SELECTION ON HERBIVORE LIFE-HISTORY TRAITS BY THE FIRST AND THIRD TROPHIC LEVELS: THE DEVIL AND THE DEEP BLUE SEA REVISITED

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Abstract.—The timing of life-history events in insects can have important consequences for both survival and reproduction. For insect herbivores with complex life histories, selection is predicted to favor those combinations of traits that increase the size at metamorphosis while minimizing the risk of mortality from natural enemies. Studies quantifying selection on life-history traits in natural insect herbivore populations, however, have been rare. The purpose of this study was to measure phenotypic selection imposed by elements of the first and third trophic levels on variation in two life-history traits, the timing of egg hatch and pupal mass, in a population of oak-feeding caterpillars, *Psilocorsis quercicella* (Lepidoptera: Oecophoridae). Larvae were collected from the field throughout each of two generations per year for three years and reared to determine the effects of the date of egg hatch on both the risk of attack from parasitoids and the pupal mass of the survivors. The direction and strength of phenotypic selection attributed to aspects of the first and third trophic levels, as well as their combined effects, on the date of egg hatch was measured for each of the six generations. Heritabilities of and genetic correlations between pupal mass and the date of adult emergence from diapause (the life-history trait expected to have the largest influence on the timing of egg hatch, and thus larval development) were estimated from laboratory matings. In four of the six generations examined, significant directional selection attributed to the first trophic level was detected, always favoring early-hatching cohorts predicted to experience higher leaf quality than late-hatching cohorts. Directional phenotypic selection by the third trophic level was detected in only one of three years, and in that year the direction of selection was in opposite directions during the two successive generations. The combined effect of selection by both trophic levels indicated that the third trophic level acted to either reduce or enhance the more predictable pattern of selection attributed to the first trophic level. In addition, I found evidence of truncation selection acting to increase the mean and decrease the variance of pupal mass during the pupa-adult transition in the laboratory. Pupal mass and diapause duration were found to vary significantly among full-sibling families; upper bounds for heritability estimates were 0.57 and 0.30, respectively. Furthermore, these two traits were found to be positively genetically correlated (families with larger pupae had longer diapause durations), resulting in a fitness trade-off, because larger pupae enjoy higher survival through metamorphosis and female fecundity but emerge later, when average leaf quality for offspring is generally poorer.

Key words.—Diapause, heritability, life-history evolution, plant-herbivore interactions, *Psilocorsis quercicella*, *Quercus alba*, tritrophic interactions.

Temperate insect herbivores have some of the most complex life histories on record (Dixon 1977), often involving the production of multiple generations within a season, each of which is subject to its own combination of environmental stresses. For these insects, selection should favor life histories that increase the coincidence of stages involved in growth and development with periods of high-quality food, while decreasing the overlap of vulnerable stages with peak periods of natural enemy abundance (Tauber et al. 1986). As such, herbivore populations have been described as being caught ''between the devil and the deep blue sea'' (Lawton and McNeill 1979), because herbivores must avoid attack by natural enemies (the third trophic level), but still be able to obtain food that is of adequate nutritional quality to permit development (the first trophic level).

The impact of the first trophic level on the timing of life-history events in seasonal insects often comes about due to temporal changes in host plant quality and/or availability (Feeny 1970; Crawley and Akhteruzzaman 1988; Hunter 1992). For example, the degree of asynchrony between larval eclosion of the winter moth, *Operophtera brumata*, and budburst of its host plant, *Quercus robur*, has been shown to affect adult size, and thus expected fitness (van Dongen et

al. 1997). In general, leaf quality (e.g., nitrogen and water content) tends to decline with leaf age, resulting in decreased performance of late-feeding herbivores (Mattson 1980; Scriber and Slansky 1981; Krischik and Denno 1983). As a result, declining leaf quality has been suggested to select for herbivore traits that increase the synchronization of feeding activity with new leaf production (Coley 1983; Nothnagle and Schultz 1987; Hunter 1991).

The seasonal pattern of mortality caused by the third trophic level may also be an important selective force on the timing of life-history events. Because parasitoids have dramatic effects on fitness (i.e., they almost always kill their hosts prior to reproduction; Godfray 1994), life histories that are timed to avoid peak periods of parasitoid attack are likely to be favored by selection. Nevertheless, because parasitoids themselves are subject to seasonal fluctuations in host availability and/or susceptibility to attack by their own natural enemies, parasitoid activity periods may not be entirely synchronous with herbivore activity periods, allowing the possibility of temporal escape from attack, or enemy-free space (Jeffries and Lawton 1984; Clancy and Price 1986; Godfray 1994; Kaitaniemi and Ruohomäki 1999). Despite these theoretical considerations, few empirical studies have been conducted to determine how the seasonal pattern of parasitoid attack selects on specific traits within natural insect herbivore populations (but see Weis et al. 1992; Kato 1994a,b), and even fewer have examined how selection by parasitoids

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varies over time (but see McGregor 1996). Unpredictability in the form and direction of selection by parasitoids may act to maintain variation in the timing of pertinent host life-history traits as a form of bet-hedging (Via and Lande 1985; Kalisz 1986; Frank and Slatkin 1990; McGregor 1996).

The timing of life-history events in insects often has been shown to have a genetic basis (Morris and Fulton 1970; Istock et al. 1975; Dingle et al. 1977). For example, the timing of diapause release, which is generally manifested through an individual insect's sensitivity to changes in temperature and/or photoperiod, has been shown to be under strong genetic control in the fall webworm, *Hyphantria cunea* (Morris and Fulton 1970). Because diapause in insects is generally considered to be the primary means of achieving seasonal synchronization (i.e., for mating or food availability; Tauber et al. 1986), the timing of diapause release may experience strong selection due to its pervasive effects on the schedules of growth and reproduction during nondiapause conditions. For example, seasonality in the availability of high-quality foliage or the risk of natural enemy attack would select for individuals with diapause release times that permit feeding stages to exploit these high-quality resources or that minimize natural enemy attack. The net effect of selection will likely depend on the interaction between the two forces; the first and third trophic levels could oppose or enhance one another in determining the final distribution of timing-related traits.

The goal of this study was to determine the joint effects of selection imposed by elements of the first and third trophic levels on an herbivore population containing substantial variation for two life-history traits, date of egg hatch and pupal mass. My approach was to collect cohorts of larvae of known age from the field and rear them in the laboratory to determine how the date of egg hatch (within a generation) affected: larval mortality (from parasitoids and overall) and pupal mass attained by survivors (a predictor of both survival to adulthood and fecundity). The former is an estimate of the impact of one component of the third trophic level and the latter can be attributed, at least in part, to the first trophic level, because the leaf quality of the host plant varies predictably over the season as the leaves age (declining in water and nitrogen concentrations and increasing in phenolics; Wold and Marquis 1997; J. T. Lill and R. J. Marquis, unpubl. data) and leaf quality is known to influence pupal mass of the herbivore (see Study System below). In this study, I examined the fitness consequences associated with variation in date of egg hatch and pupal mass for an oak-feeding moth, *Psilocorsis quercicella*, using phenotypic selection analysis. I then used laboratory matings to estimate the broad-sense heritabilities of pupal mass and diapause duration. Together, these data provide insights into the ecological and genetic factors that may be responsible for shaping observed patterns of life-history variation in *P. quercicella*.

