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GENETIC CONSTRAINTS TO LIFE-HISTORY EVOLUTION IN THE PITCHER-PLANT MOSQUITO, *WYEOMYIA SMITHII*

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Abstract.—Life-history theory relies heavily on the hypothesis that genetic tradeoffs among the components of fitness constrain their independent evolution and joint maximization. Herein we show that selection on preadult development time in the pitcher-plant mosquito, *Wyeomyia smithii,* leads to a correlated response in cohort mean generation time but no correlated response in survivorship, fecundity, or cohort replacement rate. Lines selected for fast development achieve a higher capacity for increase (r_c) than lines selected for slow development, independently of larval density. These results imply that tradeoffs due to underlying antagonistic pleiotropy affecting growth, development, survivorship, and reproduction are not necessary constraints to life-history evolution. Previous work with *W. smithii* has shown a positive genetic correlation between development time and a general, genetically coordinated diapause syndrome. We propose that the observed nontradeoffs among the components of r_c may be subsumed into an even more fundamental tradeoff between performance during the summer generations and synchronization of development and reproduction with the changing seasons. Consequently, critical tests of genetic tradeoffs as a constraint to the independent evolution or simultaneous optimization of fitness components may need to consider the seasonal context.

Key words.—Diapause, mosquito, pleiotropy, tradeoffs, *Wyeomyia*

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We consider tradeoffs among life-history traits in the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.). Life-history traits have had great appeal to both theoretical and empirical biologists because these traits are intimately associated with, and may be direct components of, fitness. Consequently, life-history theories have broad application to evolutionary theory in general. As models of evolution, predictions of life-history theory, whether involving reproduction or other components of fitness, must be confirmed or rejected at the genetic level (Reznick 1985, 1992; Partridge and Harvey 1985; Bell and Koufopanou 1986; Willis et al. 1991). Because of their direct contribution to fitness, life-history traits should be maximized by natural selection and consequently might be expected to retain little genetic variation. Despite this expectation, populations can maintain a remarkably high level of additive genetic variation for life-history traits (Istock 1983; Mousseau and Roff 1987; Roff and Mousseau 1987; Houle 1992).

A major explanation for the persistent maintenance of additive genetic variation of fitness traits in populations (Hegmann and Dingle 1982; Istock 1983; Rose 1991; Roff 1992) is tradeoffs among those traits due to underlying pleiotropy. Alleles that have positive pleiotropic effects on fitness traits will be fixed by selection, those that have negative pleiotropic effects will be lost, while those that affect some fitness traits positively and some negatively should remain longer at intermediate frequencies in populations (Lande 1980, 1982; Rose 1982, 1985). Standing genetic variation in fitness traits should therefore reflect the effects of pleiotropic loci. Indeed, "the basic hypothesis underlying most analyses of the evolution of life history traits is that variation is constrained in large measure by tradeoffs between traits" (Roff 1992, p. 1).

Genetic correlations do exist and such correlations can be important in determining the short-term correlated responses to selection (Rose and Charlesworth 1981ab; Hegmann and Dingle 1982; Palmer and Dingle 1986; Dingle et al. 1988). Life-history traits are potentially all interconnected, even in complex life cycles. Some pairs of variables may show negative genetic correlations "but it is equally clear that positive genetic correlations between other pairs of variables are possible, and indeed necessary, in sufficiently complex multivariate systems" (Charlesworth 1990, p. 352). For this reason, one cannot test the appropriateness of tradeoffs in life-history evolution by simply looking at a series of genetic correlations and tallying the correlations that are consistent or inconsistent with the concept (Pease and Bull 1988). One must also evaluate the impact of tradeoffs on fitness itself and if and where in the entire life cycle the tradeoffs are being made.

We show that selection on development time in the pitcher-plant mosquito, *W. smithii* (Coq.) elicits a correlated response in cohort mean generation time but no correlated response in survivorship, fecundity, or cohort replacement rate. These results indicate no tradeoffs among the major components of fitness under summer conditions. We then argue that the absence of tradeoffs is possible if fitness in a seasonal environment represents a compromise between performance in the favorable season and the optimal timing of diapause.

