Larval Performance in Relation to Labile Oviposition Preference of *Crocidolomia pavonana* [F.] (Lepidoptera: Pyralidae) Among Phenological Stages of Cabbage

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ABSTRACT *Crocidolomia pavonana* (=*binotalis*) [F.] demonstrates oviposition peaks in the field that we believe to be correlated with host plant phenology. In previous two-choice laboratory experiments, we found the highest relative proportion of oviposition on cabbage to correspond either to plant growth stages ≈7–8 wk or ≈9–11 wk old, depending on the alternate host plant with which it was presented. In cabbage-only trials, leaves from 7- to 8-wk-old plants were preferred. Inconsistency in preference led to the question of whether oviposition on either cabbage growth stage would confer adaptive advantages in offspring performance. We simulated oviposition on four phenological stages of cabbage in two ways. In a study of complete immature development, growth rate, pupal weight, and survivorship were measured. We also compared food utilization efficiency during the fourth larval instar by analyzing growth rate, efficiency of biomass accumulation, and frass production by analysis of covariance (ANCOVA). For both experiments, cabbage plants of defined phenological stages were designated at the time of oviposition, and larvae were fed from these as plants continued to grow throughout larval development. Our data indicate adaptive advantages in larval growth rate and food conversion efficiency to oviposition on cabbage at ≈7–8 wk from planting. Oviposition on later cabbage growth stages resulted in comparatively poor larval performance. Possible explanations for *C. pavonana* oviposition behavior in light of these results are discussed.

KEY WORDS food utilization, plant-herbivore interactions, plant phenology, larval development

Crocidolomia pavonana (=*binotalis*) [F.] IS ONE OF the most destructive pests of crucifer crops in the Old World tropics. This moth is common in southern Africa, Madagascar, and India, through Southeast Asia, the southwest Pacific, Guam, and Queensland, Australia (USDA 1968, CAB 1979). Eggs are laid in partially overlapping, shingled masses on the undersides of leaves. Three to four days after the eggs hatch, larvae migrate toward the growing center of the cabbage, where they conceal themselves in webbing. Then, they can destroy the plant's apical meristem and ruin the entire cabbage head.

When the fate of offspring is tightly linked to the site of oviposition, as with *C. pavonana*, optimality models in evolutionary ecology predict a close correlation between offspring performance and oviposition preference on the part of the mother (Jaenike 1978). A majority of tests support this (Mayhew 1997), but numerous exceptions also exist (reviewed in Thompson 1988 and Thompson and Pellmyr 1991). Many of these may involve ecological factors not measured in the laboratory that can affect larval performance in the field.

Correlations have been found between larval performance and oviposition on host plants of different taxa, different plant genotypes of the same species, and different tissue types within plants (Valladares and Lawton 1991). We examined the effect of *C. pavonana* oviposition at differing, phenologically defined, growth stages of cabbage on larval performance.

In the Old World highland tropics, cabbage is planted continuously. For this reason, *C. pavonana* females may have an opportunity to select among plants from 1 mo (at time of transplant) to 4 mo (harvest) of age. In a previous study (Smyth et al. 2003), we found that *C. pavonana* females could discriminate between phenological stages of cabbage (as described by Andaloro et al. 1983), and the pattern of oviposition preference strongly suggested that *C. pavonana* field oviposition peaks are related to cabbage plant phenology. When only cabbage stages were compared, stage 4 cabbage (7–8 wk old) was significantly preferred over stage 5 cabbage (9–11 wk old) (Smyth et al. 2003). When these, as well as stage 6 cabbage (≈12 wk old), were presented simultaneously in two-choice tests with alternate host plants, however, in several cases, stage 5 cabbage was con-

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sistently more preferred than stage 4 cabbage, relative to the alternate host (Smyth et al. 2003). This lack of hierarchical simplicity stimulated the question of whether there is an effect of cabbage plant phenology on offspring performance and whether differential oviposition in *C. pavonana* can be interpreted as adaptive.

Two experiments were conducted to compare larval performance consequent to simulated oviposition on four sequential phenological stages of cabbage. One followed mean growth rates, pupal weights, and percent survivorship for the four diet groups. The second analyzed food use during a 24-h period on initiation of the fourth larval instar for individuals from the four diet groups.

