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Parental effects in *Pieris rapae* in response to variation in food quality: adaptive plasticity across generations?

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Abstract. 1. Herbivores using seasonal resources must cope with variation in the quality of their host plants. The effects of variation in protein concentration of artificial diet and glucosinolate concentration in canola, *Brassica napus*, on *Pieris rapae* parental and progeny growth were investigated.

2. The hypothesis that parents respond to variation in food quality by altering the phenotype of their progeny to enhance progeny fitness was tested. Consistent with previous studies, *P. rapae* was not affected strongly by variation in the protein concentration of artificial diet and had equal mass on completing development.

3. The mass of individual eggs of *P. rapae* progeny was correlated negatively with the amount of protein in the diet on which parents fed. Moreover, mothers reared in extreme conditions (high and low protein) produced progeny that grew best under those conditions. These potentially adaptive parental effects were detected early in progeny growth but not later in their development.

4. Early larval growth of *P. rapae* was affected negatively by increasing glucosinolates in *B. napus* plants, although no effects of glucosinolates were detected later in growth or on the progeny's phenotype.

5. Thus, evidence is presented that variation in food quality (protein concentration) has major consequences for the progeny of *P. rapae*. Given the multivoltine life history of *P. rapae* and the seasonal differences in food quality it encounters, such parental effects may be adaptive.

Key words. Cabbage white butterfly, canola, egg mass, maternal effects, nutritional ecology of insects, phenotypic plasticity, plant–insect interactions.

Introduction

A central goal in ecology and evolution is to determine the causes and consequences of phenotypic variation among individuals. The dogma is that the phenotype of an individual is determined by its genotype, the environment it experiences, and the interaction between these two factors. Not until recently have theories and experimental studies considered the effects of the parental environment on an individual's phenotype (Mousseau & Fox, 1998a). Parental effects, those components of a progeny's phenotype that are determined by a parent's environment, can have remarkable consequences for the life history of the progeny. In other words, parents not only determine the genotype of their progeny but also influence the expression of their progeny's genes (Mousseau & Fox, 1998a). These effects are common among plants and animals, and may be adaptive under some conditions (Roach & Wulff, 1987; Mousseau & Dingle, 1991; Bernardo, 1996a; Fox *et al.*, 1997; Donohue & Schmitt, 1998; Mousseau & Fox, 1998a; Agrawal *et al.*, 1999).

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An adaptive parental effect is a modification of a progeny's phenotype, attributable to the parental environment, that increases progeny fitness (Mousseau & Fox, 1998b). Because organisms generally live in spatially and temporally variable environments, any correct predictions made by a parent about the environment that its progeny will experience could enhance progeny fitness; however tests of adaptive parental effects are exceedingly rare (Mousseau & Fox, 1998a). Parental care, oviposition behaviour of mothers, and provisioning to eggs or seeds are some probable mechanisms by which parents can adjust their progeny's phenotype to increase performance in the predicted environment (Mousseau & Fox, 1998a; Wade, 1998).

For herbivorous insects using seasonal resources, cues in a parent's environment can indicate future conditions. For example, host plant quality may change predictably throughout a season or in response to herbivory (Kause *et al*., 1999). These changes take many forms including alterations of leaf (1) physical properties, such as toughness, (2) nutritional properties, such as protein concentration, or (3) defences, such as secondary compounds (Karban & Baldwin, 1997; Kause *et al*., 1999; Simpson & Raubenheimer, 2001).

The earliest fitness-related trait, and a trait that is probably subject to parental effects, is egg quality (Rossiter, 1993, 1996). Most simply, larger eggs are often associated with greater nutritional provisions (Berrigan, 1991; Fox & Czesak, 2000), meaning that larger eggs result in larger larvae that are potentially better suited for coping with low resource quality. There is usually a trade-off between egg size and number, however, and each is likely to affect fitness differentially depending on the environment (Berrigan, 1991; Mousseau & Fox, 1998b; Fox & Czesak, 2000). In addition to a change in nutritional provisioning, parents can alter other traits (i.e. structural, physiological, ontogenetic, or behavioural) that can change the phenotype of their progeny greatly (Agrawal *et al*., 1999; Shine & Downes, 1999; Fox *et al*., 2001; Buechler *et al*., 2002). For multivoltine insects, in particular, parental effects may match the progeny phenotype to the seasonally varying host-plant resource.

