0 (2)
3	Stkhlm	20	18/21	7	29.1±0.5 (11)	29.3±0.4 (17)	31.1±0.6 (23)	32.4±0.8 (10)
4	Stkhlm	20	18/20	4	27.6±0.3 (26)	28.4±0.3 (22)	30.8±0.4 (5)	— (0)
5	Stkhlm	20	18/20	6	30.6±0.5 (24)	30.3±0.3 (21)	33.4±0.7 (5)	32.0 (1)
6	Stkhlm	20	18/20	8	29.5±0.4 (25)	29.6±0.3 (26)	32.0±0.0 (2)	30.0±0.0 (2)
7	Stkhlm	17	18/20	8	38.0±0.0 (2)	42.2±0.8 (6)	44.6±1.3 (12)	45.9±1.2 (13)
8	Stkhlm	20	18/20	8	24.9±0.2 (14)	25.8±0.2 (21)	26.8±0.6 (8)	— (0)
9	Stkhlm	23	18/20	8	21.8±0.3 (19)	22.0±0.3 (17)	23.9±0.6 (89)	25.0 (1)

E, Experiment number; T, temperature (°C); L, photoperiod (light period in a 24 h cycle) or sequence of photoperiods; D, day of transfer between photoperiods; *N* in parentheses. The first two rearings were from single parental pairs whereas the remaining were offspring from several females.

day after pupation) and adult morph for all rearings, and in most cases also on hatchling weight and pupal development time. From these data growth rates were calculated. Growth rate is here defined as a measure of weight gain (or loss). It can be expressed as weight gained per unit time (e.g. mg day^{-1}) or growth can be scaled to unit weight as well as time (e.g. (mg mg^{-1}) day^{-1}). In this study growth rates were calculated according to a formula which is a logarithmic version of the latter calculation and expresses the approximately exponential growth which is typically found in insects:

$$\log(\text{growth rate}) = (\log(W_f) - \log(W_0))/D$$

where W_f is final (pupal) weight, W_0 hatchling weight and D development time in days from hatchling to pupa. The formula returns a relative growth rate figure such as 1.25, representing a 25% mean daily weight gain.

Developmental rate is here defined as a measure of development in ontogeny, i.e. cell differentiation and morphogenesis. It is most often measured simply as the inverse of the duration of a developmental stage (1 day^{-1}). Thus, a negative correlation (trade-off) between development rate and weight equals a positive correlation between development *time* and weight. In a butterfly, development occurs in all stages of the life cycle but growth occurs only in the larva. Larval development may be strongly coupled with larval growth, as when moltings occur at specific weights, but growth and development can also be more or less decoupled as when dwarfs are produced on poor-quality host plants.

The potential trade-off between development rate and size/weight cannot be studied in isolation from other life-history traits. Assuming a strong correlation

between pupal weight and adult size (this assumption is tested below), the size/weight of an adult butterfly can be described as the result of an interplay between three life-history traits: besides development time from hatchling to pupa, pupal weight may be influenced by two other aspects of 'intermediate structure', i.e. hatchling weight and/or larval growth rate (cf. Sibly & Calow, 1986; Sibly & Monk, 1987). When the two latter traits are relatively constant, or at least do not covary with experimental categories, we can expect to see trade-offs between development time and size. In addition, pupal development time is also of interest because variation in this trait affects total development time, but not pupal weight and (in a holometabolous insect) probably not adult size/weight. Thus, it is decoupled from the studied trade-off but may yet affect its expression.

Variation among categories

Transfers from 12 h to 22 h light at high temperatures eight days after hatching are close to 100% effective at producing the light morph (Nylin, 1989) and to produce mixed broods conditions had to be found which were less prone to induce direct development. As females varied in their tendency to produce directly developing offspring, and there was no constant critical daylength, this was essentially a trial-and-error process. Mixed broods were included when found, which accounts for some unbalanced designs. Conditions are given below, but it should be noted that in all cases individuals of all categories in one experiment experienced the same temperatures and photoperiods, so that the exact conditions generally are not crucial for interpretation. In two cases, constant photoperiods were used to control for the fact that, using a fixed day of transfer, fastly and slowly growing larvae differ slightly in the photoperiods experienced at a particular stage. Experiments 1–2 were single family rearings in order to control for genetical or maternal effects on both populations. Use of families increases the genetic similarity between individuals and help assure that they will be divided among environments in a random manner with respect to genotype. Experiment 3 was made with the pooled offspring from three females. Experiments 4–6 and 7–9 were made with the pooled offspring from four and three different female lines, respectively.

Variation among environments

Experiments 7–9 were made at three different temperatures, as noted above. Two experiments, one on each population, were designed to investigate the effects of photoperiods indicating the progression of the season on variation in life-history traits. Both experiments were made with split broods.

RESULTS

Main life cycle regulation

Photoperiod

The rearing of a Stockholm single female family split between photoperiods at 21°C gave a conclusive result concerning the effects of changing daylengths in life cycle regulation (Fig. 1; cf. Nylin, 1989, for a discussion). Thus, at constant daylengths of either 16 h or 18 h a low proportion of individuals developed into

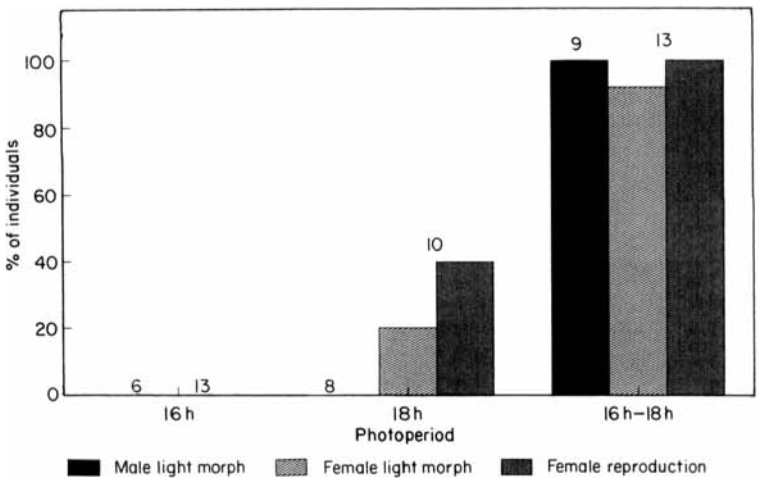

Figure 1. The proportion of male and female individuals in a family of *Polygonia c-album* that developed into the light morph, and the proportion of females ovipositing or carrying eggs, in two constant photoperiods and when larvae had experienced a change from the shorter to the longer photoperiod. N for males and females, respectively, is given above bars.

the light morph whereas with a change between the same daylengths experienced by the larvae almost all individuals did so (χ^2; $P < 0.05$). This corresponds to a high proportion of females scored as being in reproductive diapause in the first two categories, whereas all females in the last category were scored as direct developers (Fig. 1). A few dark morph females did however, produce eggs, which demonstrates that the correlation between morph and diapause occasionally breaks down at near-critical conditions and thus that adult morph and maturation of gonads can be determined independently to some extent.

