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REACTION NORMS FOR AGE AND SIZE AT MATURITY IN *LASIOMMATA* BUTTERFLIES: PREDICTIONS AND TESTS

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In recent years there has been a strong increase in the interest in animal life-history plasticity (e.g., Stearns and Koella 1986; Gebhardt and Stearns 1988; West-Eberhard 1989; Kindlmann and Dixon 1992; Newman 1992; Hensley 1993; Reznick and Yang 1993; Via 1993; Bernardo 1994), which has brought into focus the question of how to determine when variation in reaction norms is adaptive (beneficial, and possibly maintained by selection), and when plasticity can even be said to be an adaptation in the strict sense, that is, the origin of the adaptation can be linked to the same selective advantage as the current function.

Not all plasticity is beneficial, in the sense that it increases fitness compared with a different reaction norm (Newman 1992). Reaction norms with nonzero slopes can occur because of “constraints” (factors that are external to the system under investigation, including adaptations shared with many populations or species), rather than because of adaptation to the local environment. One example is when a poikilotherm animal speeds up development at high temperatures. This may be incidental in a given case, but it may serve a function if the animal is, for example, an amphibian inhabiting a temporary pond, and higher temperatures signal that the pond will dry up faster (Newman 1992). If these amphibians respond differently to temperature than related species inhabiting more stationary waters, there may be evidence for adaptation. That a given form of plasticity is likely to be an adaptation can be demonstrated in basically two ways: either by showing experimentally that the shape of reaction norms correspond closely to a priori predictions based on optimality criteria, or by using comparative methods to show that *differences* in reaction norms between species or other categories of individuals (reflecting evolutionary modifications) correspond to predictions (see Gotthard and Nylin 1995). There are few examples in the literature of such attempts at predicting the shape of plasticity. Exceptions include Stearns and Koella’s (1986) models predicting reaction norms for age and size at maturity, and Ford and Seigel’s (1989) and Reznick and Yang’s (1993) predictions regarding how allocation patterns to reproduction should respond to varying food levels in the checkered garter snake, *Thamnopsis marcianus*, and in the guppy, *Poecilia reticulata*, respectively.

In the present study, we used a combination of the two techniques described above to demonstrate that life-history plasticity observed in butterflies of the genus *Lasiommata* (Nymphalidae: Satyrinae) may be adaptations to seasonal

change in environmental conditions. We focused on effects of photoperiod on the life history, because seasonal constraints act strongly on most insects, and photoperiod is the main cue used by insects to detect the progress of the season (Danilevskii 1965; Beck 1980). Typically a large proportion of the year is unfavorable for insect growth and reproduction, and this season can be survived only in diapause, in a species-specific developmental stage or stages. Each individual must complete development up to the diapausing stage before the onset of the unfavorable season, independently of when in the season it started to grow and independently of weather conditions (Reavey and Lawton 1991). This necessity must form a strong selection pressure in favor of life histories promoting this outcome and, hence, some predictions are possible regarding what should constitute the optimal life-history response to seasonal cues (Nylin 1994).

It has been observed that insects may shorten developmental times in day lengths indicating progressively later dates in the season, in crickets (Masaki 1978) and in butterflies (Nylin et al. 1989, 1995; Nylin 1992). A possible interpretation of such patterns is that the alternative “solution” (i.e., rapid development up to the hibernating stage regardless of time of the season, followed by a waiting period of variable length) may not be feasible in these insects, because rapid growth and development is too costly, or because the hibernating stage is less safe than earlier stages, or both. There are two ways that a butterfly can have a short developmental time: either by pupating at a low weight or by growing fast to the same weight. Life-history theory assumes that there must be some cost associated with a short developmental time, because otherwise organisms should have infinitely short generation times. Small adult size is the most commonly assumed cost (e.g., Pianka 1970; Roff 1983). We have found, however, that short developmental times in butterflies seem to be associated more strongly with high growth rates than with low pupal weight and small adult size (Nylin et al. 1989, 1993, 1995; Nylin 1992, 1994; Wiklund et al. 1991). A theoretical model of this relationship (Abrams et al. 1996) suggests that an organism should, if possible, shorten its developmental time when the time left to the optimal maturation date is shorter and that it should do so more by increasing growth rates than by maturing at a small size, unless the cost of high growth rates (e.g., Gotthard et al. 1994) increases faster than linearly.