Few studies have manipulated parental and progeny environments reciprocally; such manipulations allow for the assessment of the adaptive value of parental effects by comparing the consequences of variation in the parental environment for their progeny (Fox & Czesak, 2000; LaMontagne & McCauley, 2001). In the work reported here, the effects of variation in food quality for *Pieris rapae* parents and progeny were addressed to consider two questions: (1) How does food quality affect *P. rapae* parental growth, development, and reproductive allocation? (2) How does the environment (i.e. food quality) experienced by *P. rapae* parents affect the egg mass, growth, and development of their progeny? More specifically, parental effects associated with variation in the amount of protein in artificial diet and glucosinolate concentration in *Brassica napus* plants, two traits that show large variation in natural hosts of *P. rapae* (Slansky & Feeny, 1977), were addressed.

Methods

Manipulating protein concentration

The cabbage white butterfly *Pieris rapae* (Pieridae) is native to Europe but is naturalised and abundant across North America. *Pieris rapae* larvae are specialist herbivores, consuming leaf tissue of plants in the mustard family (Brassicaceae) (Richards, 1940), including cultivated canola, *Brassica napus*. To assess the effects of variation in the amount of available protein on the growth and development of *P. rapae* and its progeny, the protein concentration of artificial diet in two separate experiments was manipulated. For both experiments, *P. rapae* eggs were obtained from a laboratory colony started from wild individuals collected 6 months earlier. Larvae were reared singly in 35 ml plastic containers on ≈7 g (wet mass) of artificial diet at ambient room temperature (≈23 °C) and light conditions. Webb and Shelton's (1988) recipe for making an optimal diet for *P. rapae* was followed. The diet treatments contained either an optimal amount of protein (i.e. 2.7% of the fresh mass, henceforth 1 protein equivalent), or 0.25, 0.5, 0.75, or 1.5 protein equivalents ($n = 11$ each). Larvae were weighed on days 8 and 12, and 4 days after pupation. The number of days to pupation and sex were recorded. In this first experiment, the parental effects on the progeny were not examined because the butterflies were not mated successfully.

In the second experiment, the effects of parental environment on progeny performance on variable diets were tested. Larvae for the parental generation were reared singly on artificial diet as described above, however the diet contained either 0.5 ($n = 46$), 1.0 ($n = 32$), or 1.5 ($n = 39$) protein equivalents. These values were chosen to represent the greatest variation in larval performance observed in the first experiment. Larvae were weighed on day 12 and at pupation as described above, and the number of days to pupation was recorded. The dry mass of frass produced, an indication of consumption and digestive efficiency, and the sex ratio of *P. rapae* reared on the different protein diets were compared. All emerged butterflies from a single protein treatment were allowed to mate within a 0.35-m^3 mesh-lined cage in a greenhouse and were supplied with a source of artificial nectar (Monarch Watch, Lawrence, Kansas). *Pieris rapae* butterflies require a space at least this large in order to mate successfully (K. Rotem, pers. obs.). This design lumps the contributions of maternal and paternal effects on the progeny phenotype. After 1 week, females [protein level 0.5 ($n = 22$), 1.0 ($n = 22$), 1.5 ($n = 26$)] were placed singly within 2-l unwaxed ice cream containers with artificial nectar and a substrate on which to lay eggs (Parafilm® wrapped around cabbage). Twenty-four hours later, eggs were collected, weighed to the nearest microgram using a Mettler-Toledo UMT-2 balance (Hightstown, New Jersey) ($n = 5$ per mother), and placed singly on 0.5, 1.0, or 1.5 protein diets ($n = 3$–5 per female, per protein diet). Eggs were not weighed from all mothers because in some cases there were too few eggs. In all analyses, individual adult

butterflies were treated as the unit of replication and the average value of the multiple progeny assayed was used as a single data point. The mass of progeny was measured on days 4, 8, 12, and as pupae, and the number of days to pupation was recorded.