An increase in photoperiod from 16 h to 18 h during the early stages of larval development is not unrealistic in the Stockholm area if civil twilight is excluded. If it is included, a change from 18 h to 20 h is more realistic, and this was the contrast used in most other experiments. Note also that in the field, following such an initial increase in photoperiod, larvae will normally experience decreasing photoperiods towards the end of larval development and this will induce the diapausing morph and univoltinism (Nylin, 1989).

Strongly contrasting photoperiods, e.g. transfers from 12 h to 22 h, were often 100% effective at inducing the light morph (e.g. experiment 2b–c of Table 6) but more moderately increasing photoperiods at a temperature of 20°C produced mixed broods of both morphs in the Stockholm population (Table 1). Note also from Table 1 that the day of transfer between photoperiods did not crucially affect the frequency of light morph adults (experiments 4–6). The studied range, 4–8 days from hatching, is admittedly narrow but this result suggests that larvae had responded to the short photoperiods of spring already during the first days of development.

The result that the proportion of light morph individuals, and of direct developers among females, was slightly higher in a constant long photoperiod than in a constant shorter photoperiod (Fig. 1; n.s.) could indicate that the system for photoperiodic regulation in *P. c-album* is a modification of the 'long-

day'-type (cf. Danilevskii, 1965) found in related species. That is, an artificially constant long day (which is consequently experienced during late larval development, when the development pathway is finally determined) is interpreted as a date relatively early in the summer (close to summer solstice) and a shorter day indicates a later date and therefore less time for a second generation.

Temperature

Low temperature apparently strengthened the induction of diapause (experiments 7–9). The proportion of dark morph individuals at 17°C was 75.8% (sexes pooled) as compared with 18.6% and 20% at 20°C and 23°C, respectively ($P < 0.001$, χ^2, both comparisons). The results of this single experiment suggest a threshold temperature rather than a proportional effect. They also indicate that besides photoperiod, low temperature may be a complementary proximate explanation for the univoltinism of the Stockholm population. Larval development in the field occurs in May–June and, according to statistics from the Swedish Meteorological and Hydrological Institute, a typical daily mean field temperature during June in the Stockholm area is 15°C whereas a typical daytime maximum temperature is 20°C.

Weight and size

Pooling all individuals in experiment 2a, the correlation between pupal weight and adult size (forewing length) was significant ($P < 0.001$; $N = 35$) but the explanatory power (r^2) was rather low, or 26.8%. In the two other (light morph only) rearings where forewing length was measured the two variables were likewise significantly correlated (2b: $P < 0.01$; $N = 19$, 2c: $P < 0.001$; $N = 44$) but again variation was high. To a large extent, this was due to differences between the sexes and morphs in the relationships between pupal weight and adult size. In all three experiments the tendency was for males to be slightly, but not significantly, heavier in the pupa but significantly smaller in size as measured by forewing length (e.g. experiment 2a: males 2.43 ± 0.01 mm, females 2.51 ± 0.03 mm; $P < 0.001$; ANOVA). Note, therefore, that a brood may be sexually dimorphic in one of the two traits (usually size) but not the other.

The correlations were considerably better among females than among males in all three experiments (r^2 for males, light morph only: 20.0%, 27.6% and 35.6%, respectively; females 80.0%, 74.3% and 75.0%). The correlation was also better for dark morph males than for light morph males in experiment 2a (where the comparison was possible), as r^2 was 96.6% vs 20.0%. Hence, light morph males varied strongly in size relative to pupal weight, whereas dark morph males and light morph females displayed good correlations between these two life-history variables (data on dark morph females was insufficient in this experiment, as in most mixed broods).

The search for trade-offs: morphs and sexes

Total development time

There were more or less consistent differences in development time between morphs and sexes in both studied populations (Table 1; Figs 2, 3). Owing to the

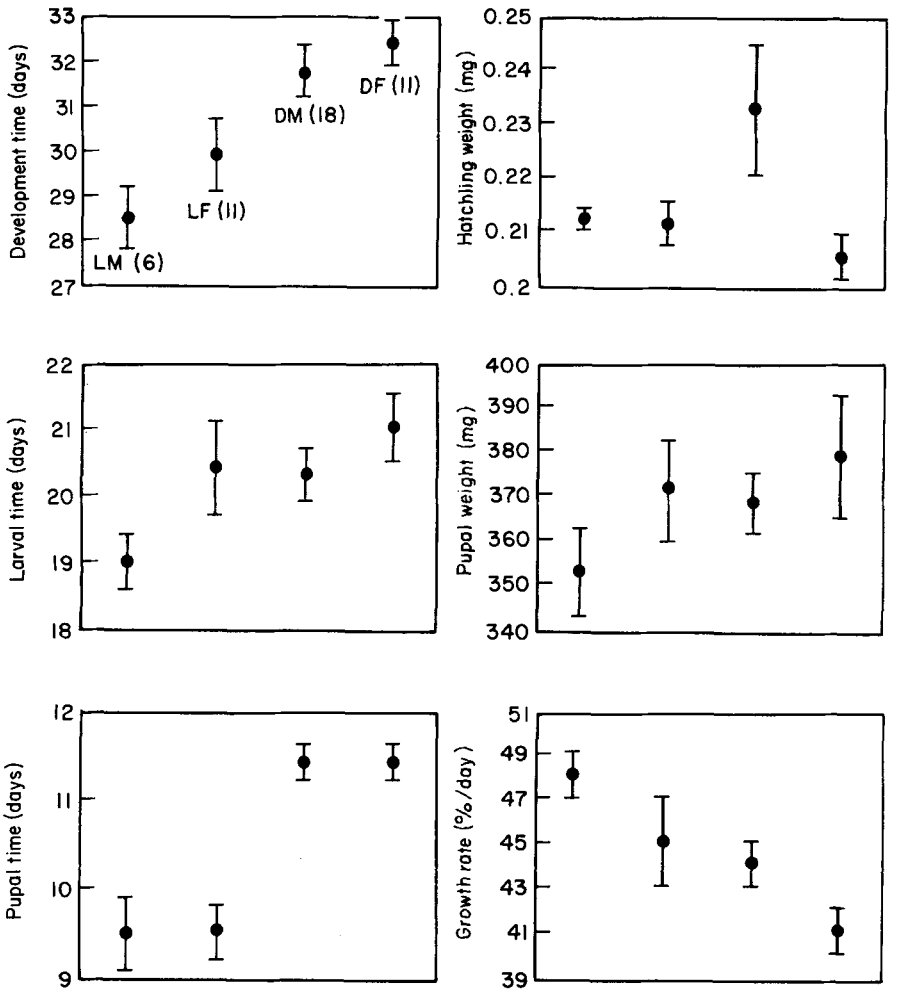

Figure 2. Life-history data (means ± SE) for four categories of individuals (LM: light morph males, LF: light morph females, DM: dark morph males, DF: dark morph females; *N* in parentheses) of *Polygonia c-album* in a family of the Oxford population.