Lasiommata petropolitana and *Lasiommata maera* are

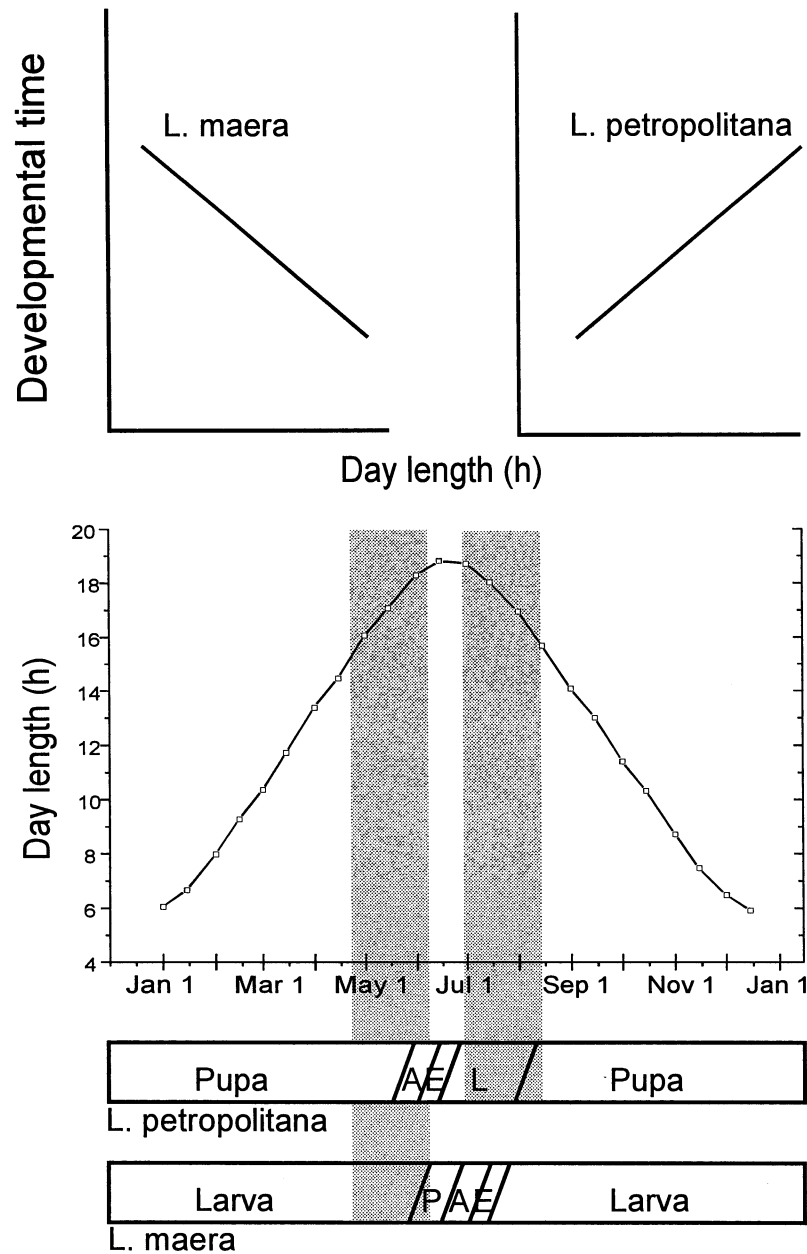


FIG. 1. (Bottom) Phenology of *Lasiommata petropolitana* and *Lasiommata maera* in Sweden. A, Adult; E, Egg; L, Larva; P, Pupa. (Center) Variation in day length in central Sweden over the year. Shaded areas extending from the phenologies of *L. petropolitana* and *L. maera*, respectively, highlight day lengths experienced by late larval instars of each species. (Top) Predicted reaction norms, assuming short developmental times at dates late in the season.

closely related species that are very similar in most respects. There is no phylogeny available for the genus *Lasiommata*, which includes five to six species in Europe and Asia. The two investigated species may be sister species, because they share details of the male genitalia that are unique among at least the European *Lasiommata* (Higgins 1975). They differ in that *L. petropolitana* hibernates in the pupal stage (in Sweden), whereas *L. maera* hibernates as a half-grown larva. Both species are univoltine in Sweden. A consequence of the difference in overwintering stage is that the late larval instars of *L. petropolitana* occur only in late summer, after summer solstice, whereas in *L. maera* they occur only in spring, before

summer solstice (Fig. 1). The late larval instars and the pupal stage have been found to be the most flexible (in terms of rates of growth and development) in the closely related *Pararge aegeria* (Nylin et al. 1989) and other butterflies. Consequently, we predicted that both species would show adaptations to speed up development through these late developmental stages in photoperiods indicating a later date in the season but that the reaction norms relating developmental time to day length would have a positive slope in *L. petropolitana* and a negative slope in *L. maera* (Fig. 1, top). In the case of *L. petropolitana*, we expected larvae emerging from eggs laid in midsummer (when day lengths are long)

to display long developmental times, whereas we expected larvae to speed up development later in the summer (in short day lengths) in order to reach the hibernating pupal stage safely before winter. In the case of *L. maera*, we expected larvae that have emerged from hibernation to display long developmental times, and the resulting pupae to develop slowly, if they occur in spring (short day lengths). We expected them to display shorter developmental times if they have been delayed by a late or cold spring and occur later in the season, close to summer solstice (long day lengths), because a more rapid development would increase the probability that their offspring (i.e., the next generation) will have enough time to reach the hibernating (third) larval instar before winter.

Here, we demonstrate that the natural phenology of *Lasioommata* butterflies conforms to the description above and that life-history reaction norms in response to day length are according to predictions based on optimality and on our empirical findings from other butterflies. We conclude that the observed differences in plasticity seem to be adaptive and that the reaction norms of the two species may be adaptations to seasonal changes in environmental conditions.

MATERIALS AND METHODS

Gravid females of *L. petropolitana* were caught in June of 1993 near Stockholm, central Sweden (59.5°N). They were allowed to oviposit on the host plant *Poa annua*. Five females were caught, but only the two females that laid the most eggs were used. This was done to ensure that there would be enough individuals in each photoperiod from each family to investigate whether strong family effects (indicating genetic rather than plastic variation) were present. Offspring were divided among the photoperiods 15L:9D (15h day length in the following), 17h, 19h, and 21h day length. They were reared in environmental cabinets, individually in plastic jars where *P. annua* was cultivated in ample supply. Larvae were followed to pupation when they were sexed and weighed.