Materials and Methods

Plant Culture. *Brassica oleracea* L., variety *capitata*, cultivar Gloria (Kays and Dias 1996), a commercial head cabbage commonly grown in Southeast Asia, was grown in a glasshouse under natural light in the summer months or under Lumalux high pressure sodium lamps with a 12:12 (L:D)-h photoperiod schedule. "Gloria," known in North America as "Greenboy," seed was obtained from Reed's Seeds, Cortland, NY. Plants were grown in 25-cm diameter pots in Premier Pro Mix BX (Premier Horticulture, Québec, Canada) potting soil. Pete's (Grace-Sierra Horticultural Products, Milpitas, CA) water soluble fertilizer ($20N{:}10P_2O_5{:}20K_2O$) was administered to the soil in the plant pots at a 1:15 concentration once each week.

Cabbages were categorized according to phenological stages as described by Andaloro et al. (1983). Within the length of time in which cabbages retained phenological characteristics, plants used in these experiments were as close in age as possible. The plants reached stage 4 from 43 to 51 d after planting, had 11 or 12 true leaves, and the base of the stem and bases of all leaves were still visible when viewed from above. Stage 5 cabbages were 56–66 d old, had 13 true leaves, and the base of the stem and bases of all leaves were no longer visible from above. The innermost heart leaves were growing upright, were concealed by outer leaves, and were not yet forming a firm center. Stage 6 cabbages were 86–91 d old, had >13 true leaves, and the inner heart leaves were as in stage 5 but forming a firm center. Stage 7 cabbages were 120–122 d old, and the inner heart leaves were forming a firm ball ≤10 cm in diameter.

Colony Rearing. Larvae were obtained from a colony that had been established at the USDA-approved ARS quarantine facility at Cornell University for ≈15 mo and had originated from 150 *C. pavonana* pupae collected in the Puncak region of West Java <3 mo earlier. A minimum population size of ≈300 adults was maintained at all times. Eggs used for continuation of the colony were taken from cages in which moths had access to host plant leaves. Larvae were fed a mixture (each day ≥2 types) of fresh crucifer leaves: cabbage, Indian mustard (*Brassica juncea* [L.] Czernj. and Coss variety *rugosa* Bailey), Chinese cabbage (*B. rapa* L. variety *pekinensis* [Lour.] Olsson), rapeseed (*B. napus* L. variety *napus*), and sawi manis or sayur pahit (both *B. rapa* variety *parachinensis* [Bailey] Tsen and Lee). See Smyth (1999) for rearing details.

Larval Experiments. Experiments were conducted in a 2.36 by 1.75 m walk-in chamber maintained at 27.8 ± 1.4°C, 54.6 ± 5.7% RH, and a photoperiod of 14:10 (L:D) h. The chamber was equipped with full spectrum lighting. We evaluated larval development after simulated oviposition on cabbage stage 4, 5, 6, or 7 in two ways. In neither case did larvae develop on leaves of a static age. Rather, plants of the four phenological stages were designated at the time of oviposition, and larvae were fed from them as the plants continued to grow throughout the course of larval development.

Larval Development and Survival. Egg masses for this experiment had been laid on waxed paper and were selected from two or three nonsibling females. Larvae remained close to the location of the egg mass on the waxed paper for a short period after hatching and were counted and transferred on the pieces of waxed paper to bins at this time. Neonates were not directly handled. This experiment was of a completely randomized design with subsamples. Three groups of ≈50 larvae were reared on each of the four phenological stages of cabbage. Groups were contained in circular 1.82-liter Rubbermaid bins (Rubbermaid Commercial Products, Winchester, VA) that measured 18.5 cm diameter at the rim.

Larvae were provided with the open leaves growing near the center of each plant ad libitum. In the field, 4-d-old larvae migrate to the center of the growing head of cabbage; therefore, larvae in this experiment also received plant centers at the appropriate time. Two plants were needed to supply each bin of larvae reared on designated stages 4, 5, and 6 cabbage throughout the course of larval development. One plant was adequate to supply each bin of larvae reared on stage 7 cabbage.

To assess rates of weight gain, 10 larvae from each bin were randomly selected and weighed (Mettler AT460 Delta Range) on days 4, 6, and 8 after hatching. Larvae were returned to bins after weighing. All pupae were collected and weighed, and the percent of larvae surviving to pupation in each bin was recorded. Development rates were compared by mixed effect analysis of variance (ANOVA) with a repeated measure design modeled through the origin (SAS; SAS Institute 1999). Larval weights were log-transformed. Percent survivorship per bin and pupal weights (with a bin within treatment covariate) were compared by ANOVA. Tukey or Tukey-Kramer multiple comparisons were conducted to detect differences in each day's larval weights and between treatment means for survivorship and pupal weight (SAS; SAS Institute 1999). An additional ANOVA analysis of pupal weight that controlled for the number of larvae surviving in each bin was performed to test for a differing effect of competition for nutritional resources between treatments.