greater tendency for males to diapause in mixed broods of *P. c-album* and other butterflies (discussed in Wiklund, C., Wickman P.-O, & Nylin, S., 1992), equal proportions of the sexes and morphs were seldom found, which complicates comparisons between categories. Two overall trends could however be seen, especially in experiments 1 and 3, where the categories were best balanced (Table 1; Fig. 2). These trends were: (1) shorter development times for individuals which later developed into the light morph as compared to individuals developing into the dark morph, and (2) for males as compared with females, i.e. in accordance with the first two predictions in the Introduction.

The difference between morphs (of the same sex, typically 2–3 days at 20°C, a 10% difference) was found for both sexes over a range of conditions, in both studied populations and in groups of full siblings as well as with less closely related individuals (Table 1; Figs 2, 3). When comparisons were made between

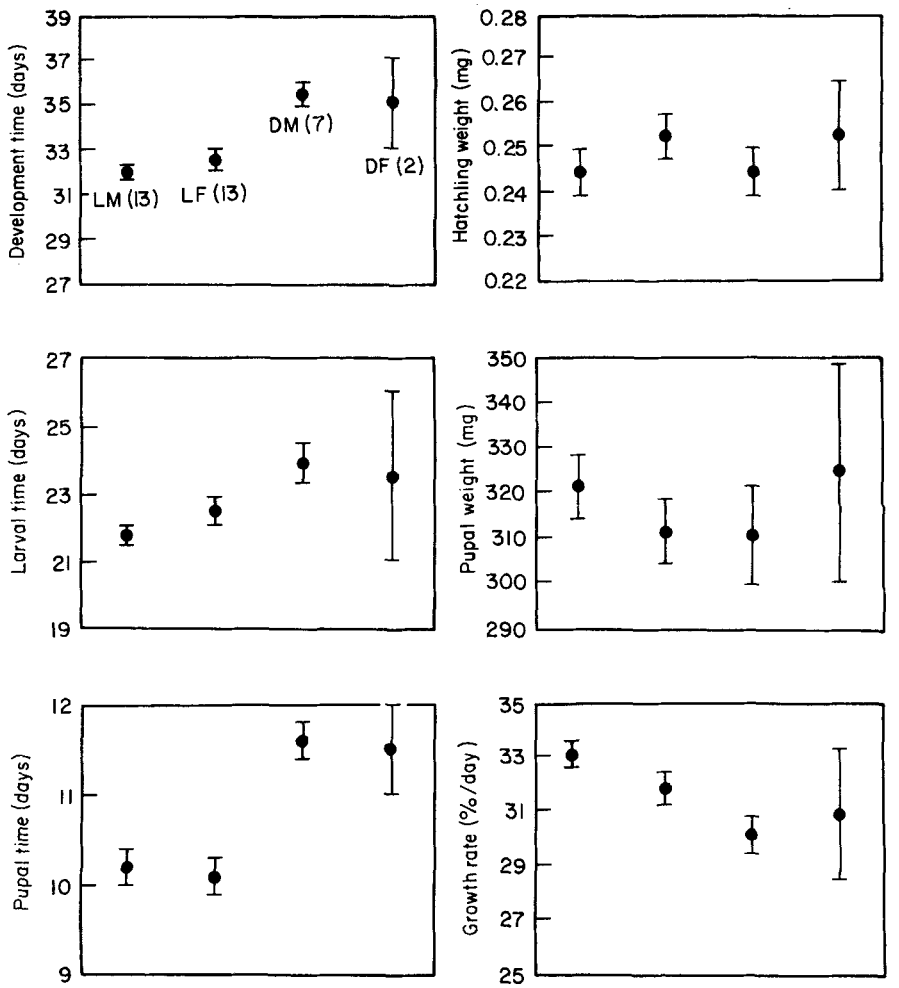

Figure 3. Life-history data (means ± SE) for four categories of individuals (LM: light morph males, LF: light morph females, DM: dark morph males, DF: dark morph females; N in parentheses) of *Polygonia c-album* in a family of the Stockholm population.

males of the two morphs, the difference was significant ($P < 0.005$–$P < 0.001$) in seven out of nine experiments (ANOVA). In the remaining (experiments 6–7), the difference was in the same direction but categories were too unbalanced for significance. For females, the difference was also consistently in the direction of shorter development times for the light morph individuals, and significance ($P < 0.05$–$P < 0.001$) was found in the three experiments where data permitted a comparison (experiments 1, 3 and 7; ANOVA). These results are consistent with the interpretation that development time in *P. c-album* follows a reaction norm where short development times are seen under environmental conditions promoting direct development (i.e. in light morph adults).

The difference between the sexes was considerably weaker and less consistent, especially for the diapausing dark morph (as predicted). However, light morph males spent shorter times in growth and development than light morph females in eight out of nine cases, and this difference was statistically significant in

TABLE 2. Life-history data (mean ± SE) for the sexes and morphs of *Polygonia c-album* from Stockholm