In June of 1994, five gravid females were caught on the Baltic island of Gotland (57.5°N). The progeny of these females were reared on *Dactylis glomerata*, another preferred host plant. In this experiment, larvae were also weighed two times a week and the larval instar reached was noted (there are four instars in both species), in order to investigate the proximate mechanism behind variation in larval developmental times. From the weights taken, a measure of growth rate of individuals (independent of pupal weight) was calculated to be used in later analyses. Growth rate was taken to be approximately equal to the slope of the regression lines for log (weight) as a function of larval age (cf. Gotthard et al. 1994).

Note that all measures of growth rate in Table 1 are given as percent weight increase per day, calculated according to the formula (cf. Nylin 1992):

$$\log(\text{growth rate}) = (\log(\text{pupal weight}) - \log(\text{hatchling weight})) / \text{larval developmental time.}$$

Because of the large loss in weight at pupation, this measure underestimates larval growth rate, and it is not independent

TABLE 1. Life-history data (means ± SE) recorded at four day lengths at 17°C, in three experiments on *Lasioommata petropolitana* (LP) and *Lasioommata maera* (LM). Growth rates are relative weight increase (%/d), calculated from hatchling weight, larval time, and pupal weight. N, total number of individuals (families pooled).

Experiment	LP I (Stockholm)				LP II (Gotland)				LM (Stockholm)			
	15h	17h	19h	21h	15h	17h	19h	21h	15h	17h	19h	21h
Males												
Larval time (d)	31.2 ± 0.5	38.6 ± 0.8	49.2 ± 1.6	55.0 ± 4.8	38.4 ± 0.8	65.8 ± 2.5	73.4 ± 4.4	80.4 ± 2.8	26.0 ± 1.0	24.8 ± 1.2	22.8 ± 0.7	19.3 ± 0.5
Pupal weight (mg)	125.9 ± 4.5	133.8 ± 3.6	133.6 ± 6.4	140.6 ± 5.8	137.8 ± 8.1	149.0 ± 3.4	138.1 ± 6.1	147.2 ± 6.7	201.4 ± 4.2	211.1 ± 6.7	202.1 ± 3.4	201.2 ± 4.7
Rate (%)	19.4 ± 0.3	15.5 ± 0.3	12.0 ± 0.3	11.0 ± 1.0	15.3 ± 0.5	9.2 ± 0.4	8.3 ± 0.6	7.4 ± 0.3	8.8 ± 0.2	9.8 ± 0.7	9.8 ± 0.4	11.0 ± 0.4
Pupal time (d)	8	8	6	4	7	10	5	8	27.5 ± 0.4	24.1 ± 0.3	24.7 ± 0.3	16.4 ± 0.6
N									11	9	18	14
Females												
Larval time (d)	32.0 ± 0.8	42.0 ± 0.9	44.8 ± 2.4	47.5 ± 1.5	43.6 ± 1.7	57.8 ± 1.7	64.3 ± 3.9	65.7 ± 5.6	34.5 ± 1.6	30.1 ± 1.3	29.8 ± 1.8	26.5 ± 0.6
Pupal weight (mg)	144.3 ± 3.2	147.5 ± 5.2	164.5 ± 3.2	155.0 ± 5.6	147.7 ± 7.9	170.9 ± 10.6	170.1 ± 9.5	161.1 ± 7.4	212.0 ± 3.6	226.0 ± 5.4	213.8 ± 4.8	209.1 ± 4.9
Rate (%)	19.3 ± 0.6	14.5 ± 0.3	13.9 ± 0.7	12.8 ± 0.5	14.1 ± 0.7	10.4 ± 0.3	9.6 ± 0.5	9.3 ± 0.6	7.1 ± 0.3	8.3 ± 0.3	8.4 ± 0.6	9.0 ± 0.4
Pupal time (d)	6	8	6	2	11	4	7	6	25.8 ± 0.4	23.5 ± 0.3	22.9 ± 0.7	16.1 ± 0.2
N									23	24	15	22

of pupal weight. It was, however, the only measure of growth rate available in two of the experiments, where weights were not taken during larval growth. For comparison with the other experiments, data on growth rate from the Gotland population given in Table 1 have been calculated according to the formula above, but this was not the measure used in statistical analyses.

After pupation, pupae were monitored for any directly developing individuals (displaying very short developmental times), which were excluded from analyses and figures. In 1994 (Gotland), variation in pupal developmental time was such that it was not possible to make an entirely clear distinction between diapausing and directly developing individuals. For this reason, all individuals are shown in figures, and statistical analyses were performed first on the whole data set and then excluding individuals that possibly developed directly (emerged from the pupa within 40 d).

After the 1993 rearing, the pupae were moved outdoors in late summer and they were allowed to hibernate, protected from wind on the roof of the Department of Zoology building. Emergence in spring was noted to investigate phenology under seminatural conditions.