Wyeomyia smithii

Wyeomyia smithii is distributed in North America from the Gulf of Mexico to Labrador and northeastern Saskatchewan (30–54°N). Throughout its range, this mosquito completes its preadult development only in the water-filled leaves of its carnivorous host, the purple pitcher plant, *Sarracenia purpurea* L. The leaves of *S. purpurea* persist through the winter and *W. smithii* overwinters in these leaves in a larval diapause that is initiated, maintained, and terminated by photoperiod (Bradshaw and Lounibos 1977). Any study that purports to show a positive correlation or nontradeoff among fitness components must satisfy concerns about spurious positive or compensating correlations that arise in novel environments (Stearns 1976; Gupta and Lewontin 1982; Bell 1984; Service and Rose 1985; Bell and Koufopanou 1986; Clark 1987).

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Indeed, "the technical difficulties of experimentally measuring the relevant parameters in a realistic setting are not to be taken lightly" (Roff 1992, p. 7). We would not be attempting this study were it not for the unique opportunity provided by *W. smithii* to minimize the effects of novel environments and, consequently, to make meaningful inferences about constraints to and opportunities for the evolution of natural populations.

First, we ran our experiments in the mosquito's natural habitat, the water-filled leaves of intact pitcher plants on a fixed diet of whole prey (freeze-dried adult *Drosophila melanogaster* Meigen) provided over a three-week period to simulate the prey-capture pattern of the host plant (Bradshaw 1983).

Second, we recreated a summer physical environment common to all populations. *Wyeomyia smithii* normally experience a fluctuating daily thermoperiod, and fluctuating temperatures sustain a higher fitness than constant temperatures (Bradshaw 1980). Consequently, we reared *W. smithii* and performed all experiments on a warm:cool = 29:13°C (mean = 21°C) smooth, sine-wave daily thermoperiod. Intermediate day lengths affect the rate of development in *W. smithii* (Bradshaw and Lounibos 1972). To avoid the three-way interaction among population, photoperiod, and development time, we ran all experiments at a light : dark = 18:6 h photoperiod incorporating two, half-hour twilights that provided unambiguous long days promoting direct (nondiapause) development in all populations (Bradshaw and Lounibos 1977). Since the phase angle difference between the light and temperature cycles can affect the interpretation of photoperiod, the thermoperiod was programmed to lag the photoperiod by 3 h, mimicking their natural phase relationship during the summer (Bradshaw 1980). To mimic the wet bogs and pine savannahs where pitcher plants grow, we provided a constant high (80%) relative humidity.

Third, unlike any previous study to our knowledge, we interspersed generations of diapause between generations of selection, thereby providing the opportunity to maintain any genetic correlation structure between diapause and nondiapause syndromes.

Finally, we used a species-wide approach to address the question of opportunities for and constraints to the evolution of fitness in *W. smithii.* Instead of selection on replicate lines within a single population, we used a single line from each of 6 populations spanning most of *W. smithii*'s range from the Gulf of Mexico to Canada (two in Florida [30–31°N] and one each in North Carolina [34°N], Massachusetts [43°N], Maine [46°N], and Ontario [49°N]). A previous study showed an average heritability of development time of 0.05 ± 0.02 (2 SE) among these six populations of *W. smithii* and a significant correlated response in photoperiodism in each of them (Hard et al. 1993). If our programmed environment were sufficiently novel to create a spurious nontradeoff due to genotype by environment interaction, then it must create a bias common to these disparate populations.

METHODS

Collection and Selection

These experiments used lines previously selected for fast and slow development time (days from oviposition to adult eclosion) with an unselected control. The methods for the collection of the populations, the establishment of the experimental lines, and the selection on development time are provided in Hard et al. (1993). Approximately 2000 larval *W. smithii* were collected from the 1987–1988 overwintering generation from each of the six localities. To maximize the opportunity for genetic equilibrium, we selected populations of *W. smithii* that appeared to be living in stable local habitats. Pitcher plants are slow growing and long lived. We sampled mosquitoes from localities that had contained abundant large pitcher plants for at least 15 years. We transported the larvae to the lab and, to minimize residual field effects, reared populations to the F_2 of wild-caught mosquitoes before initiating selection.

For each of the six populations, we established 3 lines: selection for fast development (oviposition to adult eclosion), selection for slow development, and an unselected control. To permit simultaneous selection by truncation for a temporal character in diverging lines, selection was imposed only every other generation and the intervening generation was synchronized by inducing and maintaining larval diapause and then terminating this diapause simultaneously in all lines. Over the 12 generations of selection and diapause, average effective population size ($1/N_e = 1/4N♂ + 1/4N♀$) varied from 51 to 97 and the cumulative inbreeding coefficients ranged from 3.4–8.4% over the selection process (Table 1 in Hard et al. 1993).