		Category			
		Light morph		Dark morph	
E	Factor	Males	Females	Males	Females
4	Larval time (d)	18.7±0.3	19.2±0.3	19.6±0.4	—
	Pupal time (d)	8.8±0.1	9.2±0.1	11.2±0.4	—
	Hatchling (mg)	0.241±0.003	0.241±0.004	0.213±0.009	—
	Pupa (mg)	340.3±6.4	334.8±8.8	348.2±12.8	—
	Growth (%/d)	47.6±0.7	45.9±0.7	46.0±0.9	—
		(26)	(22)	(5)	(0)
5	Larval time (d)	20.8±0.4	20.3±0.3	21.4±0.7	20.0
	Pupal time (d)	9.8±0.1	10.0±0.1	12.0±0.3	12.0
	Hatchling (mg)	0.234±0.005	0.238±0.004	0.216±0.011	0.265
	Pupa (g)	347.8±7.5	354.9±6.5	345.8±14.6	390.2
	Growth (%/d)	42.5±0.9	43.5±0.7	41.5±1.7	44.0
		(24)	(21)	(5)	(1)
6	Larval time (d)	20.1±0.3	20.2±0.3	20.0±0.0	19.0±0.0
	Pupal time (d)	9.4±0.1	9.4±0.1	12.0±0.0	11.0±0.0
	Hatchling (mg)	0.246±0.004	0.242±0.004	0.248±0.006	0.247±0.0
	Pupa (mg)	341.4±5.6	332.7±6.3	366.8±39.4	366.6±2.5
	Growth (%/d)	43.7±0.8	43.3±0.7	44.0±0.6	46.8±0.1
		(25)	(26)	(2)	(2)
7	Larval time (d)	24.5±0.5	26.5±0.7	27.9±1.1	29.2±1.0
	Pupal time (d)	13.5±0.5	15.7±0.4	16.7±0.3	16.7±0.4
	Hatchling (mg)	0.252±0.032	0.263±0.010	0.243±0.006	0.247±0.008
	Pupa (mg)	286.0±0.6	318.2±13.8	316.5±6.2	299.2±12.8
	Growth (%/d)	33.3±1.5	30.8±1.0	30.0±1.5	28.1±1.3
		(2)	(6)	(12)	(13)
8	Larval time (d)	16.4±0.3	17.5±0.3	17.6±0.7	—
	Pupal time (d)	8.4±0.3	8.2±0.2	9.1±0.4	—
	Hatchling (mg)	0.273±0.007	0.280±0.005	0.284±0.008	—
	Pupa (mg)	284.4±7.3	309.4±6.1	306.6±14.3	—
	Growth (%/d)	52.9±1.0	49.5±0.9	49.6±3.0	—
		(14)	(21)	(8)	(0)
9	Larval time (d)	14.3±0.3	14.6±0.3	15.1±0.5	16.0
	Pupal time (d)	7.5±0.2	7.4±0.2	8.8±0.3	8.0
	Hatchling (mg)	0.286±0.005	0.290±0.005	0.292±0.005	0.310
	Pupa (mg)	310.6±5.3	312.5±7.3	309.7±11.3	263.5
	Growth (%/d)	63.5±1.5	61.6±1.5	59.2±2.7	52.4
		(19)	(17)	(8)	(1)

experiments 4, 7 and 8 (Table 1; ANOVA, $P < 0.05$). The observed difference between sexes was in the expected direction and is most probably due to selection for protandry. The weak difference observed in especially the experiments on Swedish insects may relate to the fact that in the univoltine Swedish population selection for protandry as regulated by pre-diapause development time should be very weak, since all individuals normally hibernate.

Components of total development time

Total development times for the four categories of individuals in a mixed brood of siblings of the Oxford population (experiment 1) are shown in Fig. 2, together with the traits which may be involved in causing the differences in development time and in trade-offs. Figure 3 shows the same traits from data

collected in experiment 2a (Stockholm population), also a group of full siblings. These experiments were singled out to illustrate results. Data from the remaining experiments are summarized in Table 2 (full data were not collected in experiment 3).

Several observations can be made from Figs 2, 3 and Table 2. One is that a tendency towards a trade-off between total development time and pupal weight among categories of morphs and sexes is sometimes seen (Fig. 2), but most often not (Fig. 3; Table 2). Another is what could be part of an explanation: the differences in development time between light- and dark morph individuals were caused at least as much by differences in time spent in the pupal stage as in time spent in the larval stage. The former type of variation could not affect pupal weight (as measured the day after pupation).

From experiment 1 (Oxford), data were also available on time spent in the first four larval instars together, in the final instar and in the pupa. The difference in total development time between light and dark morph males in this experiment (3.2 days) was due, in increasing order of importance, to differences in early larval time (17%), late larval time (23%) and pupal time (60%). For females, the corresponding figures were 2.5 days, 12%, 15% and 73%.

From the Stockholm population complete data were available only on total larval time and pupal time, and a good comparison could be made only for males in experiments 2a and 4–9 (cf. Fig. 3 and Table 2). In these experiments the proportion of the differences which could be ascribed to different durations of the pupal stage rather than the larval stage ranged from 37% (experiment 8) to 100% (experiment 6). The difference between morphs in the duration of the larval stage was significant in only one case: males in experiment 2a (ANOVA, $P < 0.01$). The differences in pupal time were significant for both sexes in experiments 1 and 6 (ANOVA; both sexes $P < 0.001$) and for males also in five of the six remaining experiments (ANOVA; experiments 2a, 4–5 and 9, $P < 0.001$, experiment 6 $P < 0.01$). Together, these results show that the differences in development time between morphs mainly accumulated late in development, and at least as much through differences in pupal developmental rates as in larval developmental and growth rates. This is especially striking in view of the fact that the duration of the pupal stage was typically only half that of the larval stage (Figs 2, 3; Table 2).

In contrast, in most experiments the differences in development time between the sexes were entirely due to differences in duration of the larval stage, whereas pupal times were similar for the sexes in both morphs (Figs 2, 3; Table 2). In experiment 1, where data were available, the durations of the final larval instar differed more between sexes than instars 1–4 together (light morph 1.0 vs 0.4 days, dark morph 0.6 vs 0.1 days). Hence, the sexual differences in development time accumulated mainly during the last stage of larval development, but not at all in the pupa. This demonstrates that the variation in development time among categories of sexes and morphs, respectively, is determined by two separate processes. Moreover, the two processes have very different implications regarding the studied trade-off between development time and weight.

Larval development time, hatchling weight and growth rate

As stated above, variation between categories of morphs and sexes in larval (rather than total) development time were generally relatively slight. However,

variation was generally seen in the predicted directions, so why the absence of consistent trade-offs with pupal weight? Two possibilities are that the observed variation in larval development time could be explained by variation in hatchling weight or growth rate, rather than by individuals ceasing to grow at different weights.

Hatchling weight was similar among categories. The longer larval times for the dark morph compared to the light, and for females compared to males, could not be explained by lower hatchling weights as no such consistent differences were found (Fig. 2, Table 2). However, it can be noted from Fig. 2 and Table 2 that the difference in larval development time between morphs was reflected by variation in growth rates. The differences in growth rates between morphs in a given sex were not significant in any single experiment (ANOVA), but the consistent patterns have a low probability of occurring by chance. Thus, light morph males both displayed shorter larval development times and grew faster than dark morph males in all six experiments where data were available (and N at least 5 in both categories), whereas light morph females grew faster than dark morph females in both of the two experiments where the same comparison could be made ($P = \frac{1}{2}^8$; $P < 0.01$).