Five females of *L. maera* were caught in July near Stockholm. After oviposition on the host plant, *D. glomerata*, larvae were reared outdoors in late summer and allowed to hibernate under seminatural conditions as above. In spring, when still in diapause, larvae were moved back indoors, divided among photoperiods, and reared as above on *D. glomerata*. Three families were used at this stage. The durations of the late larval stages and the pupal stage were noted, as well as sex and pupal weight. In addition to this experiment, 50 larvae were hibernated outdoors and allowed to break diapause in spring, grow, pupate, and emerge under seminatural conditions.

RESULTS

Phenology under Seminatural Conditions.—Except for a single individual, which emerged from the pupa already on April 24, all individuals of *L. petropolitana* emerged during the latter half of May, the first on May 14 and the latest on June 1. Females emerged later than males, that is, there was clear protandry. Considering that the females need time to feed, mate, and oviposit and that their offspring need time to develop through the egg stage and early larval instars, it is evident that the late instars III and IV normally occur after summer solstice (June 21) in this population, with the possible exception of the very first eggs laid in a warm year. In an earlier outdoor experiment, pupation in individuals destined for hibernation took place in late July and early August under similar conditions (Wiklund et al. 1983), which also agrees well with this conclusion (Fig. 1, bottom).

In the outdoor rearing of *L. maera*, all individuals, following hibernation as third instar larvae, pupated between May 15 and June 12; that is, the late larval instars occurred before summer solstice in each case (Fig. 1, bottom). Adults emerged between June 16 and June 27 (23 males) or between June 23 and July 3 (28 females); that is, protandry was evident also in this species.

To summarize, adults emerged about a month later in *L.*

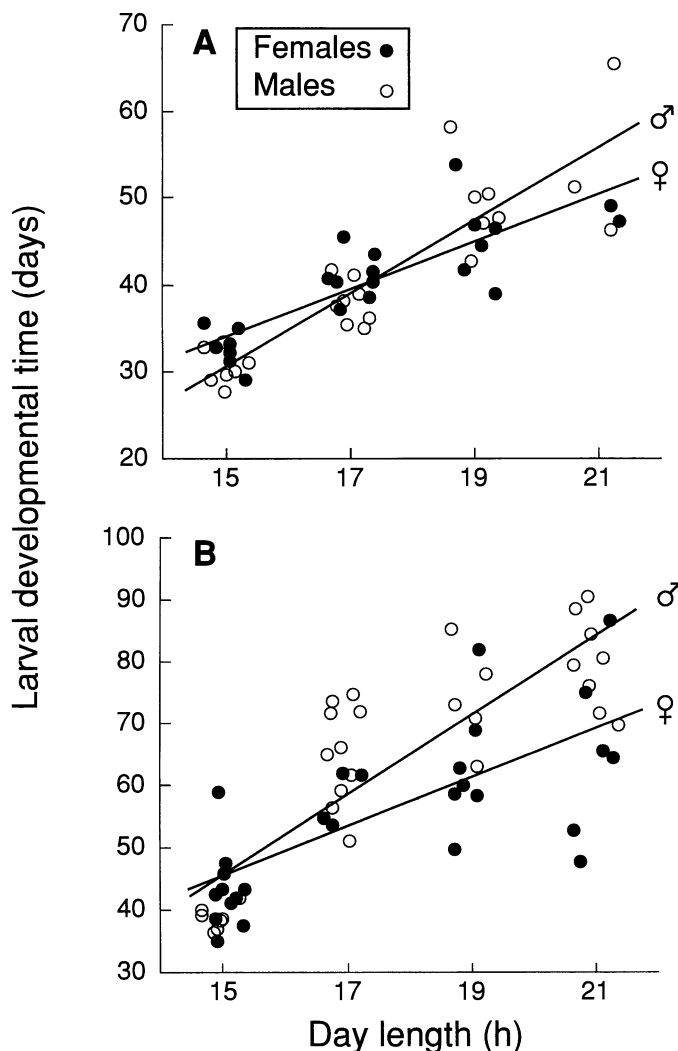


FIG. 2. Reaction norms relating larval developmental time to day length in males and females of *Lasiommata petropolitana* from (A) Stockholm and (B) Gotland. Lines show the results of linear-regression analyses.

maera (late June) than in *L. petropolitana* (late May), and this conforms closely to observations of the two species in the field in Sweden and northern Europe, where they fly from mid-June to July, and from mid-May to mid-June, respectively, without overlap (S. Nylin et al., pers obs.; Higgins and Hargreaves 1983).

Reaction Norms in L. petropolitana.—In the 1993 experiment on the Stockholm population, only total larval developmental time and pupal weight were noted as measures of larval growth and development. Table 1 and Figure 2A shows that there was a positive relationship between day length and larval developmental time (regression $P < 0.001$; $N = 47$). Some individuals developed directly at 21h, and one individual at 19h, and they were excluded from Figure 2A and analyses. Because the sexes differed in developmental time and pupal weight in both of the studied species (albeit not significantly in all analyses), sex was included as a factor in