Manipulating glucosinolate concentration

The following experiments were designed to assess the effects of variation in the concentrations of glucosinolates in *Brassica napus* seedlings on the growth and development of *P. rapae* and its progeny. Glucosinolates and their breakdown products (i.e. isothiocyanates) are nitrogen- and sulphur-containing compounds characteristic of the Brassicaceae; these compounds have been implicated in plant defence against herbivores, including *P. rapae* (Stowe, 1998; A. A. Agrawal and N. S. Kurashige, unpublished). For these experiments, seeds from 11 double haploid lines of *B. napus* were obtained. Each double haploid family is assumed to be true breeding and completely homozygous (Li *et al.*, 2000; L. Kott, unpublished). The 11 lines were *a priori* put into three groups based on glucosinolate concentration of the seeds [mean $\pm$ SE μM glucosinolate per gram fresh mass; group 1: 9.41 ± 0.150 ($n = 3$ lines); group 2: 11.88 ± 0.37 ($n = 3$); group 3: 16.76 ± 1.00 ($n = 5$); ANOVA: $F_{2,8} = 21.070$, $P = 0.001$]. The values for the glucosinolates were estimated using three measurements, each of 10 seeds from each line using a blood glucose meter then converted to glucosinolate concentrations (L. Kott, unpublished). In other work with *Brassica*, seed glucosinolate concentrations have been shown to correlate with leaf glucosinolate concentrations and resistance to herbivory (Glen *et al.*, 1990; Bodnaryk, 1997), however these lines represent extremely low levels of variation in glucosinolates compared with the levels in wild plants in the Brassicaceae, which are often orders of magnitude greater (Glen *et al.*, 1990; Bodnaryk, 1997). Five seeds from each of the *B. napus* lines were planted in 500 ml pots in Pro-Mix soil (Red Hill, Pennsylvania). Approximately 0.6 g of slow-release Nutricote fertiliser (13:13:13 N:P:K) (Vicksburg Chemical, Vicksburg, Mississippi) were added to each pot and pots were fully randomised on a greenhouse bench.

In the first experiment, two newly hatched *P. rapae* larvae were placed on each plant (at the two to four true leaf stage) and were kept in the greenhouse for 8 days. Larvae were not caged on the plants because they are sluggish and tend to remain on the plant on which they are placed. Larvae were weighed on day 8 then placed in plastic containers with excised leaves from the plant on which they had developed. This procedure was used because larvae exhibit a wandering stage before pupation. Containers were placed haphazardly on a laboratory bench at ambient temperature and light conditions. Pupae were weighed and the number of days to pupation and sex were recorded.

In the second experiment, larvae were reared as above except that the greenhouse chamber was much cooler and larval mass was assessed in the fifth instar on day 18. From this point on, larvae were reared on excised leaves until pupation. Adults were separated based on the three glucosinolate levels on which they were reared and each group of butterflies was allowed to mate as described in the protein manipulation experiment. After 4 days, as before, females were placed singly within egg-laying containers with a source of nectar and a substrate on which to lay eggs [group 1 ($n = 9$), group 2 ($n = 8$), group 3 ($n = 8$)]. Twenty-four hours later, the eggs were collected, weighed to the nearest microgram, and placed singly on standard artificial diet (i.e. 1 protein equivalent; Webb & Shelton, 1988). The mass of progeny was measured on days 4 and 8 ($n = 2$–5 per female, but again the average per female is reported).

Statistical methods

The direct effects of variation in food quality were assessed with response-curve analyses using ordered ANOVA contrasts to test for a trend in the effect of increasing food quality (protein or glucosinolates) on the growth and development of *P. rapae* larvae (Dawkins, 1983). The polynomial contrast procedure in Systat version 9 (SPSS Inc., Chicago, Illinois) was employed. In all analyses, the results represent the first-order polynomial (linear); no higher-order polynomial analyses were significant. The effects of experimentally imposed food quality variation in the parental generation on the growth and development of progeny were assessed using a factorial ANOVA, with parental diet and progeny diet as factors explaining the egg mass, growth, and development of *P. rapae* progeny. When a significant interaction between the two factors was detected, a univariate ANOVA was conducted to investigate the trends within each parental treatment more thoroughly (Day & Quinn, 1989). Moreover, the growth of progeny on each diet from the different parental treatments was compared using Tukey's HSD multiple comparison *post-hoc* test. Differences in degrees of freedom between assay times within a data set are due to mortality, however there was no effect of treatment on mortality in any of the experiments. A *G*-test was used to determine the direct effect of variation in food quality on sex ratio.