Concerning the sexual difference in larval development time the pattern varied greatly, so that trade-offs between development time and weight (and female-biased weight dimorphism) were sometimes, but not always, seen. Note in this context that in experiment 1 (Fig. 2), where there was a tendency towards a correlation between larval time and pupal weight among categories ($P < 0.01$ calculating from category mean values, ignoring individual variation), there was such a weight difference and this was more female-biased among light morph insects. This result (also cf. Table 3) is predicted by the hypothesis that selection for protandry may influence sexual size dimorphism (Singer, 1982; Wiklund & Solbreck, 1982; Wiklund *et al.*, 1991). However, compare e.g. experiment 2a (Fig. 3) where the difference in protandry between generations also was in the expected direction but size dimorphism patterns were in reverse to those expected, demonstrating that in this case light morph insects achieved protandry by speeding up male growth rates relative to females rather than through size dimorphism.

The search for trade-offs: environments

Temperature

Total development time (from hatchling to adult) was strongly dependent on temperature (Table 1, experiments 7–9; $P < 0.001$, ANOVA), in accordance with the third prediction in the Introduction. This was due to longer durations of both the larval and pupal stages at lower temperatures (Table 2), corresponding to lower growth and developmental rates. Pupal weights were however not affected by temperature (Table 2; ANOVA), and in fact did not significantly contribute to variation in development time among individuals, pooling experiments 7–9 (ANOVA).

Photoperiod and quantitative variation in development time

The importance of a short development time should increase with the progression of the season, as less and less time remains for the completion of a

TABLE 3. Life-history data (mean ± SE) for a family of *Polygonia c-album* of the Oxford population in different sequences of photoperiods. *N* (in parentheses) show the proportion of each morph and thus the tendency for direct development

	Sequence of photoperiods			
Category	12 h–18 h	18 h–20 h	18 h–20 h–18 h	20 h–18 h
Light males	(12)	(9)	(6)	(0)
Larval time (days)	20.9 ± 0.3	20.4 ± 0.9	19.0 ± 0.4	—
Pupal time (days)	11.1 ± 0.1	9.6 ± 0.4	9.5 ± 0.4	—
Pupal weight (mg)	379.0 ± 9.3	361.4 ± 6.5	352.5 ± 9.9	—
Light females	(14)	(14)	(11)	(0)
Larval time (days)	21.4 ± 0.4	20.9 ± 0.5	20.4 ± 0.7	—
Pupal time (days)	11.1 ± 0.3	9.4 ± 0.3	9.6 ± 0.3	—
Pupal weight (mg)	401.5 ± 6.0	392.0 ± 3.7	370.5 ± 11.5	—
Dark males	(0)	(2)	(18)	(8)
Larval time (days)	—	23.5 ± 1.5	20.2 ± 0.4	20.0 ± 0.8
Pupal time (days)	—	10.5 ± 1.5	11.4 ± 0.2	10.8 ± 0.3
Pupal weight (mg)	—	386.7 ± 35.6	367.7 ± 6.7	382.6 ± 8.6
Dark females	(0)	(0)	(11)	(18)
Larval time (days)	—	—	20.9 ± 0.5	21.8 ± 0.5
Pupal time (days)	—	—	11.2 ± 0.2	11.3 ± 0.3
Pupal weight (mg)	—	—	379.1 ± 13.8	383.0 ± 7.2
Direct development (%)	100	92	37	0

generation of offspring. Do the reaction norms of individuals reflect this fact, and does this result in a trade-off with weight/size? Given the system for photoperiodic regulation described above, this can be tested using changing photoperiods mimicking naturally changing daylengths or possibly by using constant photoperiods where a short day indicates a later date (i.e. after summer solstice).

Figure 4 (and Table 3) shows the response of directly developing (light morph) individuals in a family of the Oxford population to three sequences of photoperiods indicating progressively later dates (as evidenced by a decreasing proportion of light morph individuals; Table 3). It can be seen that both males and females speeded up development in both the larval and the pupal stages in response to "later" photoperiods. With the exception of female pupal times, the regressions were significant ($P < 0.01$–$P < 0.001$) when development times of individuals were regressed against either a rank 1–3 representing a date in the season, or against the proportion of individuals developing directly when larvae had experienced a given sequence of photoperiods. There was a clear tendency (significant in females; $P < 0.05$) for pupal weights to decrease when development times decreased and there was no corresponding trend in hatchling weight ($P > 0.4$). This indicates that a trade-off occurred between pupal weight and development time in this case. Although a family is not a clone, it must be assumed that this trade-off was made at the level of individual phenotypic plasticity, since individuals were assigned to environments randomly with respect to genotypes.

From Table 3 it can be noted that individuals destined for diapause (dark morph) showed tendencies towards the same trends, but much less consistently.