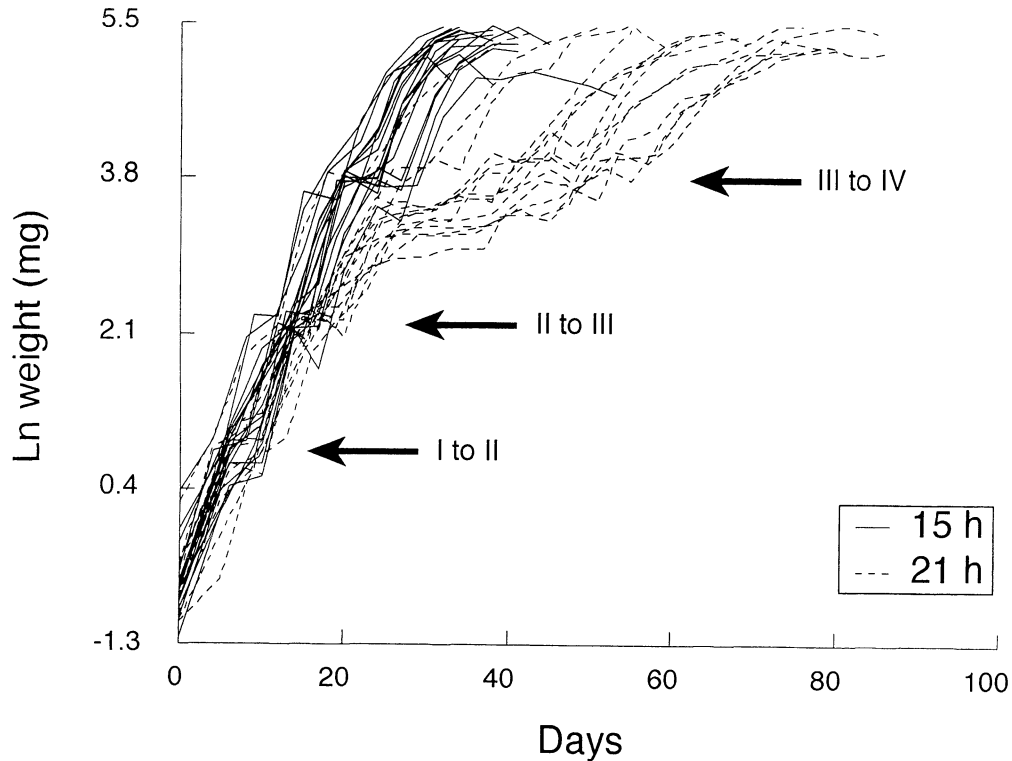


FIG. 3. Growth trajectories of individual larvae in different day lengths (according to legend) in the experiment on the Gotland population of *Lasiommata petropolitana*. For clarity, only the two extreme day lengths are shown. Arrows indicate the more horizontal sections of the growth trajectories, which show when moltings to new instars (I–IV) occurred.

this and all the following analyses (when not stated otherwise).

A regression model including day length, sex and the interaction between these two factors explained 75.4% of the variation in larval developmental time. The reaction norms of the sexes differed significantly in both elevation ($P < 0.05$) and slope (interaction between sex and day length, $P < 0.05$). In contrast, there was no significant effect of family on developmental time (ANOVA, $P > 0.39$). This demonstrates that the variation observed was mostly plastic rather than genetic but does not rule out that family effects could have been found in samples of more families. Pupal weights differed between day lengths and were lower in short day lengths where developmental times were short (Table 1; regression; $P < 0.01$). This implies that the observed variation in developmental time was associated with variation in pupal weight, as well as with variation in growth rate (which was not measured directly, but see Table 1). When controlling for effects of sex in the model, there was also a significant positive relationship between larval developmental time and pupal weight among individuals in this experiment (regression, $P < 0.001$; $r^2 = 0.28$).

The 1994 experiment on the Gotland population gave similar results concerning the effect of day length on larval developmental time but different results for pupal weight. The relationship between day length and developmental time was significantly positive (Table 1 and Fig. 2B; regression, $P < 0.001$; $N = 58$). The same regression model as used above (sex and interaction included) explained 68.0% of the vari-

ation in larval developmental time. Sex also influenced this relationship, at least through an interaction with day length (effect of sex itself: $P > 0.06$; interaction: $P < 0.05$). Differences between the two families included did not significantly influence the results (ANOVA, $P > 0.41$).

When all individuals with pupal development times of fewer than 40 d (potentially nondiapausing) were excluded, a similar positive relationship between day length and larval developmental time was found ($P < 0.001$; $N = 36$; $r^2 = 0.803$), as well as similar effects of sex (effect of sex itself: $P < 0.02$; interaction: $P < 0.05$). Log-transforms of developmental time to improve homogeneity of variances did not change the qualitative outcome of any analyses.

In the 1994 Gotland experiment, larval weights were taken two times a week, and the larval instar reached was then noted, which means that it is possible to investigate whether the differences in developmental time between day lengths accumulated early or late in development. Most of the variation in larval developmental time accumulated during the last two instars (Fig. 3), a pattern also found in other facultatively multivoltine butterflies (Nylin et al. 1989; Nylin 1992). However, larvae in 15h were already slightly ahead of the others at the time of molting to the third instar, and the regression larval developmental time versus day length is significant ($P < 0.001$) and positive in three separate analyses: instars I–II combined, instar III, and instar IV, respectively. Sex (or rather the interaction between sex and day length) influenced the results only in instar III, and this

caused the effects of sex seen for total larval developmental time (Fig 2B).