MATERIALS AND METHODS

Study System

Psilocorsis quercicella Clemens (Lepidoptera: Oecophoridae) is a common moth found throughout eastern North America (Covell 1984). Larvae feed exclusively within leaf ties, shelters formed by binding adjacent leaves together with
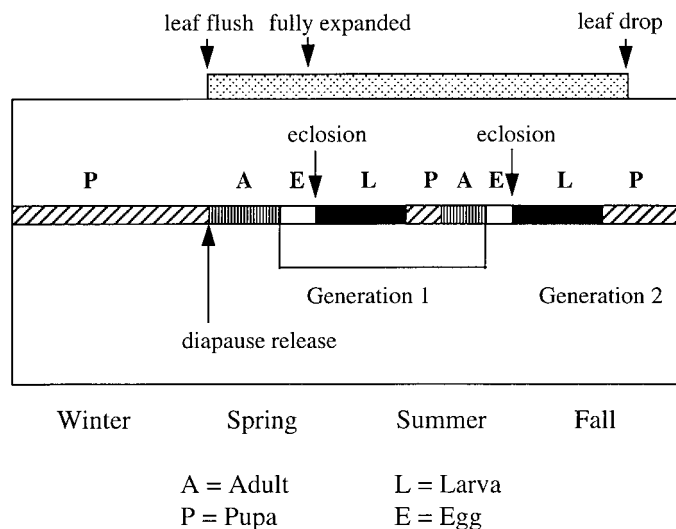

FIG. 1. Life cycle diagram of *Psilocorsis quercicella* depicting the chronology of life cycle stages observed during both generations and the pattern of leaf phenology for its host plant.

silk, primarily on oaks (*Quercus* spp.). *Psilocorsis quercicella* is bivoltine, with a summer and a fall generation (G1 and G2 hereafter; Fig. 1). Adults of *P. quercicella* begin to emerge from overwintering pupae in late May in Missouri. After mating, G1 eggs are laid on overlapping, mature leaves and hatch within a few days (Carroll and Kearby 1978). Larvae feed by skeletonizing the leaf surfaces inside the ties, passing through five instars before dropping to the litter to pupate. G1 adults emerge approximately 10 days later to mate and lay G2 eggs. G2 larvae can be found from mid-August to leaf drop at the end of October; G2 pupae then diapause in the litter until spring. Pupal mass is highly variable with as much as a fourfold difference between the lightest and heaviest pupae (range = 5.0–19.5 mg). Diapausing pupae (G2) are about 15–20% heavier than nondiapausing (G1) pupae, and female pupae are on average 18% heavier than male pupae (Lill 1999b). Leaf quality has been shown to influence pupal mass in *P. quercicella* (Lill and Marquis 2001). Specifically, the mean concentration of total phenolics in the foliage of white oak trees is a significant predictor of the mean female pupal mass for groups of larvae reared on foliage from plants of known quality (pupal mass = 16.16–70.07 [concentration of total phenolics]; $r^2 = 0.76$, $F = 19.23$, $P = 0.0046$, $N = 8$ trees; data reanalyzed from Lill and Marquis 2001). Development time is also variable, with G2 larvae requiring an average of 2.2 days longer to complete development than G1 larvae, and males developing 1.4 days faster than females (Lill 1999b). Larvae of *P. quercicella* are host to a diverse assemblage of parasitoids, which are described in detail in Pasek and Kearby (1984) and Lill (1999a).

Field Site

Collections of *P. quercicella* larvae were made at Cuivre River State Park, located near Troy, Missouri. The park is a northern extension of the Ozark Plateau and is a second-growth mixed oak-hickory forest with an understory of flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras al-*

bitum Nees), sugar maple (*Acer saccharum* Marsh), redbud (*Cercis canadensis*), and various oak saplings and an overstory consisting mostly of white oak (*Quercus alba* L.), black oak (*Q. velutina* Lamarck), and hickory (*Carya* spp.). Larvae were collected exclusively from understory leafties of *Q. alba*, the most abundant tree species in the park.

Trait Variation and Measurement of Selection

To quantify trait variation and phenotypic selection, a total of 807, 814, and 573 *P. quercicella* larvae were collected from the study site throughout G1 and G2 for the years 1995–1997, respectively. Within each generation, larvae were collected every 7–10 days from understory foliage consisting of white oak saplings and larger trees with low branches. All collections were made in the northern section of the park, an area encompassing approximately 500 ha. The majority of leaf ties contained a single *P. quercicella* larva (>80%), but occasionally there were multiple larvae per tie. Because parasitism was found to be unrelated to the number of larvae per tie (Lill 1999a), larvae were considered independent samples in all analyses. Larvae were brought to the laboratory and placed individually into 480-ml plastic containers. Within 24 h of collection, the head capsule of each larva was measured to the nearest 0.01 mm using a stereomicroscope fitted with a video camera allowing measurements of images using Digital Image Analysis System software (C-Squared Corporation 1993). These measurements were used to assign instars (1–5) to each larva at the time of collection using previously established ranges (Carroll 1977). The date of eclosion from the egg (''egg hatch,'' hereafter) was estimated for each larva based on instar at the time of collection and the average number of days a larva spends in each instar during laboratory rearings (2, 3, 3, 4, and 5 days for instars 1–5, respectively). Due to variation in development time among individuals collected in a given instar, egg hatch dates were grouped into cohorts consisting of all the individuals estimated to have hatched within a calendar week. Larvae were then reared on a diet of fresh white oak leaves collected regularly from the field site. Rearing chambers were kept at 23°C under a set of fluorescent lights set to either a 14/10 (G1) or a 12/12 (G2) light/dark cycle. High humidity was maintained in rearing chambers with moist filter paper to maintain leaf turgor. Leaves were replaced weekly (or more often if needed).

The fate of each larva was recorded as pupated, parasitized, or died of unknown causes. Larvae were recorded as parasitized when parasitoid larvae and/or pupae were found associated with the remains of *P. quercicella* larvae during rearing. Surviving pupae were sexed (Villiard 1975) and weighed to the nearest 0.1 mg using an electronic balance. All diapausing G2 pupae were placed individually into 200-ml scintillation vials containing moist cotton and these vials were kept in a cold room at 4°C for the winter. To examine the effect of pupal mass on survival through metamorphosis, adult emergence was also recorded for all G1 pupae (nondiapausing) and G2 (diapausing) pupae during 1995–1996.

Heritabilities and Genetic Correlations

Broad sense heritability estimates of pupal mass and diapause duration (and the genetic correlation between these traits) were estimated using laboratory matings of *P. quercicella* adults. In 1996, field-collected (as larvae) G1 moths of opposite sex that emerged on the same day were placed in mating chambers containing fresh foliage. These individuals constituted the parental (P_1) generation. The oviposition chambers were exposed to a 14/10 light/dark cycle, and leaves were replaced as necessary. Once mature eggs or neonate larvae were observed, or when both moths had died, leaves were removed from the chamber and examined with a stereomicroscope to determine the number of F_1 eggs laid by each female.