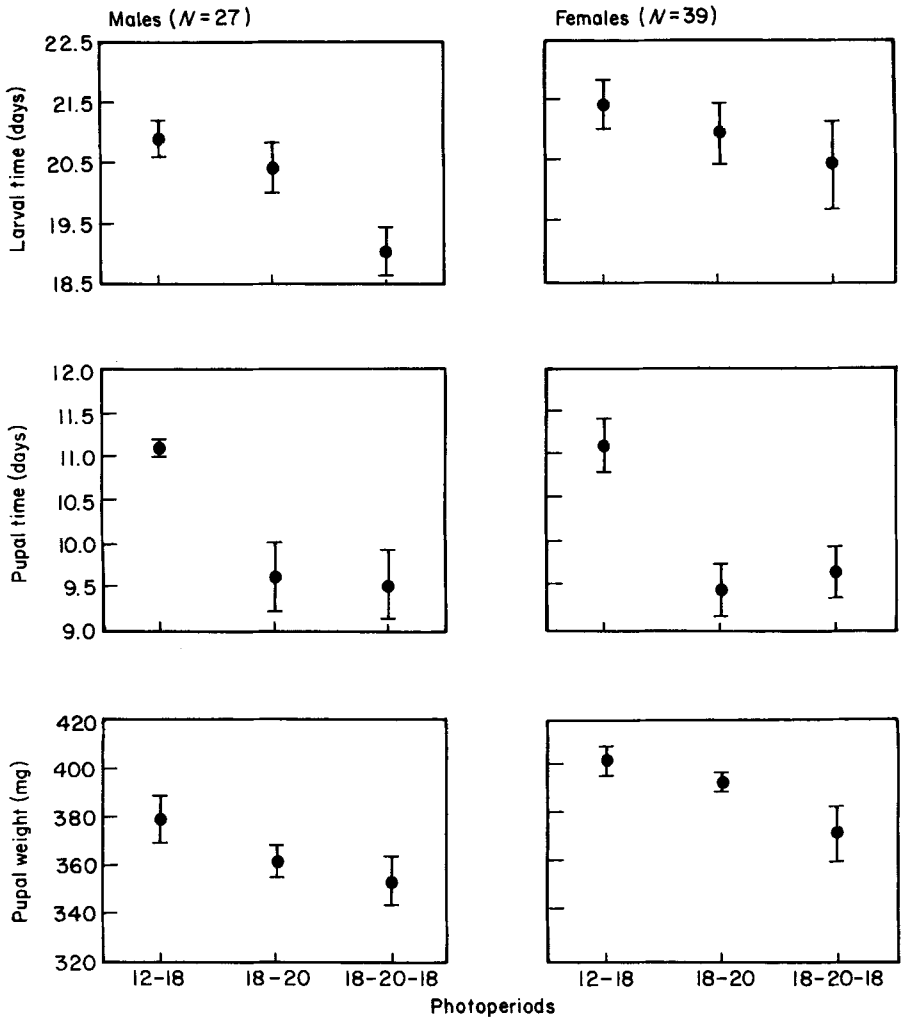

Figure 4. Life-history data (means ± SE) for light morph males (left) and females (right) in a family of the Oxford population when larvae had experienced three sequences of photoperiods (daylength is given below each diagram) indicating progressively later dates in the season.

Note also that pupal times of light morph individuals in the sequence 12 h–18 h (indicating spring conditions and thus comparatively light time stress for direct developers) were close to those typical of dark morph individuals in mixed broods, i.e. about 11 days, so that the differences seen at critical conditions (Figs 2, 3) seems to be a product not only of the main developmental pathway chosen but also of regulation within pathways. The difference in larval times and the corresponding decrease in weight between the sequences 18 h–20 h and 18 h–20 h–18 h occurred also in the experiment on the Stockholm population (Table 5; data on hatchling weight and pupal times were not collected), but the data were unbalanced and results somewhat inconsistent due to the problems in achieving direct development under different photoperiodic conditions in Stockholm insects.

The effects of constant photoperiods were also tested (Tables 4, 5). Note from

TABLE 4. Life-history data (mean ± SE) for a family of *Polygonia c-album* of the Oxford population in different constant photoperiods. *N* (in parentheses) show the proportion of each morph and thus the tendency for direct development

	Photoperiod		
Category	20 h	18 h	12 h
Light males	(12)	(8)	(0)
Larval time (days)	20.7 ± 0.6	18.5 ± 0.6	—
Pupal time (days)	10.2 ± 0.3	9.1 ± 0.3	—
Pupal weight (mg)	349.6 ± 11.0	367.8 ± 7.4	—
Light females	(12)	(15)	(0)
Larval time (days)	20.6 ± 0.6	19.0 ± 0.4	—
Pupal time (days)	10.4 ± 0.3	9.5 ± 0.2	—
Pupal weight (mg)	379.7 ± 10.9	369.7 ± 8.3	—
Dark males	(4)	(2)	(13)
Larval time (days)	24.8 ± 1.8	21.0 ± 1.0	20.3 ± 0.5
Pupal time (days)	11.8 ± 0.8	11.5 ± 0.5	11.5 ± 0.2
Pupal weight (mg)	394.8 ± 11.3	351.8 ± 10.6	358.7 ± 9.0
Dark females	(0)	(1)	(15)
Larval time (days)	—	18.0	20.7 ± 0.5
Pupal time (days)	—	10.0	12.1 ± 0.2
Pupal weight (mg)	—	398.7	358.2 ± 9.4
Direct development (%)	86	88	0

these results, first, that dark morph individuals again spent considerably longer times in the larval and pupal stages than light morph individuals, which shows that the variation seen under changing photoperiods was not an artefact of the fixed day of transfer. Second, the times spent in the larval and pupal stages were

TABLE 5. Life-history data (mean ± SE) for a family of *Polygonia c-album* of the Stockholm populations in different photoperiods. *N* (in parentheses) show the proportion of each morph and thus the tendency for direct development

	Photoperiod or sequence of photoperiods			
Category	18 h–20 h	18 h–20 h–18 h	20 h	18 h
Light males	(5)	(0)	(2)	(1)
Larval time (days)	22.2 ± 0.7	—	20.0 ± 1.0	21.0
Pupal weight (mg)	307.4 ± 6.8	—	342.7 ± 11.8	306.8
Light females	(5)	(3)	(3)	(0)
Larval time (days)	23.4 ± 0.4	17.7 ± 0.9	18.7 ± 1.8	—
Pupal weight (mg)	320.5 ± 12.2	277.6 ± 22.2	303.9 ± 6.7	—
Dark males	(5)	(5)	(11)	(14)
Larval time (days)	22.6 ± 0.9	21.2 ± 0.2	22.5 ± 0.5	22.0 ± 0.6
Pupal weight (mg)	306.8 ± 5.2	301.2 ± 6.8	313.7 ± 5.1	302.4 ± 7.3
Dark females	(4)	(5)	(5)	(8)
Larval time (days)	24.8 ± 1.2	20.0 ± 0.3	24.2 ± 1.2	22.9 ± 0.6
Pupal weight (mg)	283.6 ± 9.3	296.6 ± 10.2	308.8 ± 11.1	317.4 ± 3.0
Direct development (%)	53	23	24	4

generally longer in 20 h than in 18 h, which is in accordance with predictions. The shorter development times in 18 h sometimes but not always was associated with a weight loss. Third, the fastest dark morph category (12 h) was in fact faster in the larval stage than the slowest light morph category (20 h) in the Oxford experiment (Table 4), again demonstrating the importance of plasticity within pathways for creating the differences seen between them at near-critical conditions.

The search for trade-offs: individuals

The growth rates of individuals were calculated according to a formula including hatchling weight, pupal weight and larval development time (see Methods). Rearranging this formula, larval time is a function of the logarithmic values of the other three variables. Hence, hatchling weight, pupal weight and growth rate should all correlate with larval time to some degree, and the varying degrees of correlation with these variables are to some extent indicative of how different larval development times were proximately achieved.