In contrast to the experiment on the Stockholm population, pupal weights did not differ significantly between photoperiods in this experiment (Table 1; ANOVA, $P > 0.12$; $N = 58$), indicating that variation in larval developmental time was instead mainly associated with variation in growth rates. Moreover, we could use larval weight data to investigate growth patterns more directly. In a regression model investigating the effects of growth rate (calculated independently of pupal weight) and pupal weight on larval developmental time, growth rates strongly affected larval developmental time ($P < 0.001$), whereas pupal weight and the interaction between the two variables had less clear effects on the larval developmental time of individuals ($P > 0.10$ and $P > 0.06$, respectively). The explanatory power of this model was 92.2%.

The growth patterns of individual larvae in the two extreme day lengths can be seen in Figure 3. The horizontal or negatively sloping sections of the growth curves (indicated by arrows), intervening between sections of rapid growth, show moltings to new instars. It can be clearly seen that the shorter developmental times in shorter day lengths were associated with earlier entry into new instars (see especially the last molt, which occurred around day 20 in 15h and between days 25–55 in 21h), but the growth curves also suggest faster growth within instars (steeper slopes of the growth curve in shorter day lengths). Interestingly, the larvae in 15h (who all entered pupal diapause) grew faster than even the potentially directly developing individuals found in the other three day lengths. The growth curves end at the maximum size recorded for each individual (for clarity, the weight loss of prepupae and pupae has been omitted) and the absence of a relationship between a long developmental time and a large final size (statistics above) is obvious. Rather, both moltings to new instars and the cessation of growth before pupation seemed to occur at relatively fixed weights.

Reaction Norms in *L. maera*.—At the start of this rearing after larval hibernation, larvae were very similar in weight (23.0 ± 0.3 mg), indicating a synchronizing effect of diapause. This simplifies comparisons of larval developmental time between photoperiods. It should nevertheless be noted that “larval developmental time” in Table 1, Figure 4A, and below refers to postdiapause larval development only (mid third instar to end of fourth instar).

The reaction norm relating larval developmental time to day length in *L. maera* had a negative slope (Table 1, Fig. 4A; regression, $P < 0.001$, $N = 137$). After removing the nonsignificant interaction term, sex also had a highly significant effect on larval developmental time ($P < 0.001$). This model explained 41.8% of the variation in larval developmental time.

Furthermore, the reaction norm relating pupal developmental time to day length also had a negative slope (Table 1, Fig. 4B; $P < 0.001$; $r^2 = 0.701$), and again significant effects of sex ($P < 0.001$) were found when the nonsignificant interaction term was removed. Effects of family were not significant in either the case of larval or pupal developmental time.

Pupal weight was not related to day length (Table 1; re-

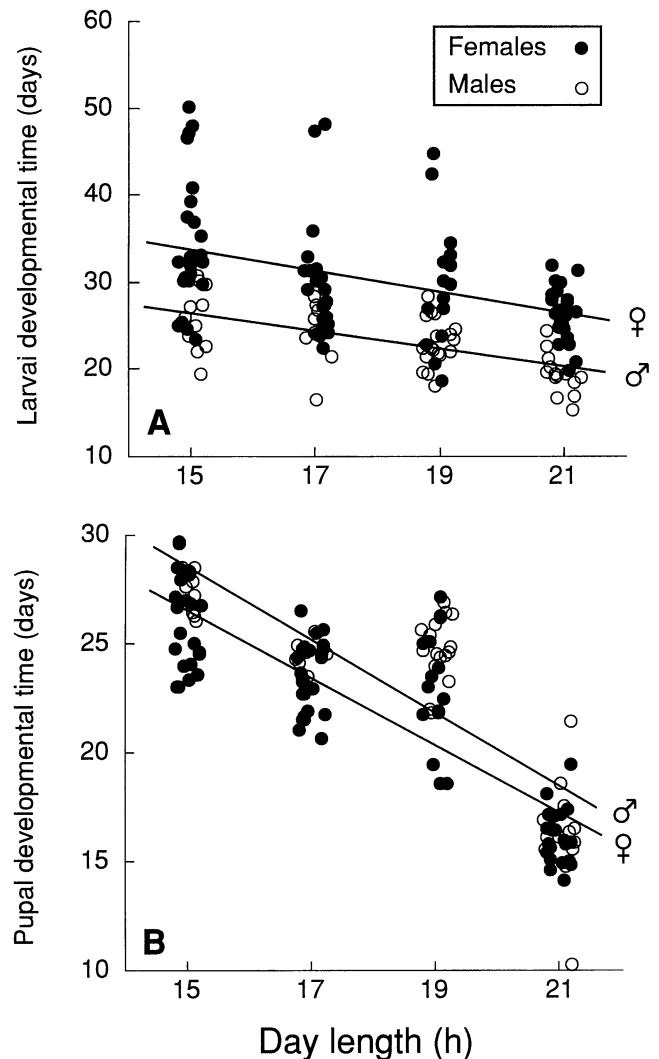


FIG. 4. Reaction norms relating (A) larval and (B) pupal developmental time to day length in males and females of *Lasiommata maera* from Stockholm. Lines show the results of linear-regression analyses.

gression; $P = 0.36$). We did not find the negative relationship that would be expected if the short larval developmental times observed at long day lengths (Fig. 4A) were associated with individuals ceasing to grow at a lower weight. Across day lengths, the relationship between larval developmental time and pupal weight was negative (regression, $P < 0.01$) rather than positive. Similarly to the situation in at least the experiment on the Gotland population of *L. petropolitana*, this means that short developmental times must instead have been associated with high growth rates (Table 1).