Results

Manipulating protein concentration

In the first experiment, examining only the parental generation, larval mass on days 8 and 12 was found to be increased with increasing protein in artificial diet over a range of 0.25–1.5 protein equivalents (ordered ANOVA day 8, $F_{1,23} = 7.550$, $P = 0.011$; day 12, $F_{1,18} = 8.558$, $P = 0.009$; Fig. 1); however pupal mass and days to pupation did not differ across protein levels (ordered ANOVA pupal mass, $F_{1,15} = 0.049$, $P = 0.827$; days to pupation, $F_{1,16} = 1.999$, $P = 0.177$). In the second experiment, larval (i.e. the parental generation) mass at day 12 did not differ

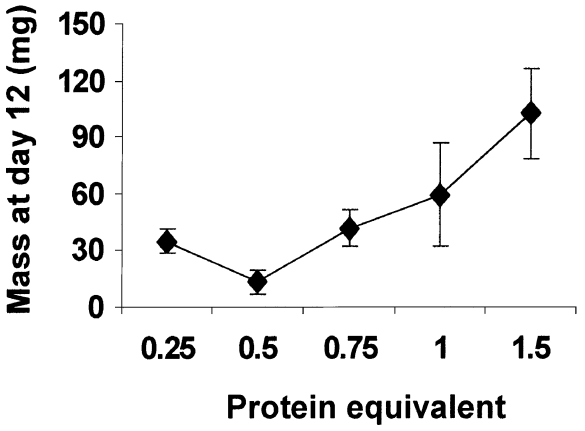

Fig. 1. Mass of larvae reared on 0.25, 0.5, 0.75, 1.0, and 1.5 protein equivalent diet on day 12. One protein equivalent contains 2.7% protein by fresh mass of the diet. Points represent mean ± SE.

among the 0.5, 1.0, and 1.5 relative protein treatments (ordered ANOVA, $F_{1,141} = 0.124$, $P = 0.725$). Likewise, the number of days to pupation and pupal mass in the parental generation did not differ across protein treatments (ordered ANOVA days to pupation, $F_{1,137} = 2.186$, $P = 0.142$; pupal mass, $F_{1,136} = 0.068$, $P = 0.795$; Fig. 2a). Total dry mass of frass decreased with increasing protein in the artificial diet (ordered ANOVA, $F_{2,37} = 22.532$, $P < 0.001$; Fig. 2b), indicating that larval consumption rate decreased or utilisation efficiency increased on higher protein diets. There was no effect of protein level on sex ratio of the adults produced by the larvae ($G = 0.29$, $P = 0.86$).

The mass of individual eggs produced by butterflies that had experienced variable protein diets as larvae decreased with increasing parental protein diet (ordered ANOVA, $F_{1,47} = 13.036$, $P = 0.001$; Fig. 2c). In a combined two-way analysis of the effects of parental and progeny environment on mass at day 4, an interaction between these main effects was found (Table 1, Fig. 3a). To decompose the interaction between effects of parental and progeny diet quality on progeny growth, ordered ANOVAs were conducted for each parental treatment. There was a positive dose-dependent response to progeny protein level on the mass at day 4 in progeny from mothers reared on 1.5 protein equivalents, but this was not found in progeny from mothers reared on 0.5 or 1.0 protein equivalents [parental treatment, (0.5) $F_{1,14} = 2.240$, $P = 0.151$, (1.0) $F_{1,19} = 1.497$, $P = 0.236$, (1.5) $F_{1,23} = 37.863$, $P < 0.001$; Fig. 3a].