Correlated Responses of Life-History Traits

The sixth generation of selection was completed in the F_{12} lab generation, lines were synchronized in diapause and the direct response of development time and correlated response of critical photoperiod determined in the F_{14} generation (Hard et al. 1993). The F_{15} was again synchronized in diapause and the F_{16} and F_{17} used to determine the correlated responses of life-history traits in the present study.

Eggs of the F_{16} generation were removed from adult cages three times per week and examined for hatching daily. On the day of hatch, 20 first instars were placed in 15 ml distilled water in the leaves of intact pitcher plants and fed 25 freeze-dried adult *D. melanogaster.* Larvae were fed 100, 50, and 25 *D. melanogaster* after 7, 14, and 21 days, respectively. Each selected line consised of 5 cohorts of 20 larvae, each cohort having been oviposited on a single day and hatched on a single subsequent day. Starting on the 21st day, leaves were censused every 4–5 days and the pupae were removed, sexed, weighed, and transferred to dishes of distilled water in 12-liter acrylic adult cages. For oviposition, the cages were provided with a distilled water-filled, freshly cut leaf of *S. purpurea.* Pupae from replicate cohorts were pooled so that each selected line was represented by a single adult cage (18 total cages). Three times per week thereafter, pupal exuviae were removed, sexed, and counted; eggs were removed, counted, and floated on distilled water in large (150 × 25 mm) petri dishes. *Wyeomyia smithii* has determinate embryogenesis and first instars hatch without the requirement of a hatching stimulus after 4–7 days. Ten days after oviposition, the first instars in each dish were counted to determine percentage hatch. These first instars of the F_{17} generation were then used to repeat the entire above experiment but at a higher density of 40 larvae per leaf. This density is sufficient to reduce r_c by about 50% (Bradshaw and Holzapfel 1989).

After collection of all the data, we calculated the cohort replacement rate (R_o), mean generation time (τ), and capacity for increase ($r_c = \ln R_o/\tau$) for each line at each density:

$$R_o = L_O/L_P \quad (1)$$

where L_O = total number of larvae hatching in the offspring generation, and L_P = total number of first instars comprising the parent generation.

$$\tau = \Sigma x E_x/\Sigma E_x \quad (2)$$

where E_x = number of offspring eggs oviposited on day x since oviposition of the parents.

$$\%\ \text{Hatch} = L_o/\Sigma E_x \quad (3)$$

$$\%\ \text{Eclosion} = (\text{total number of adult exuviae collected})/L_p \quad (4)$$

$$\text{Fecundity} = \Sigma E_x/(\text{total number of female exuviae collected}) \quad (5)$$

$$\text{Growth rate} = (\text{pupal weight})/(\text{days oviposition to pupation}) \quad (6)$$

Statistical Treatment of the Data

To approximate a normal distribution, frequencies of hatching and eclosion were subjected to arcsine-square-root transformation prior to analysis. To reduce heteroscedasticity due to positive skew, R_o, pupal weight, and fecundity were subjected to $\log_e$ transformation prior to analysis. All analyses were performed using the SAS ANOVA procedure (SAS Institute 1985). Capacity for increase (r_c), R_o, τ, percent hatch, percent eclosion, and fecundity were subjected to a balanced, full factorial ANOVA with selected lines (fast, control, slow) and larval densities (20, 40) as treatments (fixed effects) and with 6 populations per cell. We treated population as a random effect and used a model II design to test for significant effects of selected lines ($F_{2,10} = MS_{line}/MS_{line*population}$), density ($F_{1,5} = MS_{density}/MS_{density*population}$), and their interaction ($F_{2,10} = MS_{line*density}/MS_{line*density*population}$). A posteriori testing of line means used Ryan's Q pairwise comparisons to control for experimentwise error rates (Day and Quinn 1989). Pupal weight and growth rate were subjected to a similar model II ANOVA but with sex added as an additional treatment.

RESULTS

As shown in Figure 1, ANOVA of mean generation time (τ) showed significant species-wide correlated responses of τ to direct selection on development time ($F_{2,10} = 19.07$; $P < 0.001$). There was also a significant effect of density ($F_{1,5} = 42.65$; $P < 0.001$) but no significant line by density interaction ($F_{2,10} = 0.06$; $P > 0.05$). Following ANOVA, Ryan's Q test showed ($P < 0.05$) that mean τ was shorter in the lines selected for fast development than in the controls and was longer in lines selected for slow development than in the controls. τ was also longer at higher than lower density. Thus, direct selection for fast and slow development resulted in shorter and longer mean generation times, respectively, regardless of density.