Food Assimilation. Groups of ≈65 larvae were reared in circular 1.82-liter bins on leaves from cabbage plants that initiated the experiment at phenological stages 4, 5, 6, and 7. As fourth instars, usually 7–12 d from egg hatching, *C. pavonana* larvae feed and grow most rapidly. Within 8 h of molting to the fourth instar, ≥20 randomly selected individuals from each diet treatment were transferred to 14-cm diameter petri dishes lined with filter paper moistened with 2 ml deionized water. Each larva was given one-half of a leaf from a plant of the same phenological category as that on which it had been fed previously. Individual petri dishes were not sealed but assembled and placed in large, closed plastic bags to minimize leaf drying and larval movement in the growth chamber.

Twenty-four hours later, larvae, frass, and leaves were weighed, placed in −80°C storage, and freeze dried. Fresh weights of leaves and larvae were used for preliminary analyses only. ANOVAs preparatory to analyses of covariance (ANCOVA) (Fisher 1932, Neter et al. 1990) and ANCOVAs were calculated on a dry weight basis.

For dry weight calculations, a "before treatment" dry weight of larvae and leaves was estimated from percent dry matter of similar aliquots. Leaves from the four plant growth stage categories were cut in half, with midrib sections excluded. One-half of each leaf was used to determine percent dry weight of the leaf, and the other half was fed to a larva. "Before treatment" larval dry weight estimates were obtained from a regression of percent dry weight to fresh weight of aliquot larvae reared simultaneously and from the same pretreatment diets as experimental larvae. These were weighed and frozen at the start of the experiment and later freeze dried. Larval consumption and gain in biomass were derived from final dry weights − initial dry weights of leaf halves and larvae, respectively.

Data were analyzed by ANCOVA, a statistically more detailed and accurate approach for food utilization studies than ratio-based indices (Raubenheimer and Simpson 1992, Horton and Redak 1993). Tukey-Kramer simultaneous tests were conducted to detect differences between treatment means (SAS; SAS Institute 1999). Reported least square means have been adjusted for the covariates.

Food Utilization Estimates. Because larvae were selected from cabbage stage pretreatment diets and thus not assigned randomly to treatments, this experiment differs from most insect dietary studies. The objective here was to compare aspects of food utilization for fourth instar larvae in the course of development that initiated on hosts of different ages. This design also avoided possible effects of diet switching. In such observational studies, ANCOVA covariates may serve purposes not usually considered in randomized experiments. For example, variables that differ among the groups, e.g., initial biomass of larvae, may be deliberately chosen as covariates to remove bias (Cochran 1957). One can also distinguish between multiple treatment effects (Cochran 1957), for example, by removing the effect of diet on consumption from larval gain in biomass or frass production. Although the use of covariates that may be affected by treatment is normally cautioned against (Cochran 1957, Smith 1957, Raubenheimer and Simpson 1992) for removing variation caused by the treatments themselves, the usefulness of the consumption covariate in insect diet studies is supported by Horton and Redak (1993), with examples from Cochran and Cox (1957), Cox (1958), Steel and Torrie (1980), and Packard and Boardman (1988). We considered it essential to distinguish between biomass increase caused by increased consumption from biomass increase caused by differences in assimilation of treatment cabbage leaves.

To estimate the effect of diet on weight gain during the 24-h experimental period, final dry mass was analyzed using initial larval dry mass as a covariate (Raubenheimer and Simpson 1992). Results from this analysis and that of larval gain in biomass with initial dry mass as a covariate, suggested as an alternative by Horton and Redak (1993), were statistically the same. Only the former is reported. The efficiency of conversion of ingested food to biomass was estimated by measuring the biomass gain of larvae using consumption as a covariate. The effect of diet on frass production was estimated using consumption as a covariate.