To assess whether the parental effects were adaptive, the interactive effects in Fig. 3a were decomposed further. Progeny from 0.5 and 1.5 adults grew best on 0.5 and 1.5 protein equivalent diets respectively, relative to the progeny from other parental treatments (Tukey's HSD test; Fig. 3a). In addition, progeny from each of the three parental treatments grew best qualitatively on their home diet, relative to their own performance on other diets (Fig. 3a). By day 8, however, there was no detectable difference between larval

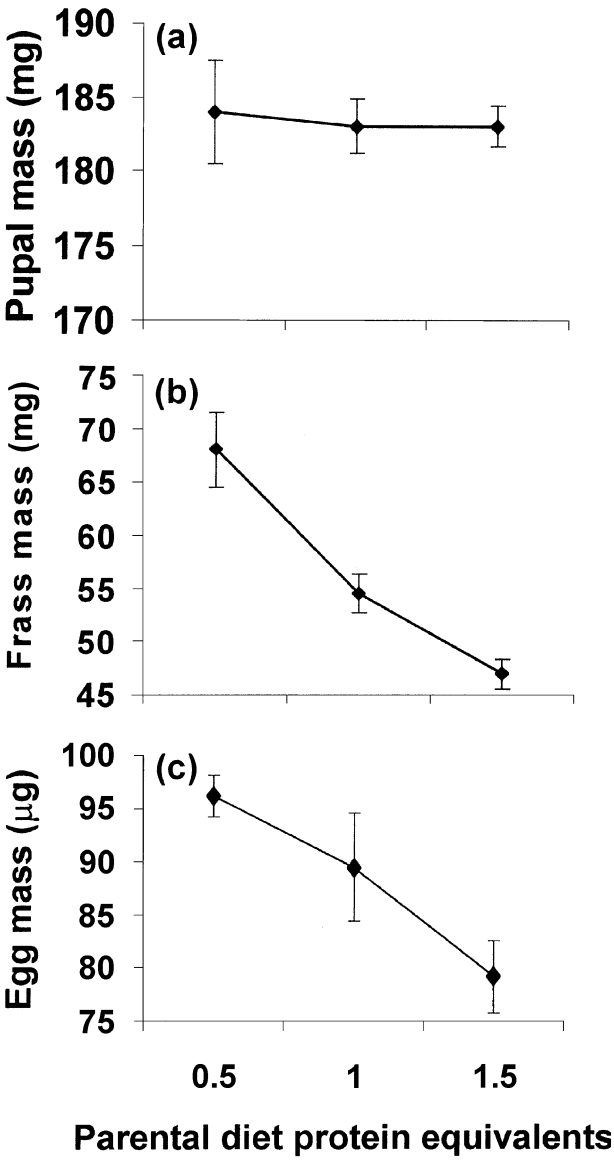

Fig. 2. (a) Mass of pupae, (b) total dry mass of frass produced by individual larvae, and (c) mass of individual eggs produced by adults that fed on either 0.5, 1.0, or 1.5 protein equivalents in artificial diet. One protein equivalent contains 2.7% protein by fresh mass of the diet. Points represent mean ± SE.

mass based on parental protein diet or progeny diet (Table 1, Fig. 3b). Days to pupation and pupal mass did not depend on parental or progeny protein environment (all P-values > 0.1).

Manipulating glucosinolate concentration

Pieris rapae larval mass at day 8 was found to be associated negatively with plant glucosinolate level in expt 1 but was not affected by treatment at day 18 in expt 2 (expt 1:

Table 1. Analysis of variance for effects of parental diet and progeny diet on progeny larval mass at days 4 and 8 (see Fig. 3).

Source	SS	d.f.	MS	*F*	*P*
Day 4					
Parental diet	0.000002	2	0.000001	2.13	0.128
Progeny diet	0.000001	2	<0.000001	0.588	0.559
Parental diet × progeny diet	0.000014	4	0.000004	6.957	<0.001
Error	0.000031	61	0.000001		
Day 8					
Parental diet	0.023	2	0.012	0.811	0.452
Progeny diet	0.027	2	0.014	0.962	0.392
Parental diet × progeny diet	0.068	4	0.017	1.191	0.332
Error	0.499	35	0.014		