Species-wide ANOVA of cohort replacement rate ($\ln R_o$, Fig. 1) showed a significant effect of larval density ($F_{1,5} = 167.23$; $P < 0.001$) but no significant effect of selected line ($F_{2,10} = 1.79$; $P > 0.05$) or line by density interaction ($F_{2,10} = 0.80$; $P > 0.05$). Capacity for increase (r_c, Fig. 1) reflected significant effects of both density ($F_{1,5} = 407.59$; $P < 0.001$) and selected line ($F_{2,10} = 5.80$; $P < 0.05$) but not line by density interaction ($F_{2,10} = 0.45$; $P > 0.05$). Following the ANOVA, Ryan's Q test revealed no significant differences ($P > 0.05$) in r_c between either of the selected lines and the control but did show a significant difference ($P < 0.05$) between the lines selected for fast and slow development. These results show that direct selection on development time had the corresponding effect on cohort mean generation time but incurred no correlated cost in cohort replacement rate so that capacity for increase was greater in the lines selected for fast than slow development.

Two-way ANOVA of % Hatch (Fig. 1) showed no significant effects of density ($F_{1,5} = 3.71$; $P > 0.05$), selected line ($F_{2,10} = 1.46$; $P > 0.05$), or their interaction ($F_{2,10} = 0.98$; $P > 0.05$). Percentage eclosion (Fig. 1) was lower at higher density ($F_{1,5} = 23.00$; $P < 0.01$) but reflected no significant effects of selected line ($F_{2,10} = 3.50$; $P > 0.05$) or line by density interaction ($F_{2,10} = 0.14$; $P > 0.05$). Similarly, fecundity (Fig. 1) was lower at higher density ($F_{1,5} = 149.07$; $P < 0.001$) but showed no significant effects of selected line ($F_{2,10} = 0.19$; $P > 0.05$) or line by density interaction ($F_{2,10} = 0.28$; $P > 0.05$).

Three-way ANOVA of pupal weight (Fig. 2) showed significant effects of larval density ($F_{1,5} = 492.51$; $P < 0.001$), sex ($F_{1,5} = 673.24$; $P < 0.001$), and sex by density interaction ($F_{2,10} = 202.92$; $P < 0.001$) but no significant effects of selected line ($F_{2,10} = 0.13$; $P > 0.05$), line by sex interaction ($F_{2,10} = 1.33$; $P > 0.05$), line by density interaction ($F_{2,10} < 0.01$; $P > 0.05$), or their three-way interaction ($F_{2,10} = 1.94$; $P > 0.05$). Females weighed more than males and both sexes were heavier at the lower larval density regardless of selection on development time.

Three-way ANOVA of growth rate (pupal weight/development time, Fig. 2) showed significant effects of sex ($F_{1,5} = 168.82$; $P < 0.001$), density ($F_{1,5} = 371.37$; $P < 0.001$), sex by density interaction ($F_{1,5} = 108.30$; $P < 0.001$), selected line ($F_{2,10} = 4.19$; $P < 0.05$), and line by sex interaction ($F_{2,10} = 14.77$; $P < 0.01$), but not line by density interaction ($F_{2,10} = 0.43$; $P > 0.05$) or their three-way interaction ($F_{2,10} = 0.23$; $P > 0.05$). Both sexes clearly achieved a higher growth rate at low density but females achieved a higher growth rate than males only at low density. Following ANOVA, Ryan's Q test revealed that growth rate was significantly higher ($P < 0.05$) in lines selected for fast development than slow development, but neither the line selected for fast nor the line selected for slow development differed ($P > 0.05$) from the control line. Because of the significant sex by line interaction, we performed ANOVA of growth rate separately for the two sexes. In this case, the effect of selected lines was significant for females ($F_{2,10} =$