The resulting F_1 larvae produced by these matings were reared in the laboratory to pupation as described above, except that larvae were reared under decreasing day length (I reduced daylength by 10 min/day from 12/12 to 10/14 light/dark cycle over about 2 weeks) to simulate autumn light conditions and induce pupal diapause. Diapausing pupae ($N = 1607$ from 39 families ranging in size from four to 98 individuals) were weighed, sexed, and placed individually into 200-ml scintillation vials containing a moist cotton ball to maintain high humidity. These laboratory-reared pupae were slightly heavier than the field-collected pupae from the same generation (mean ± 1 SE = 10.31 ± 0.12 [laboratory reared] and 10.04 ± 0.10 [field-collected]) but this difference was not statistically significant ($t_s = 0.97$, $P = 0.33$). On 23 September 1996, the vials were placed in a 4°C environmental chamber for the winter. In early April 1997, surviving F_1 pupae were removed from the cold chamber and placed in plastic rearing containers with moist filter paper. These containers were placed randomly on shelves in an environmental chamber set to simulate spring conditions (12/12 light/dark cycle, 18°C, and 70% humidity). The containers were monitored daily for adult emergence until all surviving adults had emerged. The position of the containers on the shelves was periodically changed to minimize position effects within the chamber.

Statistical Analysis

Phenotypic selection

Multiple bouts of phenotypic selection were measured by examining the relationship between relative fitness and two traits of *P. quercicella*: hatching date and pupal mass. For hatching date, I measured six bouts (both generations of 1995–1997) of selection during two discrete portions of the life cycle (episodes sensu Arnold and Wade 1984a); the first episode was the period of larval development (from egg hatch to pupation) and the second episode was the period from pupation to adult reproduction. Mortality selection during the first episode was assessed directly using larval survival as the absolute fitness measure in calculating relative fitness. For the second selection episode, I used pupal mass (of those individuals surviving the first episode) as an indirect measure of fitness, assuming that pupal mass is correlated with survival during this episode as well as adult fecundity (pupal mass was found to be a significant predictor of female fecundity in *P. quercicella* [$r^2 = 0.36$, see Results] and the relationship between pupal mass and survival to adult emergence was examined with selection analysis; see below). For simplicity, I will refer to this measure as ''pupal size selec-

tion'' hereafter. To examine the pattern of selection on hatching date across both episodes ("combined selection" hereafter), I again used pupal mass as the measure of absolute fitness but also included in the analyses those individuals that died during the larval stage (they were assigned an absolute fitness of zero). Mortality selection acting on pupal mass (as a phenotypic trait in this case) during the pupa-adult transition was also measured. These selection gradients examine the influence of pupal mass on the probability of surviving metamorphosis and successfully emerging during both non-diapause (G1) and diapause (G2) conditions for the years 1995–1996.

For each generation and episode, phenotypic selection was measured using the methods outlined in Lande and Arnold (1983) and Arnold and Wade (1984a,b) and following Kalisz (1986). I measured directional selection (β) during the kth generation by regressing individual relative fitness (ω_k) on the phenotypic trait (z) using the model:

$$\omega_k = \beta z + \text{error.} \tag{1}$$

I quantified variance (nonlinear) selection using the model:

$$\omega_k = \beta z + (\gamma/2)z^2 + \text{error.} \tag{2}$$

Significant positive and negative values for γ indicate that nonlinear selection decreased and increased trait variance, respectively, over the selection period.

Because larvae were collected from the field in a variety of instars, the average amount of time that larvae from different egg hatch cohorts had been exposed to field conditions (e.g., exposed to parasitoids) may have varied and could have biased the results of the phenotypic selection analyses. To control for this, I regressed egg hatch cohort on the instar at the time of collection (for each generation) and used the residuals (in place of the raw data) in all selection analyses. Although they explained little variation ($r^2_{\max} = 0.04$), these regressions were significant during G1 of all three years and were always positive, indicating that larvae from later hatching cohorts were, on average, collected in later instars than larvae from earlier-hatching cohorts.

In measuring the strength of larval mortality selection on egg hatch date, I first considered all sources of mortality during larval development. Additionally, for each generation, individuals that died of unknown causes were removed to create a reduced dataset that included only mortality due to parasitism, thereby isolating selection caused exclusively by parasitoids (after McGregor 1996). A second reduced dataset was similarly created to isolate the effects of mortality due to unknown factors, which were likely a combination of first and third trophic level factors (i.e., parasitized larvae in which the parasitoids died before completing development, possibly due to multiparasitism; Godfray 1994).

Because survival is binomial, using linear regression to quantify mortality selection is likely to produce nonnormally distributed regression errors, which violates the underlying assumptions of the technique (Mitchell-Olds and Shaw 1987). As a consequence, we also calculated the mortality selection gradients using Janzen and Stern's (1998) logistic regression method. Qualitatively, the gradients produced by both methods were identical and quantitatively, they differed by much less than one standard error of the mean in all cases. Because

the other selection measures (pupal size selection and combined selection) were based on a continuous response variable (pupal mass), only the results of the linear regression method are presented here to enable direct comparisons among the different selection measures.

Heritability estimates and genetic correlations

Broad-sense heritability estimates of pupal mass were calculated by estimating the covariance among siblings within the F_1 families, all of which experienced the same average environment. I used the SAS MIXED procedure (Littell et al. 1996) to estimate the variance component associated with the random family effect in a model containing sex as a fixed effect and the sex $\times$ family interaction as a random effect. To test the significance of the two random effects (family and sex $\times$ family), I reran the mixed model twice, sequentially deleting each random effect and subtracted the $-2X$ log-likelihood of the full model from that of each reduced model (the difference follows a one-tailed chi-square distribution, with 1 df; Littell et al. 1996). When significant, this family variance component was then divided by the total phenotypic variance and then doubled to obtain the heritability estimate, because full siblings, on average, share half of their genes (Falconer 1981). Using the same methods, the covariance among F_1 siblings was used to estimate the heritability of diapause duration ("diapause intensity" sensu Morris and Fulton 1970). Diapause duration had a highly leptokurtic distribution and was therefore log-transformed prior to analysis to improve normality. In using full siblings to calculate these heritabilities, the values will tend to be overestimates because they include variance due to dominance as well as maternal effects (Arnold 1981; Falconer 1981). Finally, the genetic correlation between pupal mass and diapause duration (for individuals that successfully emerged) was calculated using F_1 generation family best linear unbiased predictors (BLUPs; Littell et al. 1996) generated from the mixed models. This correlation is a genetic correlation in the broad sense, because the family component of covariance contains additive, nonadditive, and interaction genetic covariance plus maternal covariance (Via 1984), which will tend to overestimate the correlation. In addition, calculating a full-sibling genetic correlation using family means (or in this case BLUPs) is approximate when mean family size is small, because a fraction of the within-family error variance is included in each variance or covariance (Via 1984). This will typically underestimate the genetic correlation (discussed in Via and Conner 1995), which may partially compensate for the overestimate generated from the use of full-siblings. For this analysis, the mean family size (± 1 SE) was 13.2 ± 5.3 and ranged from six to 39.