Table 1. Least squared mean adjusted weights of *C. pavonana* larvae by diet treatment (stage of cabbage at initiation of experiment) and results of Tukey-Kramer simultaneous tests of differences between treatments for each day larvae were weighed during larval development

Cabbage stage	Day	LS mean (mg)	−SE	+SE	Cabbage stages compared	*t*	*P* value
4	4	3.1897	0.5015	0.5951	4–5	3.06	0.061
5	4	1.5182	0.2395	0.2844	4–6	3.05	0.062
6	4	1.5221	0.2402	0.2852	4–7	2.84	0.083
7	4	1.6010	0.2526	0.2999	5–6	−0.01	1.000
					5–7	−0.22	0.996
					6–7	−0.21	0.997
4	6	14.9088	2.2595	2.6631	4–5	2.75	0.095
5	6	7.8694	1.1933	1.4066	4–6	2.20	0.202
6	6	8.9298	1.3545	1.5967	4–7	2.72	0.099
7	6	7.9261	1.2022	1.4172	5–6	−0.54	0.946
					5–7	−0.03	1.000
					6–7	0.51	0.954
4	8	69.6850	10.9907	13.0487	4–5	2.21	0.201
5	8	40.7890	6.4251	7.6264	4–6	1.18	0.658
6	8	52.3881	8.2659	9.8145	4–7	2.37	0.162
7	8	39.2408	6.1915	7.3514	5–6	−1.03	0.737
					5–7	0.16	0.998
					6–7	1.19	0.649

Results

Larval Development and Survival. Significant differences were detected in larval weight increase through the eighth day caused by cabbage stage treatment ($F = 1886.99$; df = 4, 8; $P < 0.0001$), larval age ($F = 4479.81$; df = 1, 348; $P < 0.0001$), and the interaction of treatment and age ($F = 3.88$; df = 3, 348; $P = 0.009$) in the full model ANOVA. Tukey-Kramer simultaneous tests, however, resulted in marginally nonsignificant differences between only some treat-

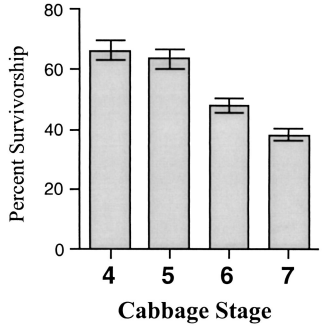

Fig. 1. Least squared mean (±SE) percent survivorship of *C. pavonana* larvae reared from egg hatch on four diet treatments, indicated by cabbage stage at the time of oviposition.

ment means (Table 1). All of these were between stage 4 and a later cabbage stage on day 4 or 6. All other tests were not significant.

Neither differences among treatments in pupal weights ($F = 0.72$; df = 3, 8; $P = 0.568$) nor survivorship ($F = 3.60$; df = 3, 8; $P = 0.065$) were significant. We note, however, that for survivorship, this may be an artifact of our experimental design, which resulted in an analysis of means among only three bins per treatment. Statistical results were not significant, although survivorship on cabbage stage 4 was nearly twice as high as on stage 7 (Fig. 1). Analysis of diet treatment effects on pupal weight, controlling for per bin survivorship, showed a significant treatment × survivorship interaction ($F = 2.84$; df = 3, 377; $P = 0.038$), indicating that treatment effects varied depending on the number of larvae surviving in each bin. Only the cabbage stage 5 treatment, however, showed the negative correlation between survivorship and pupal weight that could be anticipated from larval competition for nutritional resources.

Food Assimilation. Final larval dry weights, adjusted by the initial larval dry weight covariate, varied significantly among treatment groups ($F = 26.71$; df = 3, 47; $P < 0.0001$). Interaction terms were not significant, indicating that slopes among diet treatment regression lines did not differ. Figure 2 shows raw data and ANCOVA-fitted data for the relationship between final dry weights and initial dry weights among diet treatments. Larvae continuing on a diet of plants initially designated as stage 4 increased significantly more in weight during the 24-h period than larvae on any other cabbage stage (stage 5, $P = 0.0008$; stage 6, $P = 0.0322$; stage 7, $P < 0.0001$). Larvae continuing on diets of plants designated as cabbage stages 5 and 6 at the start of the experiment were not significantly different from each other, but grew significantly faster than those on cabbage stage 7 (both $P < 0.0001$).