ordered ANOVA, $F_{1,26} = 4.657$, $P = 0.040$; expt 2: $F_{1,39} = 0.067$, $P = 0.797$; Fig. 4a). Moreover, neither *P. rapae* pupal mass nor time to pupation differed between glucosinolate treatments (pupal mass: ordered ANOVA, expt 1: $F_{1,26} = 0.062$, $P = 0.805$; expt 2: $F_{1,36} = 0.553$, $P = 0.462$; time to pupation: ordered ANOVA, expt 1: $F_{1,26} = 3.053$, $P = 0.092$; expt 2: $F_{1,36} = 0.036$, $P = 0.851$). Sex ratio was affected marginally by glucosinolate treatment in the first experiment but was not affected in the second experiment (expt 1: $G = 5.043$, $P = 0.08$; expt 2: $G = 1.540$, $P = 0.463$). The non-significant trend in expt 1 was in the direction of higher glucosinolate lines causing a female-biased sex ratio. The mass of individual eggs produced by butterflies that had experienced variable glucosinolate diets was not affected by parental treatment (ordered ANOVA, $F_{1,22} = 0.038$, $P = 0.848$; Fig. 3b). Mass of the larval progeny at days 4 and 8 did not depend on parental

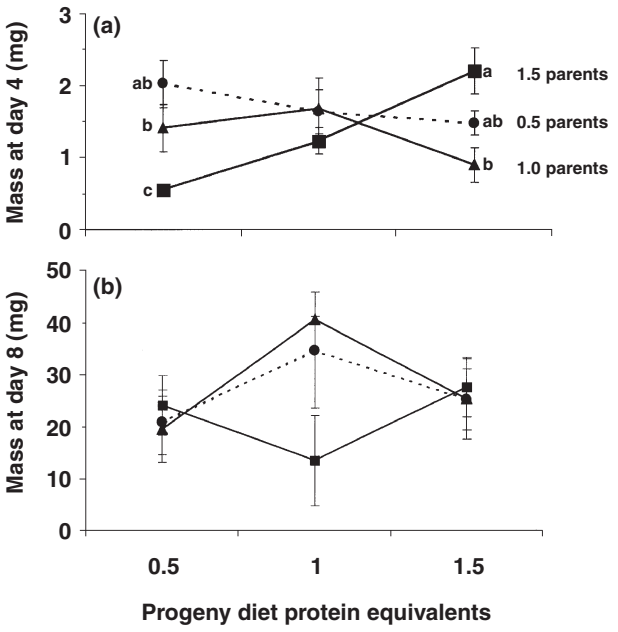

Fig. 3. Effects of parental and progeny diet (0.5, 1.0, and 1.5 protein equivalents) on mass of progeny on (a) day 4 and (b) day 8. One protein equivalent contains 2.7% protein by fresh mass of the diet. Points represent mean ± SE. In (a), letters above 0.5 and 1.5 protein equivalents represent results from a *post-hoc* Tukey HSD comparison. Different letters represent significant differences at $P < 0.05$.

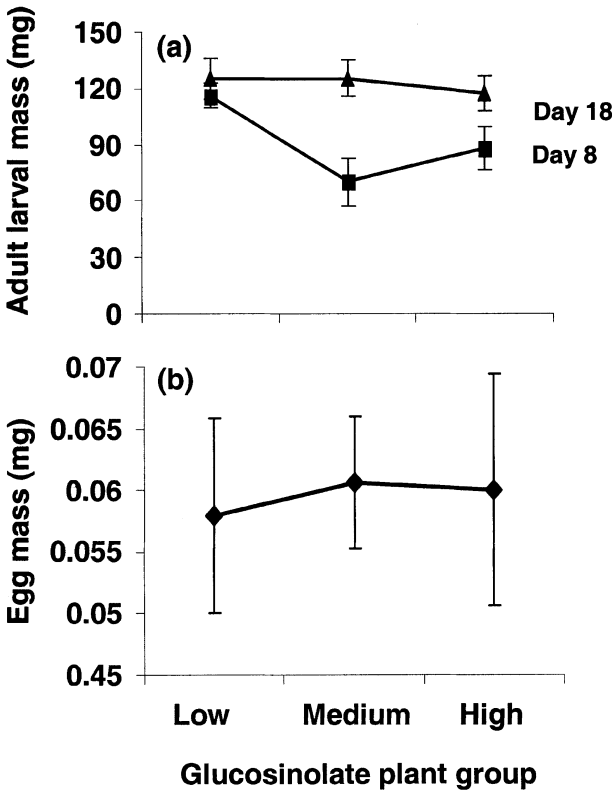

Fig. 4. (a) Mass of larvae reared on three glucosinolate plant groups on day 8 in expt 1 and day 18 in expt 2. (b) Mass of individual eggs produced by adults that fed on the three glucosinolate plant groups. Points represent mean ± SE.

glucosinolate level (ordered ANOVA, day 4: $F_{1,19} = 0.135$, $P = 0.717$; day 8: $F_{1,19} = 0.854$, $P = 0.367$).