RESULTS

Phenotypic Selection

Date of egg hatch

Within a generation, the date of egg hatch spanned a six- to eight-week period (Fig. 2). Across generations, however, there was little overlap, facilitating assignment of larvae to the appropriate generation (G1 or G2).
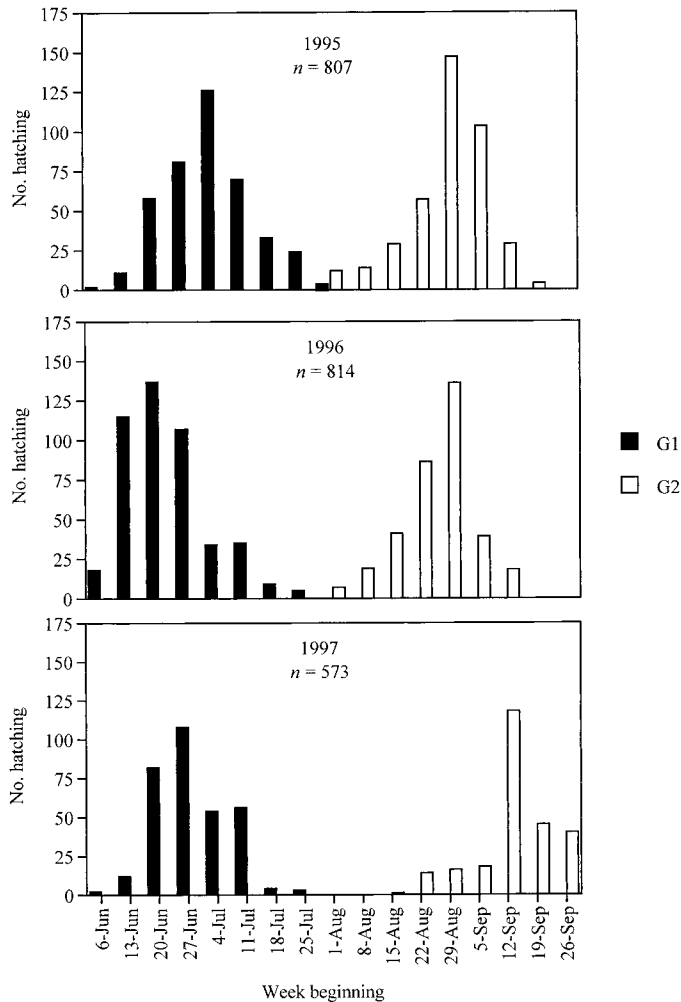
FIG. 2. Distributions of estimated hatching weeks for *Psilocorsis quercicella* larvae collected during both generations of 1995–1997.

TABLE 1. Fate of *Psilocorsis quercicella* larvae collected from the study site during both generations of the years 1995–1997.

Year	Generation	N	Survived to pupation (%)	Parasitized (%)	Other (%)
1995	1	415	50.1	15.4	34.5
1995	2	397	69.8	10.8	19.4
1996	1	460	71.1	12.6	16.3
1996	2	346	74.3	15.9	9.8
1997	1	321	69.5	21.8	8.7
1997	2	252	82.6	6.7	10.7

Larval mortality selection.—Survival of larvae collected during G1 and G2 of the years 1995–1997 varied from 50.1% to 82.6% (Table 1). Parasitism rates varied from 6.7% to 21.8%, with the remainder of mortality resulting from other (unknown) sources. In 1995, significant directional selection occurred for the date of egg hatch during both generations (Table 2a). During G1, mortality selection (all sources combined) favored survival of late-hatching cohorts over early-hatching cohorts. Directional selection gradients calculated from the reduced datasets followed the same pattern, with both parasitoids and mortality from other causes selecting against early-hatching cohorts. In addition, other sources of mortality imposed nonlinear selection, increasing the variance (i.e., the quadratic term was positive) in egg hatch cohort among the 1995 G1 survivors. During G2 of 1995, however, the overall pattern of directional selection was in the opposite direction, selecting against late-hatching cohorts. In addition, variance was reduced, as indicated by a significant negative quadratic term. The 1995 reduced datasets for G2 followed a similar pattern, with negative directional selection gradients for both parasitoids and other mortality sources and negative nonlinear selection by other sources of mortality. For 1996

and 1997, no significant directional selection acting on timing of egg hatch was detected for either generation, considering all sources as well as the reduced datasets (Table 2a). However, positive nonlinear selection acted to increase the phenotypic variance during G1 of 1997 due to higher parasitism rates in cohorts hatching near the sample mean and lower parasitism rates at the tails of the distribution.

Pupal size selection.—For the subset of individuals that survived to pupation each generation, directional selection favored early-hatching cohorts during the first generation of 1997 and during the second generation of all three years (i.e., early-hatching cohorts produced significantly larger pupae than late-hatching cohorts; Table 2b). I found significant variance selection in 1995 during both generations, but in opposite directions (G1 had increased variance, G2 had decreased variance). No variance selection was detected in either generation of 1996 or 1997.

Combined selection.—Combining the measured and predicted effects of selection on hatching date over the entire life cycle (Table 2c, Fig. 3) revealed significant directional selection in both G1 and G2 of 1995, in opposite directions in the two generations, as well as significant variance selection (also in opposite directions). In 1995, the strength of the selection gradients for the combined analyses were greater (but not significantly so) than those obtained from either selection episode alone. Similarly, during G2 of 1997 the combined effects of selection by elements of the first and third trophic level acting in the same direction resulted in significant directional selection favoring early-hatching cohorts, although this effect was attributed largely to the first trophic level (declining leaf quality). In contrast, nonsignificant mortality selection by the third trophic level offset weak pupal size selection (attributed to the first trophic level), resulting in no net selection during G2 of 1996 and G1 of 1997 (cf. Tables 2b and 2c; see Fig. 3).

Pupal mass

As expected, survival from pupation to adult emergence was much greater in the nondiapause generations (89–93%) compared with the diapausing generations (6–30%; Table 3). There was positive directional selection and negative variance selection acting on pupal mass during all four generations; however, the selection gradients were weak in G1 of both years and nonsignificant in G2 of 1995. During G1 of both years, the decrease in variance was largely a result of truncation selection, with no evidence of an intermediate fitness maximum (i.e., survival of pupae that were <5 mg was

TABLE 2. Standardized directional selection gradients (β) and variance selection gradients (γ) for date of egg hatch of *Psilocorsis quercicella* collected from the field during both generations of 1995–1997. Standard errors for the selection gradients are in parentheses. To examine selection by elements of the third and first trophic levels, as well as their combined effects, individual relative fitness was calculated using three different measures of absolute fitness: (a) survival through the larval period (0/1), (b) pupal mass (considering survivors only), and (c) pupal mass, assigning a fitness of zero to individuals that died during the larval period. N is the number of individuals examined in each generation of selection and l_k indicates survivorship during the kth generation.