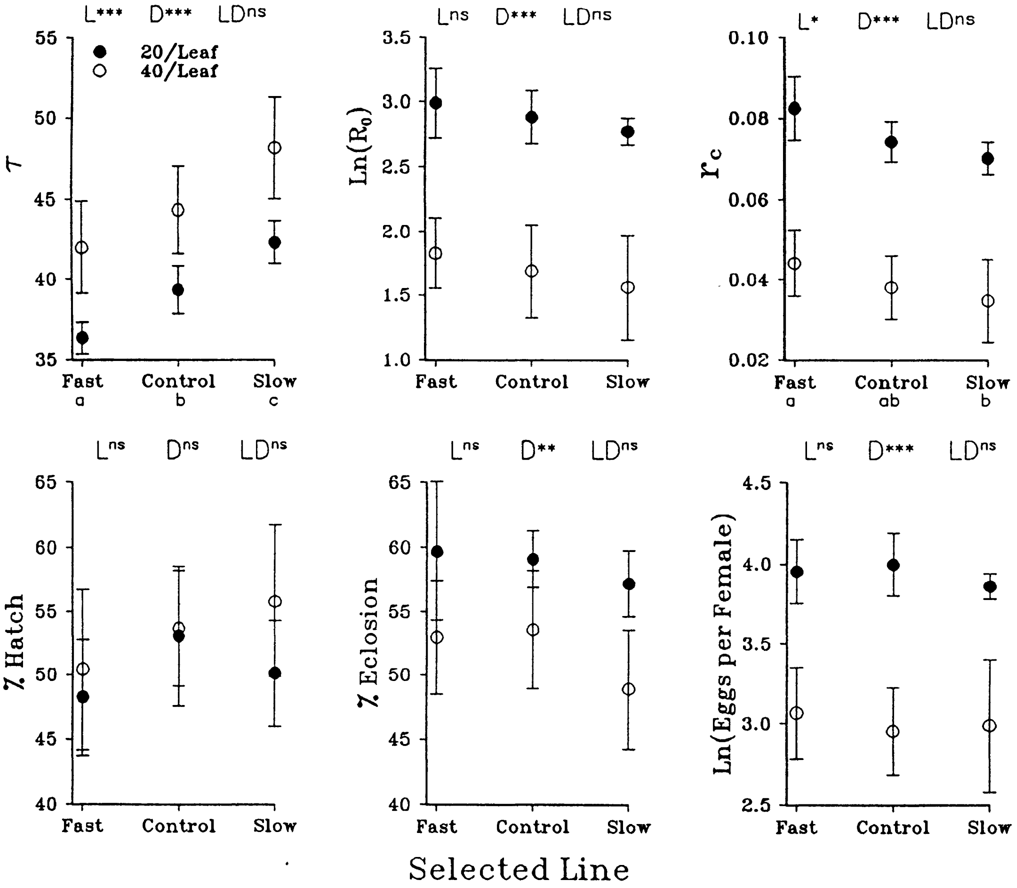

FIG. 1. Species-wide correlated responses of fitness, its components, and survivorship and fecundity to direct selection (fast, control, slow) on development time (days oviposition to adult eclosion). The plots show means ± 2 SE averaged over six populations. The legend at the top of each graph shows the results of two-way ANOVA: L, selected line; D, larval density; LD, line by density interaction. $^{ns}P > 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Line means associated with the same letter (a, b, c) are not significantly different ($P > 0.05$) by Ryan's Q test.

7.64; $P < 0.01$) but not males ($F_{2,10} = 3.05$; $P > 0.05$). As in the case of both sexes combined, Ryan's Q test revealed that female growth rate was higher in the line selected for fast than slow development ($P < 0.05$) but neither selected line differed from the control line ($P > 0.05$). Selection for fast development resulted in higher growth rate than selection for slow development, but only in females.

DISCUSSION

Nontradeoffs in W. smithii

Relative to selection for slow development, selection for fast development resulted in species-wide shorter generation time and higher capacity for increase without a concomitant cost to replacement rate (Fig. 1). The nonsignificant trend was toward a higher replacement rate in lines selected for fast development, that is, opposite that predicted from a tradeoff between R_0 and τ. Since r_c or female growth rate in lines selected for neither fast nor slow development differed from the control lines, there is no direct evidence that selection on fast development resulted in improved fitness, selection on slow development resulted in decreased fitness, or both. Still, selection on development time elicited no significant correlated response in survivorship (Fig. 1), fecundity (Fig. 1), or size (Fig. 2), contrary to what would have been expected from genetic correlations in *D. melanogaster* (Partridge et al. 1985; Partridge and Fowler 1993) or *Oncopeltus fasciatus* (Hegmann and Dingle 1982; Palmer and Dingle 1986).

Line by density interaction did not have a significant effect on r_c or any of its components (Figs. 1–2). Consequently, there is no evidence for a genetic tradeoff between performance at high and low densities within populations of *W. smithii.* This result is consistent with a lack of such tradeoffs among populations despite their evolution over a geographic gradient of density-dependent larval development (Bradshaw and Holzapfel 1989). In *D. melanogaster,* there is clear evidence for genotype by density interaction in the expression of fitness traits (Mueller and Ayala 1981; Mueller 1991). The genetic architecture of *W. smithii* from a seasonal, natural background is therefore strikingly different from *D. melanogaster* from an aseasonal, laboratory background.