Discussion

Parental environmental effects can have a strong influence on progeny fitness in insects (Mousseau & Dingle, 1991). In some cases, these effects are apparently non-adaptive, so that the relative fitness of progeny of parents that experience a detrimental environment is reduced compared with those of parents in a better environment (Mousseau & Fox, 1998a). For example, tobacco budworm *Heliothis virescens* (Noctuidae) progeny from mothers that had developed on artificial diet containing quercetin (a plant defence compound) grew more slowly on quercetin-containing diet than did progeny from mothers fed quercetin-free diet (Gould, 1988). In other cases, parental effects are adaptive, e.g. where a stressful environment results in parents producing progeny better suited to that stress than parents that were not stressed (Haukioja & Neuvonen, 1987; Mousseau & Fox, 1998a; Agrawal *et al*., 1999; LaMontagne & McCauley, 2001; Buechler *et al*., 2002).

In this study, a case of a potentially adaptive parental effect in *P. rapae* in response to variation in food quality is reported. Mothers reared in extreme conditions (i.e. 50% more or less than the optimal amount of protein) produced progeny that grew fastest under those conditions. Moreover, all progeny grew equally well on the optimal diet (Fig. 3a). These results suggest that progeny do not simply differ in overall vigour or quality, but rather are set for the particular protein environment experienced by their parents. Parental *P. rapae* growth was affected positively by the amount of protein in the diet in the first experiment in which there was a wide range of protein concentrations (i.e. 0.25–1.5 equivalents); however variation in growth was not detectable in the second experiment in which only three protein levels were assessed (i.e. 0.5, 1.0, 1.5). The lack of effects of variation in protein concentration on traits including pupal mass is consistent with a previous study which showed that *P. rapae* larvae feeding on low-nitrogen host plant species consumed food faster and had lower assimilation efficiency, but utilised nitrogen more efficiently than larvae feeding on high-nitrogen host plants (Slansky & Feeny, 1977). The earlier study and the current demonstration of decreasing total frass production on higher protein diets suggest that *P. rapae* larvae are able to adjust their feeding rates and efficiency in response to food quality to maximise growth rate. Although the growth rate of *P. rapae* larvae and consequently adult size measured as pupal mass were not affected strongly by variation in protein concentration, reproductive allocation, in terms of egg mass, was altered in response to this variation.

Little is known about the specific factors that determine lepidopteran egg size, even though it is an ecologically and evolutionarily important trait (Fischer *et al*., 2002). Across butterflies, female adult body size has been implicated in determining egg size (Fischer *et al*., 2002). Although the contribution of maternal and paternal effects on progeny phenotype could not be separated, it is assumed that maternal effects are more important because females invest more than males nutritionally and tend to spend more time associated with their progeny (Mousseau & Fox, 1998a). Because adult size (as estimated by pupal mass) was not affected by food quality in the experiments, the negative relationship between egg mass and protein treatment may be the result of differential allocation by mothers to individual eggs depending on the parental protein environment. Similarly, Wiklund *et al*. (1987) found a high amount of interspecific variation in egg size across 11 species of Pieridae collected in the field, including *P. rapae*, but demonstrated that there was no correlation between egg size and maternal adult size across these species.

As demonstrated here, a female insect can modify the mass of its eggs in response to food quality, potentially to maximise its own fitness (Awmack & Leather, 2002). Given the general trade-off between egg mass and number, females that produce relatively larger eggs do so at the expense of producing more eggs. This difference in allocation could prove to be advantageous if larger hatching size (or heavier hatching mass) is beneficial for an individual's subsequent growth, survival, and reproductive success, especially when consuming a nutrient-poor resource (Fox & Mousseau, 1996; Sinervo & Doughty, 1996). Several other studies have reported that organisms growing in resource-poor environments produced relatively larger offspring than offspring from mothers growing in resource-rich environments (Brody & Lawlor, 1984; Gliwicz & Guisande, 1992; Reznick & Yang, 1993; reviewed by Bernardo, 1996b). For *Stator limbatus* seed beetles, females lay relatively large eggs on seeds of the poor-quality host *Cercidium floridum*, and small eggs on the good-quality host *Acacia greggii* (Fox & Mousseau, 1996). The oviposition behaviour of *S. limbatus* females is potentially adaptive because producing relatively larger eggs at the expense of more eggs will result in progeny that are better able to penetrate the thick seed coat of *C. floridum*. On the other hand, producing smaller progeny on more easily penetrated *A. greggii* seeds will result in the female producing more eggs (Fox *et al*., 1997).