Year	Generation	Mortality	l_k	$β^{[1]}$	P	$γ^{[2]}$	P	N
(a) Larval mortality selection (third trophic level)								
1995	1	All	0.50	+0.107 (0.33)	0.0012	+0.156 (0.060)	0.011	415
1995	1	Parasitoids	0.77	+0.062 (0.021)	0.0029	+0.020 (0.040)	0.62	268
1995	1	Other	0.59	+0.070 (0.030)	0.0183	+0.146 (0.054)	0.007	351
1995	2	All	0.70	−0.105 (0.024)	0.0001	−0.103 (0.044)	0.0197	397
1995	2	Parasitoids	0.87	−0.037 (0.017)	0.0303	−0.006 (0.034)	0.87	316
1995	2	Other	0.78	−0.085 (0.020)	0.0001	−0.117 (0.037)	0.0016	354
1996	1	All	0.71	+0.031 (0.021)	0.15	−0.050 (0.043)	0.24	456
1996	1	Parasitoids	0.85	+0.015 (0.015)	0.32	−0.007 (0.032)	0.84	381
1996	1	Other	0.81	+0.020 (0.017)	0.23	−0.053 (0.035)	0.13	398
1996	2	All	0.74	+0.017 (0.025)	0.51	+0.016 (0.055)	0.77	343
1996	2	Parasitoids	0.82	+0.003 (0.022)	0.88	+0.068 (0.046)	0.14	309
1996	2	Other	0.88	+0.016 (0.017)	0.35	−0.048 (0.036)	0.18	288
1997	1	All	0.70	+0.012 (0.031)	0.69	+0.180 (0.086)	0.0372	319
1997	1	Parasitoids	0.76	+0.024 (0.018)	0.17	+0.245 (0.079)	0.0021	291
1997	1	Other	0.89	−0.009 (0.027)	0.73	−0.030 (0.049)	0.54	249
1997	2	All	0.83	−0.031 (0.023)	0.17	+0.062 (0.049)	0.21	251
1997	2	Parasitoids	0.92	−0.014 (0.015)	0.35	−0.001 (0.031)	0.99	224
1997	2	Other	0.89	−0.020 (0.019)	0.29	+0.065 (0.040)	0.10	234
(b) Pupal size selection (attributed to the first trophic level)								
1995	1	n/a	1.0	+0.022 (0.013)	0.095	+0.060 (0.024)	0.012	204
1995	2	n/a	1.0	−0.094 (0.010)	0.0001	−0.054 (0.020)	0.006	273
1996	1	n/a	1.0	−0.005 (0.008)	0.56	+0.009 (0.017)	0.59	323
1996	2	n/a	1.0	−0.025 (0.008)	0.0026	−0.024 (0.018)	0.18	254
1997	1	n/a	1.0	−0.041 (0.012)	0.0007	−0.028 (0.034)	0.41	221
1997	2	n/a	1.0	−0.050 (0.011)	0.0001	+0.018 (0.024)	0.46	207
(c) Combined selection (first + third trophic levels)								
1995	1	All	0.50	+0.133 (0.035)	0.0002	+0.236 (0.065)	0.0003	415
1995	2	All	0.70	−0.192 (0.025)	0.0001	−0.115 (0.046)	0.0134	397
1996	1	All	0.71	+0.026 (0.022)	0.25	−0.042 (0.046)	0.36	456
1996	2	All	0.74	−0.009 (0.027)	0.75	−0.009 (0.058)	0.88	343
1997	1	All	0.70	−0.032 (0.033)	0.33	+0.139 (0.093)	0.14	319
1997	2	All	0.83	−0.085 (0.025)	0.0009	+0.088 (0.054)	0.11	251

[1] Positive values indicate selection for increased mean hatching date, and negative values indicate selection for decreased mean hatching date.
[2] Positive values indicate selection acted to increase the variance, and negative values indicate selection decreased the variance in hatching date.
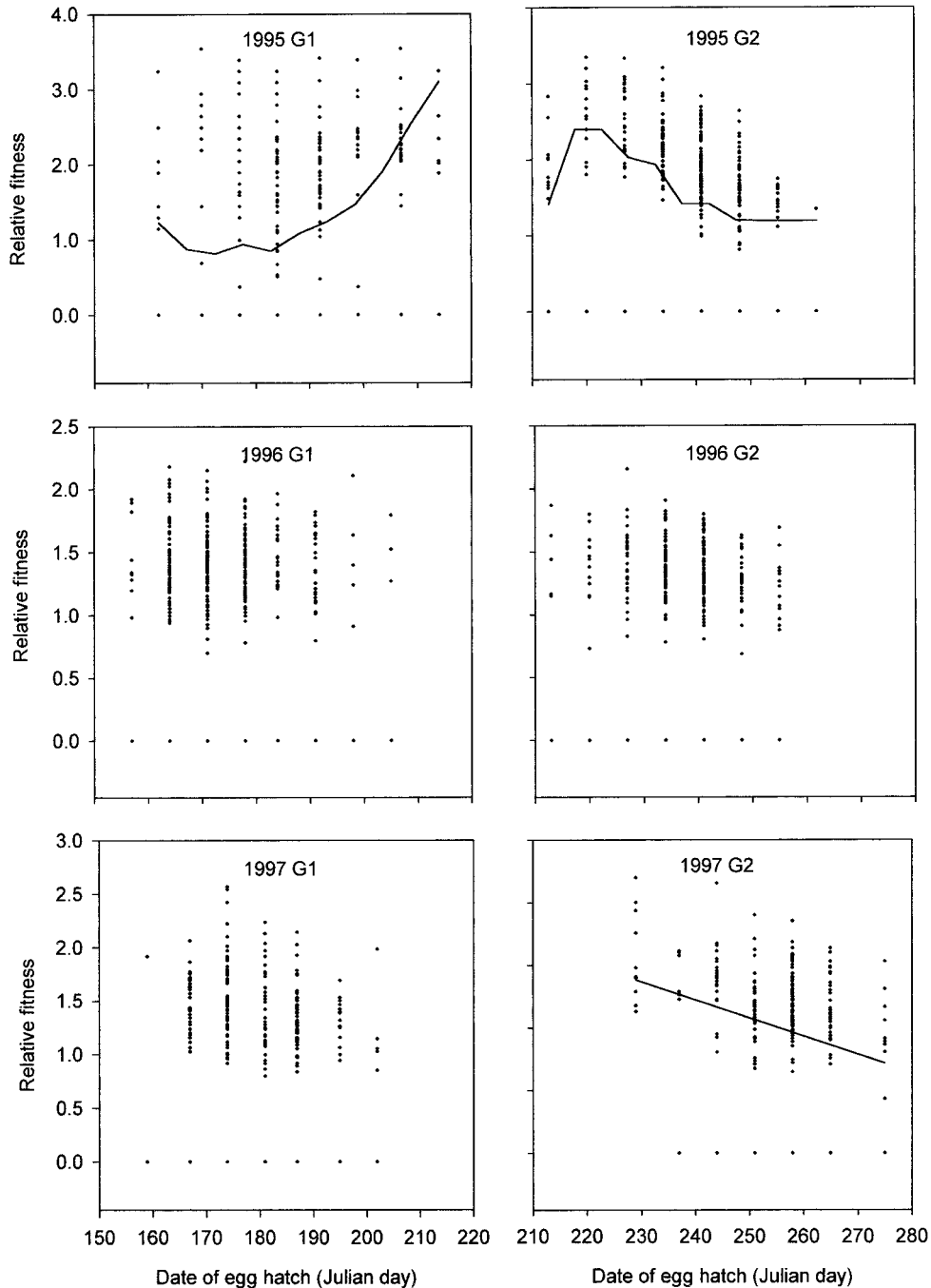
FIG. 3. Relative fitness of *Psilocorsis quercicella* larvae hatching within weekly intervals for both generations of the years 1995–1997. To reflect the combined effects of larval mortality and pupal size selection on hatching date, relative fitness was calculated using pupal mass as the measure of absolute fitness, but individuals not surviving the episode (due to parasitism or other causes) were included in the analysis (and were assigned an absolute fitness of zero). Curves were fit to the data only when the combined selection gradients were significant (see Table 2c). Significant nonlinear selection gradients were fit using locally weighted regression (10 intervals, each of which sampled 60% of the datapoints).

low but increased substantially and remained high for larger pupae; Fig. 4). During G2 of 1996, the probability of survival increased with pupal mass in a more linear fashion over the range of phenotypes, resulting in a much larger directional selection gradient.