These results indicate that the differences in fitness (r_c) between the lines selected for fast and slow development resulted primarily from the direct contribution of development time to τ and a general lack of compensating genetic correlations in other fitness traits than from a general erosion of fitness in lines selected for slow development. Our results

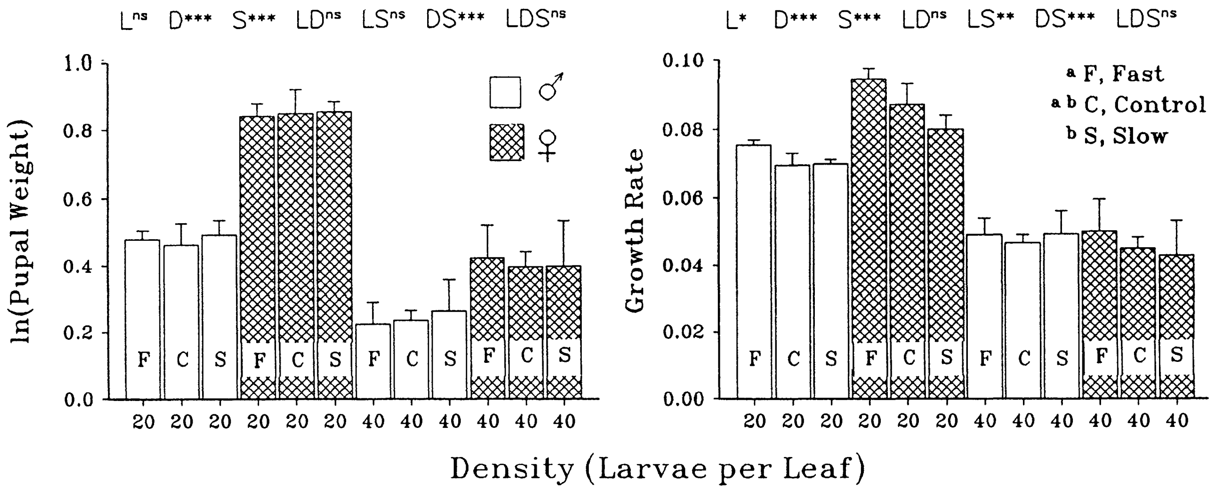

FIG. 2. Specieswide correlated responses of pupal weight and growth rate to direct selection on development time. Abbreviations and conventions as in Fig. 1 but with sex (S) added as an additional treatment in a three-way ANOVA.

do not rule out weak genetic correlations among individual traits with low heritability. Our results do imply that tradeoffs due to underlying antagonistic pleiotropy affecting intrinsic growth, development, survivorship, and reproduction are not necessary constraints to life-history evolution.

In a multivariate set of fitness components, weak negative or even positive genetic correlations are to be expected (Barton and Turelli 1987; Pease and Bull 1988; Charlesworth 1990; Rose et al. 1990; Houle 1991; de Jong and van Noordwijk 1992). Such positive genetic correlations presumably incur costs elsewhere in the life cycle. Pairs of traits may be positively correlated or uncorrelated within syndromes of life-history traits (Dingle 1986) but whole syndromes are then expected to be negatively genetically correlated with other whole syndromes (de Jong 1993). We propose that the non-tradeoffs among the components of r_c might be explained by a conflicting contribution of development time both to exploiting the favorable season (r_c and its components) and to optimizing the timing of diapause.

Comparisons with previous work on *W. smithii* in the same (Campbell and Bradshaw 1992) as well as different (Istock 1981; Scheiner and Istock 1991) populations show a genetic connection between development time and a general, genetically coordinated diapause syndrome. Individuals genetically prone to diapause respond to longer daylengths, commit themselves to diapause after exposure to fewer short days, and enter a deeper diapause, but develop more slowly under near-optimal, long-day conditions than do inviduals genetically averse to diapause. Consequently, larval "development time is a fitness component both in the strict sense of Fisher, and additionally through its timing and fitting of the generations within a single season" (Istock 1978).

We conclude that life-history tradeoffs in seasonal organisms should be evaluated not only in the context of growth, development, and reproduction, but also in the context of how these traits coordinate and potentially tradeoff with diapause or migration and with the synchronization of these activities with the changing seasons.

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