DISCUSSION

It has been observed that insects may shorten developmental times in day lengths indicating a late date in the season, for example in crickets (Masaki 1978) and in butterflies (Nylin et al. 1989, in press; Nylin 1992). The adaptive nature of this plasticity has not been questioned, but alternative explanations are sometimes possible; for example, effects of

day length on feeding patterns and indirectly on growth and development. It is therefore important to be able to demonstrate that the slope of such reaction norms relating developmental time to day length may differ even between closely related species and that they do so in a predictable manner. To the results mentioned here can be added that the closely related *P. aegeria*, which is unusual in that it may hibernate in either of the stages used by *Lasiommata* butterflies, show similar patterns relating developmental time to day length (Nylin et al. 1989, 1995). Developmental time is shorter in day lengths indicating later dates, which generally translates to a negative slope of reaction norms. The simpler *Lasiommata* systems yield clearer predictions and the fact that they are met suggests that the observed differences between species in plasticity may be adaptive. The method that we have used to find comparative evidence for adaptation follows the same logic as the "independent contrasts" family of methods (Felsenstein 1985; Harvey and Pagel 1991; Pagel 1994) and shares its strengths and weaknesses. The strength of such methods is that they compare only pairs of related species ("contrasts"), which means that a complete phylogeny is not necessary, only enough phylogenetic information to form the contrasts. The major shortcoming is that without a complete phylogeny and an outgroup, it is not possible to tell where in the phylogeny the putative adaptive change occurred. In the present case, if the two investigated species are sister species, and if they differ in their reaction norms, then the reaction norms of one or both species must have changed, but at present we cannot tell along which branch in the phylogeny. We are collecting information regarding reaction norms in other butterflies in the tribe Parargini, as well as phylogenetic information.

As has been found to be the case in other butterfly systems (Nylin et al. 1989, 1993; Wiklund et al. 1991; Nylin 1992), short developmental times in *Lasiommata* are associated mainly with increased growth rates and only to a small extent with lower pupal weights. The result that an association between pupal weight and larval developmental time was found for the Stockholm population of *L. petropolitana*, but not for the Gotland population, could be interpreted as evidence for stronger time stress in the more northern Stockholm population. We have previously found in other species of butterfly that pupal weight decreases with larval developmental time only under conditions mimicking severe time stress (e.g., Nylin 1992). This is, however, speculative at present, and it is quite possible that the underlying mechanism is very similar in both populations, because in both cases shorter developmental times were associated with higher growth rates. The results presented here thus support the present view of butterfly growth patterns; that larval growth rates are not always maximized in seasonal environments (Reavey and Lawton 1991; Nylin 1992, 1994). Rather, growth rates seem to be optimized according to trade-offs between gains associated with reaching the pupal stage at a certain date in the season (not necessarily as early as possible) and costs associated with high growth rates. Probable costs include increased risk of death by starvation, as found in *P. aegeria* (Gotthard et al. 1994) and other Lepidoptera (Stockhoff 1991). Higher mortality due to increased exposure to pred-

ators and parasites when feeding is another likely cost, which we have as yet not investigated.

In conclusion, we believe that the results of this study demonstrate the advantages of using a combination of experimental and comparative techniques to show that a given reaction norm may be an adaptation to variation in the local environment. In most systems where life-history plasticity is found, it should be possible to formulate strong and testable predictions regarding how the reaction norms of species ought to differ, and these predictions can subsequently be tested experimentally. The adaptive nature of plasticity is generally interpreted ad hoc (e.g., Nylin et al. 1989), and this is often out of necessity in single-species studies because of the complexity involved in quantitatively predicting the exact shape of a given reaction norm (cf. Stearns and Koella 1986). A life-history reaction norm is probably most often shaped by more than one selection pressure (i.e., selection on seasonal timing, size and growth rate, more or less independently of each other), and in addition it is influenced by the constraints specific to a given system. Qualitative differences between the reaction norms of categories of individuals (sexes, populations, or species) should be easier to predict, and successful predictions of this kind are needed before we can say that a life-history reaction norm is likely to have been modified by a process of local adaptation.

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LITERATURE CITED

- ABRAMS, P. A., O. LEIMAR, S. NYLIN, AND C. WIKLUND. 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*, (2d. ed.) Academic Press, New York.
- BERNARDO, J. 1994. Experimental analysis of allocation in two divergent, natural salamander populations. *Am. Nat.* 143:14–38.
- DANILEVSKII, A. S. 1965. *Photoperiodism and seasonal development of insects*. (English ed.) Oliver and Boyd, Edinburgh.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- FORD, N. B., AND R. A. SEIGEL. 1989. Phenotypic plasticity in reproductive traits: Evidence from a viviparous snake. *Ecology* 70:1768–1774.
- GEBHARDT, M. D., AND S. C. STEARNS. 1988. Reaction norms for development time and weight at eclosion in *Drosophila mercatorum*. *J. Evol. Biol.* 1:335–354.
- GOTTHARD, K., AND S. NYLIN. 1995. Adaptive plasticity and plasticity as an adaptation: A selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17.
- GOTTHARD, K., S. NYLIN, AND C. WIKLUND. 1994. Adaptive variation in growth rate: Life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* 99:281–289.
- HARVEY, P. H., AND M. D. PAGEL. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- HENSLEY, F. R. 1993. Ontogenetic loss of phenotypic plasticity of age at metamorphosis in tadpoles. *Ecology* 74:2405–2412.
- HIGGINS, L. G. 1975. *The classification of European butterflies*. William Collins, London.
- HIGGINS, L. G., AND B. HARGREAVES. 1983. *The butterflies of Britain and Europe*. William Collins, London.
- KINDLMANN, P., AND A. F. G. DIXON. 1992. Optimum body size:

- Effects of food quality and temperature, when reproductive growth rate is restricted, with examples from aphids. *J. Evol. Biol.* 5:677–690.
- MASAKI, S. 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. Pp. 72–100 in H. Dingle, ed. *Evolution of insect migration and diapause*. Springer-Verlag, Berlin.
- NEWMAN, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. *Bioscience*. 42:671–678.
- 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.
- . 1994. Seasonal plasticity and life-cycle adaptations in butterflies. Pp. 41–67 in H. V. Danks, ed. *Insect life cycle polymorphism*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- NYLIN, S., P.-O. WICKMAN, AND C. WIKLUND. 1989. Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyridae). *Biol. J. Linn. Soc.* 38:155–171.
- NYLIN, S., C. WIKLUND, P.-O. WICKMAN, AND E. GARCIA-BARROS. 1993. Absence of trade-offs in life-history evolution: The case of early male emergence and sexual size dimorphism in *Pararge aegeria* (Lepidoptera: Satyridae). *Ecology* 74:1414–1427.
- NYLIN, S., P.-O. WICKMAN, AND C. WIKLUND. 1995. Life-cycle regulation and life-history plasticity in the speckled wood butterfly: Are reaction norms predictable? *Biol. J. Linn. Soc.* 55:143–157.
- PAGEL, M. D. 1994. The adaptationist wager. Pp. 29–51 in P. Eglyton and R. Vane-Wright, eds. *Phylogenetics and ecology*. Academic Press, London.
- PIANKA, E. R. 1970. On “r” and “K” selection. *Am. Nat.* 104:592–597.
- REAVEY, D., AND J. H. LAWTON. 1991. Larval contribution to fitness in leaf-eating insects. Pp. 293–319 in W. J. Bailey and J. Ridsdill-Smith, eds. *Reproductive behaviour of Insects*. Chapman and Hall, London.
- REZNICK, D., AND A. P. YANG. 1993. The influence of fluctuating resources on life history—patterns of allocation and plasticity in female guppies. *Ecology* 74:2011–2019.
- ROFF, D. A. 1983. Phenological adaptation in a seasonal environment: A theoretical perspective. Pp. 253–270 in V. K. Brown and I. Hodek, eds. *Diapause and life cycle strategies in insects*. Dr W. Junk Publishers, The Hague.
- STEARNS, S. C., AND J. C. KOELLA. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution* 40:893–913.
- STOCKHOFF, B. A. 1991. Starvation resistance of gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae): Trade-offs among growth, body size, and survival. *Oecologia* 88:422–429.
- VIA, S. 1993. Adaptive phenotypic plasticity: Target or by-product of selection in a variable environment? *Am. Nat.* 142:352–365.
- WEST-EBERHARD, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20:249–278.
- WIKLUND, C., S. NYLIN, AND J. FORSBERG. 1991. Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly (*Pieris napi* L.). *Oikos* 60:241–250.
- WIKLUND, C., A. PERSSON, AND P.-O. WICKMAN. 1983. Larval aestivation and direct development as alternative strategies in the speckled wood butterfly *Pararge aegeria* in Sweden. *Ecol. Entomol.* 8:233–238.

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QUANTITATIVE GENETIC AND OPTIMALITY ANALYSES OF LIFE-HISTORY PLASTICITY IN THE EASTERN MOSQUITOFISH, *GAMBUSIA HOLBROOKI*

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Life-history theory predicts that organisms should allocate resources to maintenance, growth, reproduction, and storage in such a way that fitness is maximized (Gadgil and Bossert 1970; Smith and Fretwell 1974; Brockelman 1975; Giesel 1976; Stearns and Crandall 1984; Stearns and Koella 1986; McGinley et al. 1987; Winkler and Wallin 1987). Although much life-history theory is framed in terms of population-level responses to different environments, similar expectations can be applied to individual-level responses that are the product of phenotypic plasticity (Via 1987). Modification of the phenotype according to the environment (i.e., phenotypic plasticity) should evolve in habitats where organisms en-

counter equally frequent, but variable patches, as long as the cost of this phenotypic plasticity is low, suitable genetic variation is available, and the environmental cues are highly correlated with the environment of selection (Via and Lande 1985; Schlichting 1986; Via 1987; Van Tienderen 1991; Gornikiewicz and Kirkpatrick 1992; Scheiner 1993).

A number of life-history optimality models make testable predictions about the timing, level, and packaging of reproductive investment in environments that differ in food availability or “scope for growth” (for reviews, see Roff [1992] and Stearns [1992]). Phenotypic plasticity in age and size at maturity in high- relative to low-growth environments has been addressed in a variety of models, with a number predicting earlier age at maturity and increased size at maturity (Roff 1984, 1986), later age at maturity at a larger size (Ko-

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