Heritability Estimates and Genetic Correlations

For the 1996 P_1 generation, 40 pairs of moths laid a total of 2928 eggs. Mean clutch size (± 1 SE) was 73.2 ± 5.9 and ranged from seven to 183. However, nine of the clutches

TABLE 3. Directional selection gradients (β) and variance selection gradients (γ) for pupal mass during the pupa to adult transition. Values in parentheses are one standard error. All data are for field collected *Psilocorsis quercicella,* except for the 1996 G2 individuals, which were obtained from laboratory matings. N is the number of individuals entering the selection episode, and l_k is survivorship through this episode.

Year	Generation	N	l_k	β	P	γ	P
1995	1	204	0.89	+0.044 (0.010)	0.0001	−0.059 (0.011)	0.0001
1995	2	273	0.06	+0.056 (0.096)	0.56	−0.083 (0.110)	0.45
1996	1	323	0.93	+0.016 (0.008)	0.035	−0.025 (0.011)	0.027
1996	2	1470	0.30	+0.127 (0.018)	0.0001	−0.051 (0.021)	0.015

were nonviable and these were dropped from analysis. For the remainder, female pupal mass was found to be a significant predictor of clutch size (log transformed; $r^2 = 0.36$, $F = 11.23$, $P = 0.0018$, $n = 31$). In the mixed model examining the sources of variation in pupal mass among the F_1 families, family was highly significant ($\chi^2 = 25.89$, $P = 0.0001$). Sex was also highly significant ($F_{1,30} = 237.8$, $P = 0.0001$), but the degree of dimorphism did not vary significantly among families (i.e., the sex × family interaction was not significant;

$\chi^2 = 0.12$, $P = 0.46$). Family BLUPs for pupal mass (±SE) ranged from 9.10 (±0.57) to 12.60 (±0.29) for the families with the lightest and heaviest pupae, respectively. Using the variance component estimates from the mixed model, family explained 28.3 ± 8.4% of the total phenotypic variation in pupal mass, yielding a broad-sense heritability estimate of $h^2 = 0.566 \pm 0.168$.

Diapause duration for F_1 pupae was also highly variable. The first moths began emerging three weeks after pupae were
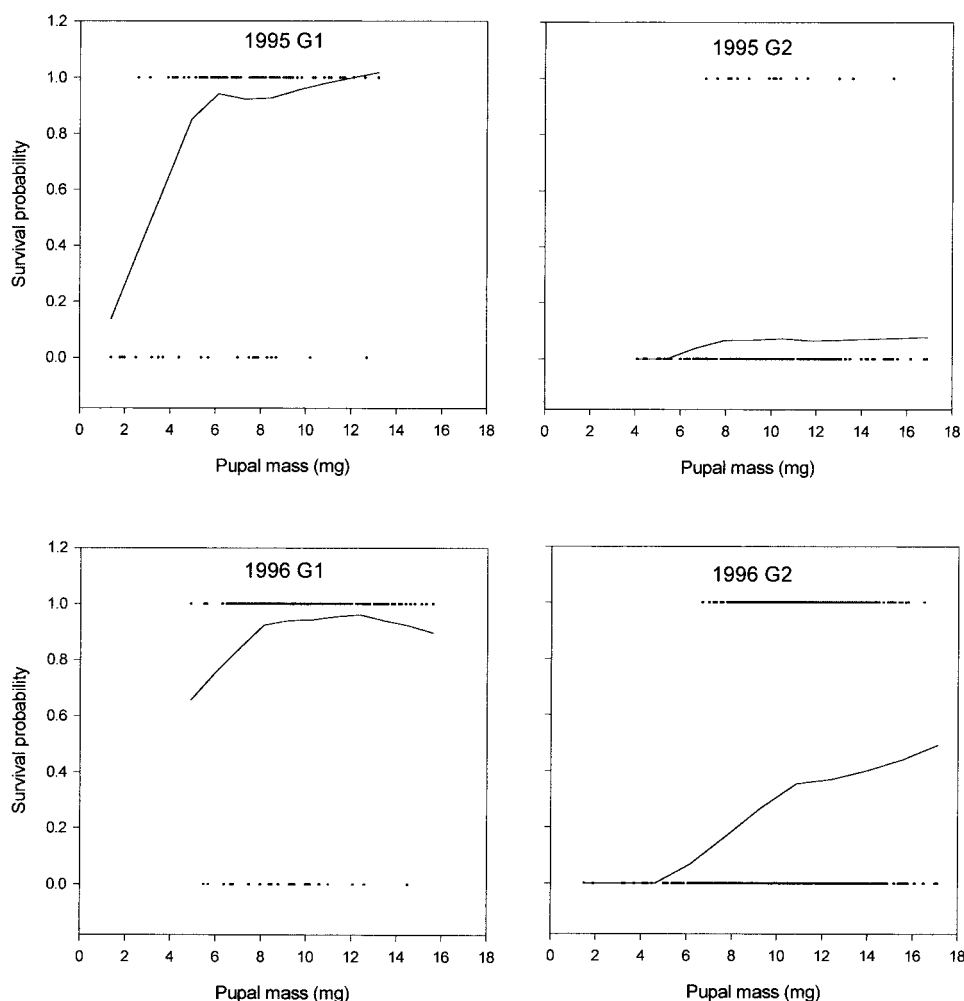

FIG. 4. Probability of adult emergence from pupae produced during both generations (G1, nondiapause; G2, diapause) of the years 1995 and 1996. Curves were fit using locally weighted regression (10 intervals, each of which sampled 60% of the datapoints).

removed from the cold room, and emergence continued for an additional six weeks. Mean diapause duration (log transformed) differed significantly among families ($\chi^2 = 6.98$, $P = 0.0043$) and sexes ($F_{1,30} = 45.25$, $P = 0.0001$), and the sex $\times$ family interaction was not significant ($\chi^2 = 1.29$, $P = 0.17$). Family BLUPs for diapause duration ($\pm$SE) ranged from 33.08 ($\pm$1.82) to 40.53 ($\pm$1.41) days for the families with the shortest and longest durations, respectively. Using the variance component estimates, family explained $15.2 \pm 6.6\%$ of the total phenotypic variation in diapause duration (log-transformed), yielding a heritability estimate of 0.304 $\pm$ 0.132 for this trait. A similar estimate ($h^2 = 0.262 \pm 0.120$) was obtained using the untransformed data. Additionally, the genetic correlation between pupal mass and diapause duration (based on family BLUPs) was significant (Pearson's $r_G = 0.57$, $n = 31$, $P = 0.0001$).