Similarly, weight gain for quantity consumed (conversion efficiency) differed significantly among diet treatments ($F = 16.91$; df = 3, 46; $P < 0.0001$). Figure 3 shows raw data and ANCOVA-fitted data for the relationship between weight gain and consumption among diet treatments. Larvae developing on a diet of

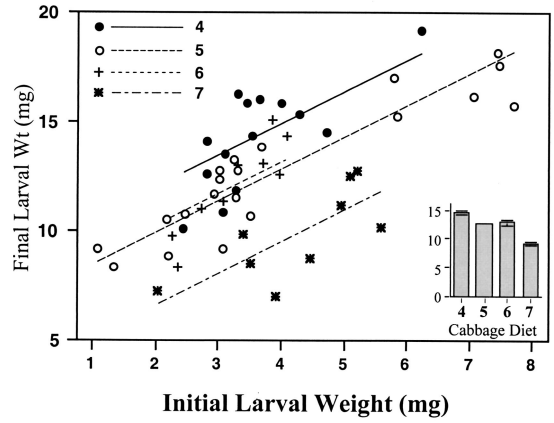

Fig. 2. Raw and ANCOVA-fitted data showing the relationship between initial (dry) weights and final (dry) weights, after 24 h, of *C. pavonana* fed four diet treatments, indicated by cabbage stage at the time of oviposition. Common slope = 1.44. Inset shows final weight ANCOVA means (±SE).

plants designated as stage 4 gained significantly more weight for leaf biomass consumed during the 24-h period than larvae on cabbage stage 5 ($P = 0.006$) or 7 ($P > 0.0001$), and marginally more than those on cabbage stage 6 ($P = 0.0724$). Larvae developing on cabbage stage 7 also gained significantly less weight for leaf biomass consumed than larvae fed cabbage stage 5 ($P = 0.0002$) or 6 ($P = 0.0003$).

Frass (egesta) biomass for quantity consumed also differed significantly among some treatments ($F = 9.36$; df = 3, 46; $P < 0.0001$). Figure 4 shows raw data and ANCOVA-fitted data for the relationship between egesta and consumption among diet treatments. Larvae developing on plants that had been designated as stage 4 excreted the highest dry weight of frass for leaf

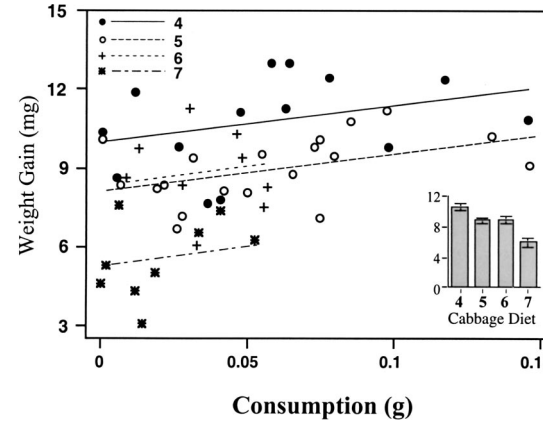

Fig. 3. Raw and ANCOVA-fitted data showing the relationship between consumption (dry) and weight gained (dry), after 24 h, of *C. pavonana* larvae fed four diet treatments, indicated by cabbage stage at the time of oviposition. Common slope = 0.0079. Inset shows ANCOVA means (±SE) for weight gained.

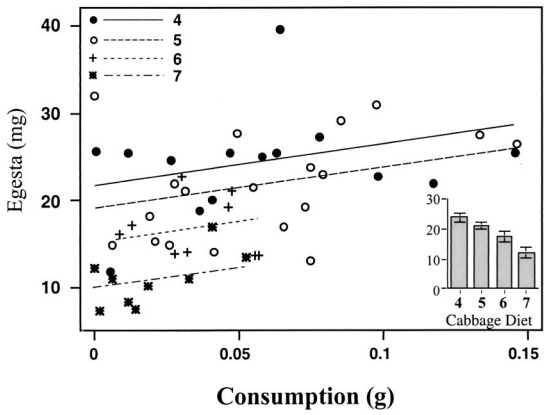

Fig. 4. Raw and ANCOVA-fitted data showing the relationship between consumption (dry) and egesta (dry), after 24 h, of *C. pavonana* larvae fed four diet treatments, indicated by cabbage stage at the time of oviposition. Common slope = 0.0272. Inset shows ANCOVA means (±SE) for egesta.

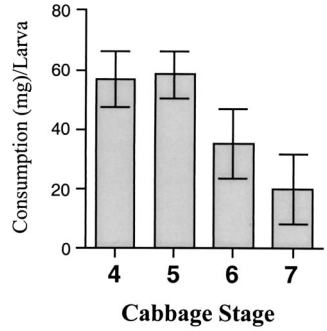

Fig. 6. Mean (±SE) consumption of *C. pavonana* larvae during 24 h on four diet treatments, indicated by cabbage stage at the time of oviposition.

mass consumed. Differences in quantities of frass were statistically significant between cabbage stage 4 and stages 6 ($P = 0.027$) and 7 ($P < 0.0001$) but not significantly different from that excreted by larvae developing on stage 5 cabbage. Dry weight of frass for stage 7 cabbage was also significantly lower than for stage 5 ($P = 0.0009$). Percent dry biomass in the four leaf types was also progressively lower for each later cabbage stage ($F = 66.52$; df = 3, 47; $P < 0.0001$; Fig. 5). Consumption was significantly different between groups ($F = 3.18$; df = 3, 47; $P = 0.033$; Fig. 6).