Time spent in the larval stage should correlate positively with pupal weight (and result in trade-offs between development rate and weight) among individuals, given that hatchling weights and growth rates are relatively constant. Pooling all categories of individuals, there were no such positive correlations, and in fact the correlations were significantly negative in experiments 4–6 ($P < 0.01$–$P < 0.001$). Concerning variation among individuals *within* categories the two variables again were not significantly positively correlated in any case, but in several cases significantly negatively correlated ($P < 0.05$–$P < 0.001$), and this was true for both morphs and both sexes.

Turning to the next variable, hatchling weights could be expected to correlate negatively with larval times given relatively constant pupal weights and growth rates. When categories were pooled a significant negative correlation was found only in experiment 6 ($r = -0.455$, $P < 0.001$). In the other experiments (including the replicate, experiment 8) the most common result was a slight positive correlation (n.s.). Within categories, the sign of the correlation coefficients varied and the only significant correlation was for light morph males in experiment 6 ($r = -0.506$, $P < 0.01$). Hence, even within categories hatchling weights generally had very little effect on larval times.

In contrast, short mean larval times were accompanied by high mean growth rates also among individuals, as could be expected if hatchling and pupal weights were relatively constant compared with growth rates. When the correlations between larval time and hatchling weight, pupal weight or growth rate, respectively, were compared the last correlation was consistently strongest (among or within categories). When the other two correlations varied greatly as to sign and level, the correlations with growth rate never were lower than $r = -0.85$ within any category (with an N of at least 5) or among categories in any experiment, and generally greater than -0.95 ($P < 0.001$ in all instances where N was at least 5). To a degree the greater strength of this correlation reflects the fact that growth rate was calculated as a function of larval time (among other variables) whereas hatchling and pupal weights were independent measurements, but the much more consistent correlations nevertheless demonstrate that growth rate variation to a much higher degree than variation

TABLE 6. Life-history data (mean ± SE) for the sexes and morphs of three families of *Polygonia c-album* from Stockholm

		Category			
		Light morph		Dark morph	
E	Factor	Males	Females	Males	Females
2a	Larval time (d)	21.8 ± 0.3	22.5 ± 0.4	23.9 ± 0.6	23.5 ± 2.5
	Pupal time (d)	10.2 ± 0.2	10.1 ± 0.2	11.6 ± 0.2	11.5 ± 0.5
	Hatchling (mg)	0.244 ± 0.005	0.252 ± 0.005	0.244 ± 0.005	0.252 ± 0.012
	Pupa (mg)	321.3 ± 7.1	311.1 ± 7.1	309.9 ± 10.9	324.2 ± 24.5
	Growth (%/d)	39.3 ± 0.8	37.5 ± 0.8	35.1 ± 1.1	36.2 ± 4.6
		(13)	(13)	(7)	(2)
2b	Larval time (d)	20.3 ± 0.2	20.6 ± 0.2	—	—
	Pupal time (d)	10.4 ± 0.1	10.2 ± 0.1	—	—
	Hatchling (mh)	0.247 ± 0.005	0.255 ± 0.004	—	—
	Pupa (mg)	327.1 ± 4.6	317.1 ± 3.7	—	—
	Growth (%/d)	42.5 ± 0.6	41.5 ± 0.6	—	—
		(18)	(28)	(0)	(0)
2c	Larval time (d)	20.2 ± 0.2	20.4 ± 0.2	—	—
	Pupal time (d)	10.3 ± 0.2	10.3 ± 0.2	—	—
	Hatchling (mg)	0.224 ± 0.006	0.222 ± 0.004	—	—
	Pupa (mg)	286.4 ± 6.1	280.1 ± 8.0	—	—
	Growth (%/d)	42.5 ± 0.6	42.0 ± 0.6	—	—
		(9)	(14)	(0)	(0)

in hatchling or pupal weight accounted for the observed individual variation in larval development time. This explains the negative correlations between development time and weight, since this is the expected pattern when some individuals can grow to a higher weight in a shorter time (e.g Van Noordwijk & de Jong, 1986).

The search for trade-offs: families

The experiments were not designed primarily to detect variation in life-history traits among families, representing different coadapted genotypes in one population. However, experiment 2a–c represented offspring from three different females, and a comparison is of some interest (Table 6). Note that the brood (2a) where the tendency to diapause was high (compared with the two broods where only the light morph was produced; 2b–2c) also displayed longer larval times for both morphs and both sexes, and that this was because of lower growth rates rather than higher pupal weights or lower hatchling weights (Table 6; compare 2a–2b). Pupal development times for the light morph were similar in all three broods. Comparing the two broods displaying short larval times, both hatchling weights and pupal weights were lower in experiment 2c than in 2b, so that growth rates were still similar and in both cases higher than in 2a (Table 6).

Hence, also when families are tentatively compared, there is no evidence of a trade-off between larval time and pupal weight. Rather, variation in larval times among genotypes, which could be correlated with differing tendency to diapause (in accordance with the prediction in the Introduction), may be due to differing basal growth rates.

The search for trade-offs: populations

An equally tentative comparison can also be made between the experiments on stock from Oxford and Stockholm. Compare, for instance, experiments 1 and 2a (Figs 2, 3). At 20°C total development time was > 10% shorter in the Oxford experiment for all categories (Figs 2, 3; Table 1), in accordance with the prediction in the Introduction. This was due to differences in both larval and pupal times. Differences in hatchling or pupal weight could not account for the difference in larval duration. In fact, Oxford insects became heavier than Stockholm insects in a shorter time, starting from a lower weight. This corresponded to 20–25% higher growth rates (Fig 2, 3). For light morph individuals, shorter pupal times added to the total difference in development time. Interestingly enough, there was no corresponding difference in pupal times for dark morph individuals (Figs 2–3), which in both populations are headed for diapause and thus have surplus time at these critical day-lengths.

From Table 2 it can be seen that in other experiments with Stockholm stock the life-history traits displayed were more similar to those found in the Oxford experiment, and values could be higher or lower (with the exception of pupal weights, which were highest in the Oxford experiment). For this reason, and since the Oxford stock originated from a single female, these results should not be seen as establishing any differences between the populations. Rather, they demonstrate that the variation in total development time which is due to variation in growth- and developmental rates in the larvae and pupae rather than to differences in final weight could potentially be sufficient to cause trade-offs with weight/size to disappear even at the among-population level. The size for British *P. c-album* given by Thomas (1986), with an average wingspan of 55–60 mm (the higher value for females), is clearly larger than the average in Sweden (where the range is 40–50 mm, e.g. Nordström & Wahlgren, 1941; Nylin, personal observations). This is counter to predictions from theory on latitudinal size patterns (lower weights and smaller sizes in the partially bivoltine Oxford population, as a result of short development times).