DISCUSSION

Selection on Timing of Egg Hatch

These results indicate that in some years (e.g., 1995) partial temporal refuges from parasitism exist for developing larvae. Such refuges have been hypothesized to have strong effects on population dynamics (Jeffries and Lawton 1984). However, the unpredictability of these partial refuges from one generation to the next or from one year to the next makes it difficult to predict their long-term effects. As with *P. quercicella*, McGregor (1996) also found evidence of partial temporal refuges for the leaf-mining moth *Phyllonorycter mespilella*, as well as intergenerational and interannual variation in the shape and direction of selection by parasitoids. The timing of egg hatch was also shown to influence the risk of parasitism in forest tent caterpillars placed in the field at periodic intervals following bud-break of their host tree (Parry et al. 1998). Another recent study (Kaitaniemi and Ruohomäki 1999) found no evidence of temporal refuges from parasitism for *Epirrita autumnata* Borkhausen, but the experiment was conducted for only a single generation in one year. The paucity of studies documenting selection by parasitoids on the timing of larval development, coupled with the fact that the life histories of those insects that have been studied differ in potentially important ways (i.e., diapause stage, voltinism, and feeding mode), precludes making any generalizations at this point.

It should be noted that my analyses treated all parasitoid species as a single selective force, potentially obscuring patterns of selection by individual species. However, it is the net effect of parasitism (all species combined) that ultimately determines the distribution of survivors in the field. Also, because larvae were removed from the field and thus were only exposed to attack during a portion of their development, levels of parasitism may have been underestimated and/or the selection gradients may have taken a different form. However, these disparities are unlikely to be large, because previous work on this species has shown that parasitism, particularly by the most common species, is concentrated in the early instars. In addition, there do not appear to be any parasitoid species that selectively attack late instars (and thus may have been missed or underrepresented in sampling; Lill 1999a).

Within a generation, pupal size selection tended to favor early-hatching cohorts, particularly in the second generation. Declining leaf quality, especially during the late summer and early fall, is likely to have produced this pattern because pupal mass in *P. quercicella* has been shown to be a function of leaf quality (Lill and Marquis 2001) and the leaf quality of white oak at the study site has been shown to decline in the late summer and fall (Wold and Marquis 1997, R. J. Marquis, J. Le Corff, E. Wold, and J. Lill, unpubl. data). As the season progresses, oak leaves in general have been shown to increase in toughness and decrease in water and nitrogen content (Feeny 1970; Schultz and Baldwin 1982; Erelli et al. 1998). At the same study site, Wold and Marquis (1997) found that the protein-binding capacity (a measure of phenolic activity) of *Q. alba* leaves was highest early and late in the season, with a decline during midsummer. A similar pattern was reported by Hunter and Schultz (1995) for *Q. rubra*. This midseason low followed by a late-season peak may partially explain the weaker relationship between date of egg hatch and pupal mass during G1 (which feed during midsummer) relative to the late-feeding G2, which likely experienced a sharp decline in leaf quality from the beginning to the end of the generation. However, because leaf quality was not measured directly in this study, invoking the first trophic level (leaf quality) as the mechanism explaining the relationship between hatching date and pupal mass is based on correlative rather than causal evidence.

The combined effects of selection on hatching date generally reflected the separate effects of the individual selection episodes. In some generations, however, the pattern of selection in the combined analysis differed from the individual patterns, either increasing or decreasing the magnitude of the selection gradients depending on whether the two forms of selection offset or enhanced one another.

Overall, the pattern of pupal size selection attributed to the first trophic level in the second generation of all three years was consistent (favoring early hatching). In contrast, mortality selection by parasitoids was highly variable, both among generations and years. Thus, in years when parasitoids exerted strong selection on the date of egg hatch, the magnitude of the overall selection gradient depended on whether this selection was in concert with, or in opposition to, the more predictable pattern of pupal size selection.

Selection on Pupal Mass

Pupal mass was positively related to survivorship during the pupa-adult transition. The opportunity for selection on pupal mass during the nondiapause generations of both 1995 and 1996 was quite low, due to the very high survivorship during the 10–12 days. Despite the low opportunity for selection, significant directional selection for increased pupal mass occurred during G1 of 1995 and 1996, and nonlinear selection acted to decrease the variance. This finding is clearly a result of the sharp decline in survivorship for pupae smaller than 7.0 mg (Fig. 4), which is consistent with the action of truncation selection. Survivorship of the diapausing G2 pupae was low in both years, and directional selection favoring larger pupae (that may have had greater fat reserves) was detected only in 1996. For insects in general, a greater store of fat reserves increases survival of diapausing individuals by providing an
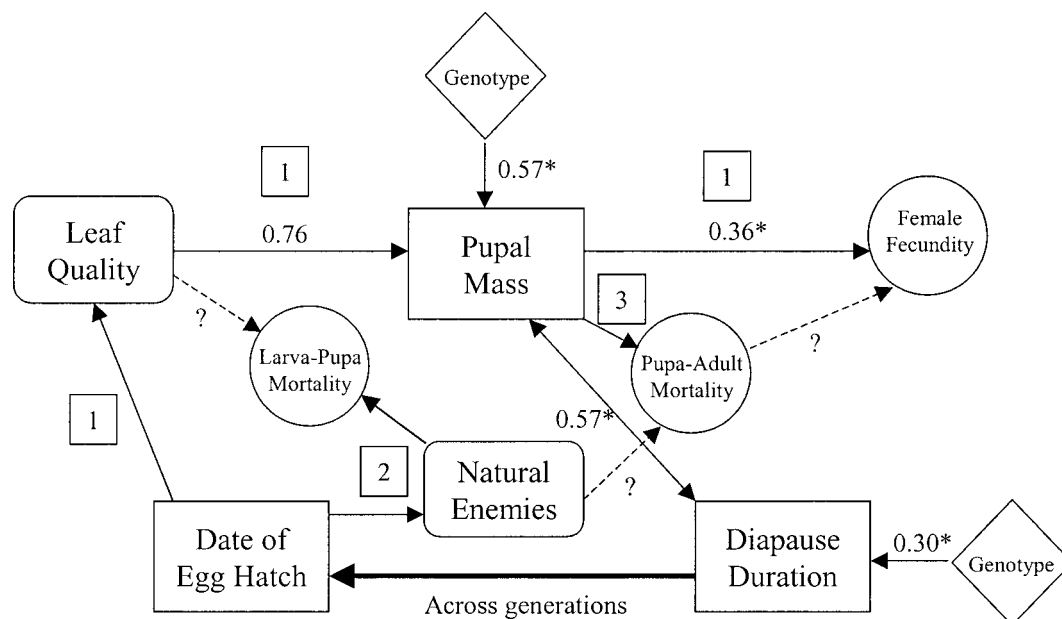
FIG. 5. Schematic summarizing the relationships among three life-history traits of *Psilocorsis quercicella* (rectangular boxes), two ecological factors (leaf quality and attack from natural enemies), and their influences on fitness components (two episodes of mortality and female fecundity). The genetic contributions to the trait phenotypes are based on broad-sense heritabilities. Numbered pathways denote relationships measured (and predicted) in the phenotypic selection analyses: 1, pupal size selection on date of egg hatch; 2, larval mortality selection by the third trophic level; 3, mortality selection on pupal mass. Values associated with these pathways vary among generations and years (see data in Tables 2 and 3). Asterisks indicate values based on laboratory-reared individuals.

energy source that can be used during the warmer days of late fall and early spring, when high temperatures increase the insect's resting rate of metabolism (Tauber et al. 1986). As a consequence, individuals entering diapause early in the fall and/or emerging late in the spring may deplete their metabolic reserves, resulting in increased mortality. McGregor (1996) found that overwintering mortality was the most important cause of selection in *P. mespilella*, suggesting a similar link between life-history timing and pupal mass. It should be noted that because pupae were kept in the laboratory, these analyses do not include the selective effects of additional mortality factors (i.e., pupal predators and parasitoids, abiotic stress) experienced by pupae in the field (see Fig. 5), and thus should be interpreted cautiously.