Discussion

Patterns of larval performance in relation to simulated oviposition on the four consecutive phenological cabbage stages were consistent in the two experiments. Although results of simultaneous comparisons between diet treatments in the experiment on complete immature development were not statistically significant, we believe this to be a consequence of the experimental design rather than of a discrepancy between treatment effects during the entire larval development versus during only one larval instar. Larvae developing from eggs beginning on stage 4 cabbage had the most rapid development rates and highest mean survivorship in this experiment. In the 24-h test, larvae on stage 4 cabbage gained weight faster, showed higher efficiency of food conversion, and produced more frass than larvae from later cabbage stages. The accelerated response to this phenological stage of cabbage seems to be both behavioral and nutritional.

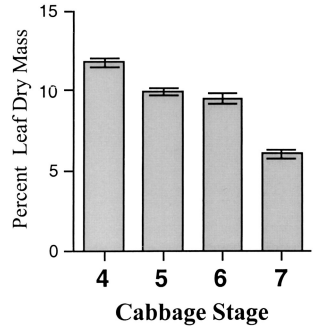

Fig. 5. Mean (±SE) percent dry mass of leaves used in experiments lasting 24 h in which *C. pavonana* larvae were fed four cabbage diet treatments, indicated by growth stage at the time of oviposition.

Larvae that hatched from eggs that would have been laid on cabbage stage 5 survived as well as those on stage 4. During the 24-h test at the start of the fourth instar, however, these larvae gained less weight and showed lower food conversion efficiency than stage 4 larvae. That stage 5 larvae showed similar consumption rates and produced similar amounts of frass while growing less than those on stage 4 indicates that the diet consequent to oviposition on stage 5 cabbage is nutritionally inferior to that beginning with the previous plant stage.

Similar to stage 5 larvae, those that hatched from eggs that would have been laid on stage 6 cabbage showed lower growth rates than stage 4 larvae but higher growth rates and food conversion efficiency than stage 7 larvae. They also produced less frass than larvae from stage 4 cabbage.

Larvae that hatched from eggs that would have been laid on stage 7 cabbage performed poorly in comparison with all others. One-half of the larvae from this category also died during the 24-h food utilization experiment. Those that survived consumed less leaf biomass, grew less, converted food to biomass less efficiently, and produced less frass. Less frass, given similar consumption, is normally thought to indicate higher food digestibility (Wheeler and Halpern 1999). The lower frass production for leaf biomass consumed may, alternatively, be the result of lower percent dry weight of leaves from this phenological category. There would have been a considerably higher volume of water to be processed by the larvae eating them.

These data indicate that preference of female *C. pavonana* to oviposit on stage 4 cabbage over other

phenological stages of cabbage (Smyth et al. 2003) is correlated with stage 4 being a nutritionally superior host for their offspring, resulting in more rapid and efficient development. These results were obtained despite stage 4 lasting only 6 d of a total 4-mo growing period, while later cabbage stages lasted 2 wk or more. Previous work (Smyth et al. 2003), however, showed that *C. pavonana* oviposition preference shifted to the next cabbage stage in the context of certain alternate hosts. Offspring development consequent to oviposition at the later stage was slower, although survivorship of larvae on the two diets was similar.

Several explanations have been offered for a lack of correlation between oviposition preference and offspring performance, such as factors that influence escape from natural enemies, variation in plant abundance (Thompson 1988 and references therein), inter- or intra-specific competition, and physiological, behavioral, or phylogenetic constraints (Mayhew 1997). Our study fits in the context of the potential adaptive importance of intraspecific host selection (Ng 1988, Jaenike 1990). The brevity of stage 4 may mean that *C. pavonana* often do not have access to this resource. Oviposition preference for stage 5 over stage 4 cabbage, which we observed when mediated by the presence of certain taxonomically differing hosts, may reflect plasticity that would be adaptive in conditions of limited resource options or interactions with attributes of the alternate host plants. Studies of larval development on hosts other than cabbage and the plant characteristics that explain differences in larval performance could contribute much to the understanding of *C. pavonana* oviposition behavior.

Acknowledgments

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