Pieris rapae mothers cue to variation in the protein concentration of their diet and alter the phenotype of their progeny. Larvae on a poor-quality diet (i.e. with less available protein) produced fewer progeny in exchange for larger single individuals, whereas females on a high-quality diet (i.e. with more available protein) produced more progeny in exchange for smaller single individuals. This conclusion is reached because the pupal mass of parents was equal among protein treatments, but the average mass of individual eggs produced was variable. Even though differences in progeny mass were undetectable by day 8, the additional allocation by females to individual progeny may contribute to a more substantial parental effect in the field. The first few days in a larva's development are vital for its establishment and survival (Zalucki *et al*., 2002), and thus parental effects influencing this stage may be critical.

Non egg-mass mediated parental effects may also contribute to progeny fitness (Rossiter, 1996). For example,

female seed beetles of *S. limbatus* that encounter *C. floridum* plants produce progeny that have survivorship 10 times higher on seeds of Texas ebony *Chloroleucon ebano* than that of progeny produced by females that do not encounter *C. floridum*, even when controlling for egg size (Fox & Savalli, 2000). One key result from the experiments presented here (Fig. 3a) implicates potentially adaptive non egg-mass related parental effects in *P. rapae*: progeny from high-protein parents had the highest 4-day growth on high-protein diet, even though eggs from high-protein parents were the least heavy of all treatments. Thus, even though egg mass could have explained the results for progeny on low-protein diets (i.e. low-protein mothers produced large eggs that had the fastest growth on low-protein diet), egg mass cannot explain the results for progeny on high-protein diet. It is predicted that a future examination of the nutritional composition of eggs and feeding behaviour of progeny from mothers in variable environments may explain some of the parental effects reported.

Slansky and Feeny (1977) found no correlation between larval growth rate and glucosinolate concentration across host plant species. The results show that early larval growth of *P. rapae* is affected negatively by increasing glucosinolates in *B. napus* seedlings, even at the low concentrations in the double haploid lines. These results are consistent with those of Stowe (1998), who showed that *P. rapae* larvae consumed a greater amount of *Brassica rapa* leaf tissue in plant lines with relatively low glucosinolate concentration compared with lines with higher levels of glucosinolates. No effects of glucosinolates were found on *P. rapae* larval growth or pupation after day 8, however, suggesting that larvae have mechanisms for tolerating or detoxifying these secondary compounds. Moreover, progeny were unaffected by parental glucosinolate environment (Fig. 4b). These results are not surprising given that *P. rapae* is a highly co-evolved specialist consumer of the Brassicaceae that encounters glucosinolates in all of its host plants.

In conclusion, variation in food quality may cause adaptive parental life-history switches in *P. rapae*. It is demonstrated that mothers in a poor-quality environment increase egg quality in terms of the total mass allocated to a single individual, and that this effect benefits larvae for a significant portion of their lives (≈25% of larval development time). Moreover, it is demonstrated that parental environments can be equally or more important for progeny growth than the environments experienced by the progeny themselves. In nature, herbivores must adjust to changes in plant quality and may do so via parental effects. In addition to herbivores responding to diet quality, plants are known to respond to herbivory within and across generations (Karban & Baldwin, 1997). For example, adaptive parental effects have been demonstrated in *Raphanus raphanistrum* (Brassicaceae) in response to herbivory by *P. rapae* (Agrawal *et al.*, 1999; Agrawal, 2001a). These potentially adaptive parental effects between *P. rapae* and its host plant will hopefully be linked in the exploration of reciprocal phenotypic responses across generations in this plant–herbivore interaction (Agrawal, 2001b).

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