DISCUSSION

Returning to the predictions outlined in the Introduction, hypotheses on variation in development time could mostly be corroborated, but not the common assumption that short development times should be associated with small final size. Plasticity in growth and developmental rates (rather than differences in initial or final size/weight) emerges as the single most important factor behind variation in development time in *P. c-album*. In addition, it seems that within wide limits environmentally enforced variation in growth- and developmental rates and associated variation in development times in *P. c-album* does not affect size/weight, and this is true for variation due to temperature (this study) as well as host plant quality. I have previously showed (Nylin, 1988) that this polyphagous species displays similar pupal weights over a range of hosts enforcing up to 25% longer development times compared to the preferred hosts.

Partly parallel cases are the studies on seasonal plasticity in two other butterflies, the satyrine *Pararge aegeria* (Nylin *et al.*, 1989) and the pierid *Pieris napi* (Wiklund *et al.*, 1991) where individuals of the studied populations were

found to regulate growth and development adaptively in response to photoperiod to a striking degree, in many cases not paying the full price in the expected currency of size or weight but instead varying growth- and developmental rates. In *P. c-album,* the loss in pupal weight associated with shorter development times in photoperiods indicating later dates was the only clear exception. This (phenotypic) trade-off occurred in the already time-constrained light morph insects as they came under even stronger pressure to develop in a short time.

Saying that growth—and developmental rates vary instead of weight over a range of developmental times (and vice versa) expressed by a range of genotypes, as is especially striking in *P. c-album,* amounts to saying that weight/size as a trait appears to be strongly canalized in its phenotypic expression. Phenotypic plasticity and canalization are probably most often thought of as contrasts, but they may rather be two sides of the same coin. The relationship can be illustrated with the strongly interrelated set of traits studied in this paper: final weight, growth rate and development time. Size is positively correlated with both of the two other variables (when everything else is equal), but they have a negative relationship with each other. Thus, holding size constant over environments and yet being able to express adaptive variation in one of the traits necessitates varying also the other trait through plasticity. If non-adaptive variation in growth rates are enforced by the environment, plastic variation in development time is the only possibility to reach the canalized weight. It is quite possible that plasticity and canalization are closely related phenomena, since both involve modification of the phenotypic expression of genes by other genes in the 'intermediate structure' (*sensu* Stearns, 1989) that shape the reaction norms of genotypes—genetic polymorphism perhaps being more of a true contrast.

A difference from the two studies on *P. aegeria* and *P. napi* mentioned is that since *P. c-album* hibernates in the adult stage rather than as larva or pupa, differences in pupal developmental rates also cause differences in development time between developmental pathways (i.e. up to the potentially diapausing stage). Therefore, it is interesting to note that differences in time spent in the pupal stage is the most important mechanism causing differences between the morphs of *P. c-album,* followed by regulation of late larval growth. This may correspond to the fact that the titre of SMPH (summer morph producing hormone; responsible for inducing the light, non-diapausing, morph) evidently peaks in the pupa, and to a lesser extent in the final larval instar, in the congeneric *P. c-aureum* (Masaki *et al.*, 1989). Given the system for photoperiodic regulation and the physiological mechanism (if it is similar in *P. c-album*), the developmental pathway is not finally determined until late in development (which makes sense in a potentially multivoltine species, selected to take opportunistic advantage of good seasons) and growth/development should consequently not be regulated according to pathway before these stages. The important role for variation in pupal development time in causing adaptive variation in total development time (also cf. Nylin *et al.*, 1989) is intriguing, since it suggests that trade-offs between development time and size/weight may differ in expression between holometabolous and hemimetabolous insects.

High rates of growth and development clearly must carry some cost, even if it is not smaller size. Three possibilities are: (1) increased risk of starvation (applies to larval growth), (2) lower survival in the larval or pupal stage through other

mechanisms and (3) lower quality of later stages, especially the adult, in some other respect than size. The poor correlation between pupal weight and adult size in the fastest developing category, directly developing males, is of interest in this context since it may reflect a cost of fast development in the pupa. If so, the mechanism is far from clear. Possibly individuals developing fast in the pupa are forced into a trade-off between achieving large adult size and high somatic quality in some other unknown respect, resulting in a mixed response.

Both *P. aegeria* and *P. napi* display latitudinal size patterns reminiscent of the "saw-tooth"-patterns predicted by theory (Nylin & Svärd, 1991; Petersen, 1947, respectively) which suggests that in these species development time and adult size are in fact not always optimized simultaneously (through variation in growth rates) when the analysis is extended to variation among populations. In contrast, the limited information available suggests that *P. c-album* may not follow a "saw-tooth"-pattern. The results of the present study suggests that this may occur because of a lack of strong trade-offs acting between development time and size at among-genotype levels, plastic variation in growth and development rates buffering the phenotype against size variation to a high degree.

The results reported above for *P. c-album*, and those from *P. aegeria and P. napi*, strongly suggest that temperate insects normally do not maximize growth- and developmental rates and minimize development times, unless forced to by severe time stress. This is consistent with the interpretation that insects, such as temperate butterflies (with generation lengths similar to the period of seasonal fluctuation) often have surplus time when they are destined for diapause, because of the constraint that hibernation can only take place in species-specific developmental stages (cf. Roff, 1980, 1983). There is thus scope for great plasticity in growth- and developmental rates which may devalue the basic trade-offs often assumed by life-history theory. Surplus time is evidently not spent wholly in the hibernating stage, or no differences in development time up to the potentially diapausing stage would be seen between- and within-developmental pathways. In conclusion, the present results together with those reported elsewhere (Nylin *et al.*, 1989; Karlsson & Wickman, 1989; Wickman *et al.*, 1990; Wiklund *et al.*, 1991) highlight the necessity to study the evolution and effects of plasticity, instead of ignoring it as environmental 'noise'. Plasticity is a necessary subject in evolutionary ecology, not only as a response to environmental heterogeneity which is analogous to genetic differentiation (Giesel, 1976; Roff, 1990) and of equal interest when testing predictions concerning adaptation (as evidenced by the study of conditional strategies in behavioural ecology, ethology and ecological physiology) but also because the roles of the two responses differ and may conflict (Bradley, 1982; Gupta & Lewontin, 1982; Via & Lande, 1985; Schlichting, 1986; Stearns, 1989, 1991; Roff, 1990). We cannot understand one without understanding the other.

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