Heritability Estimates

The analyses presented here suggest that genotype may explain up to 57% of the phenotypic variation in pupal mass and up to 30% of the phenotypic variation in diapause duration in *P. quercicella*. However, heritability estimates calculated from full-sibling analyses must be viewed as upper estimates because they may include variation due to maternal, dominance, and common-environment effects (Falconer 1981). Additionally, it is important to note that the heritability estimates reported here are for a single cohort of larvae from one generation, reared under controlled conditions on leaves of the same age and average quality (i.e., understory shade leaves). Previous field experiments with *P. quercicella* (Lill and Marquis 2001) indicated that leaf quality had significant effects on pupal mass and that the effect of leaf quality varied among full-sibling families (i.e., significant genotype × environment interactions were detected).

Linking Life-History Traits

The variance in the timing of egg hatch within a generation (6–8 weeks) was quite large in comparison to the variance in hatching dates reported for many spring-feeding forest Lepidoptera, such as the forest tent caterpillar, *Malacosoma disstria* Hübner, which typically hatches within a one- to two-week period (Parry et al. 1998). For insects in general, diapausing stage (Tauber et al. 1986), variation in the timing of oviposition (Kaitaniemi and Ruohomäki 1999), and variable microclimate may all contribute to variation in timing of egg hatch. The complex interactions among genetic factors and environmental variables producing this variation in egg hatch, as well as the consequences for the hatching larvae are summarized in Figure 5. For *P. quercicella*, in particular, the major determinant of the timing of egg hatch is the date of oviposition, because variation in the duration of the egg stage (two to four days) is low. Oviposition date, in turn, is necessarily correlated with the timing of emergence of the adults following diapause, because the moths have relatively short lifespans (a maximum of two weeks in the laboratory; pers. obs.). Thus, the date that an adult female moth emerges following winter diapause sets the clock, determining when during G1 her offspring will develop and, to a lesser degree (due to within cohort variation in development time), when during G2 her offspring's offspring will develop. This scenario (see Fig. 5) is supported by the close correspondence between the range in diapause duration observed in the laboratory (approximately six weeks) and the estimated range in date of egg hatch (six to eight weeks within a generation) observed in the field, given a typical adult lifespan of approximately 10–14 days. To the degree that diapause duration

and the timing of oviposition are correlated, the results of this study suggest that phenotypic selection on the timing of egg hatch represents maternal selection (Kirkpatrick and Lande 1989) on diapause duration. In the present case, however, the diapause duration of the mothers (whose offspring were collected from the field) was not known and thus could not be evaluated directly.

Pupal mass was found to be positively genetically correlated with diapause duration; regardless of sex, average emergence time was later for large pupae than for small pupae. It seems plausible that the set of genes controlling size at metamorphosis could have pleiotropic effects on diapause duration (or vice versa). Against a background of seasonally declining leaf quality, this correlation could generate maternally induced oscillations in pupal mass: Adults from large pupae emerge late in the generation, their offspring feed on lower-quality foliage and, as a result, produce small pupae; subsequently, these adults emerge early, their offspring feed on higher-quality foliage producing large pupae, and so forth. In this scenario, the leaf-quality environment experienced by the mother (as a caterpillar) is negatively correlated with the leaf-quality environment experienced by her offspring, and thus directly influences offspring phenotype. Because pupal mass was found to decline within a generation (particularly during G2), fecundity selection would tend to favor early emerging genotypes to take advantage of favorable leaf quality during larval development. However, because early emergence occurs more often in small pupae (which have both lower fecundity and survivorship through diapause), the net effect of selection on diapause duration will depend on the relative strengths of these opposing selective forces and the strength of the genetic correlation between pupal mass and diapause duration. Under this scenario, selection may act to decouple these two traits, the effectiveness of which will depend on the genetic mechanism of the correlation.

Maintenance of Life-History Variation

Unpredictability in the strength and direction of selection acting on the suite of traits determining the timing of life cycle events in *P. quercicella* is one factor that may contribute to the maintenance of high levels of genetic variation in these traits. In this study, mortality selection by parasitoids on the timing of egg hatch was only detectable in one of three years, and in that year, selection acted in opposite directions in successive generations. Such temporal variance in mortality has been shown theoretically to be an important force acting to maintain variation in the timing of emergence within animal populations (De Stasio and Hairston 1992). Positive assortative mating among moths with similar emergence times is a second factor that is likely to contribute to the maintenance of life-history variation in *P. quercicella*. The factors maintaining genetic variation in pupal mass are perhaps more complex. Pupal mass appears to be intimately tied to fitness, affecting survival through diapause as well as fecundity. Thus, directional selection for larger pupae would be predicted to have decreased the additive genetic variance in the trait over time (Roff 1992). It appears, however, that significant genetic variation for pupal mass remains in the population, although it is unclear how much of genetic variation is additive. One plausible factor preventing the erosion

of genetic variation in pupal mass is the genetic correlation between pupal mass and diapause duration, because this correlation may generate ecological trade-offs (negative correlations) between the leaf-quality environment experienced by successive generations of caterpillars (as discussed above).

The results of this study highlight the importance of life-history trade-offs, both between fitness components (i.e., survivorship vs. fecundity) and among life-history stages, in determining patterns of variation observed for organisms with complex life cycles. Because natural selection acts on whole organisms rather than on individual traits (Tuomi et al. 1983), measurements of its effect on a single life-history trait during a particular stage in the life cycle must consider the ensuing effects on later stages and the overall fitness of the organism.

Conclusions

This study demonstrates that the timing of life-history events for seasonal insects can experience selection from elements of both higher and lower trophic levels. In general, for *P. quercicella*, selection was found to favor life histories that maximize pupal mass, a phenotypic trait that is at least partially related to food quality. Larger pupae were found to have increased survivorship through both diapause and nondiapause generations as well as increased fecundity compared with smaller pupae. However, because pupal mass was found to be genetically correlated with diapause duration, the effects of pupating at a given size on the timing of larval feeding (and the ensuing fitness consequences) of offspring must also be considered. Variation in the timing of diapause release is likely the target of maternal selection, due to its phenotypic effects on the timing of development of successive generations of larvae. Variation in the date of egg hatch within a generation influenced pupal mass (presumably through seasonal changes in leaf quality) as well as the risk of parasitism, and the overall pattern of selection depended on whether natural enemies enhanced or opposed the more predictable pattern of selection attributed to the first trophic level.

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