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The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly (*Lycaeides melissa samuelis*)

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Abstract Larvae of the Karner blue butterfly, *Lycaeides melissa samuelis*, feed solely on wild lupine, *Lupinus perennis*, from the emergence to summer senescence of the plant. Wild lupine is most abundant in open areas but Karner blue females oviposit more frequently on lupines growing in moderate shade. Can differences in lupine quality between open and shaded areas help explain this disparity in resource use? Furthermore, many lupines are senescent before the second larval brood completes development. How does lupine senescence affect larval growth? We addressed these questions by measuring growth rates of larvae fed lupines of different phenological stages and lupines growing under different shade conditions. The habitat conditions under which lupines grew and plant phenological stage did not generally affect final larval or pupal weight but did significantly affect duration of the larval period. Duration was shortest for larvae fed leaves from flowering lupines and was negatively correlated with leaf nitrogen concentration. Ovipositing in areas of moderate shade should increase second-brood larval exposure to flowering lupines. In addition, larval growth was significantly faster on shade-grown lupines that were in seed than on similar sun-grown lupines. These are possible advantages of the higher-than-expected oviposition rate on shade-grown lupines. Given the canopy-related trade-off between lupine abundance and quality, maintenance of canopy heterogeneity is an important conservation management goal. Larvae were also fed leaves growing in poor soil conditions and leaves with mildew infection. These and other feeding treatments that we anticipated would inhibit larval growth often did not. In particular, ant-tended larvae exhibited the highest weight gain per amount of lupine eaten and a relatively fast growth rate. This represents an advantage of ant tending to Karner blue larvae.

Key words Host plant quality · *Lupinus perennis* · Phenology · Shade · Butterfly conservation

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Introduction

Habitat structure affects the suitability of an area for butterflies in many ways (Singer 1972; Greatorex-Davies et al. 1993). This is especially true for oviposition. For instance, habitat structure can affect abundance and distribution of host plants (Stanton 1982), nectar plants (Murphy 1983), predators (Montllor and Bernays 1993), and ants tending larvae (Pierce and Elgar 1985). Structure can affect larval growth (Grossmueller and Lederhouse 1985) and survival (Rausher and Papaj 1983). Habitat variations in sun and shade can also affect aspects of host plant chemistry such as total plant nitrogen and annual patterns of change in nitrogen (Scriber and Slansky 1981; Jackson et al. 1990; Ravenscroft 1994). Despite this variety of effects, plants selected by female butterflies for oviposition usually support faster larval growth and higher larval survivorship than do plants not selected (Rausher 1981; Ng 1988; Thompson 1988). Thus, the specificity of cues used in selecting oviposition sites can greatly affect persistence of a butterfly population in a changing habitat (New 1991).

Understanding the specificity of oviposition cues is therefore critical for the proper management of endangered butterflies. Previously, we showed that populations of the endangered Karner blue butterfly, *Lycaeides melissa samuelis* Nabokov (Lepidoptera: Lycaenidae), differentiate among conspecific host plants during oviposition, based on canopy structure above the plants (Grundel et al., in press). During the second brood, fe-

males preferentially oviposit on shade-growing wild lupine, *Lupinus perennis*, the sole larval host plant. In this case, the usual larval growth advantage attributed to sunnier and warmer microhabitats cannot explain the preferred oviposition location along the sun-shade gradient (Grossmueller and Lederhouse 1985; Weiss et al. 1988, 1993). A direct effect of canopy cover on host plant quality is, therefore, a likely reason for the preference for shade-growing plants.

Changes in canopy cover have been implicated in the decline of the Karner blue. The Karner blue butterfly inhabits savanna and barren sites, today principally in the Great Lakes region of North America and in eastern New York (Captive Breeding Specialist Group 1992; Andow et al. 1994a). A defining characteristic of these sites, historically, was a heterogeneous landscape of canopy cover and openings. Declining fire frequency over the past 150 years, due to loss of fires set by Native Americans and suppression of wildfires (Curtis 1959), has produced a more densely wooded landscape with fewer canopy openings (Nuzzo 1986; Cole and Taylor 1995). This change can be detrimental to Karner blue populations (Clough 1992; Andow et al. 1994b; Dirig 1994). Conversely, while Karner blue populations persist in very open habitats, the long-term viability of such populations is not clear (Andow et al. 1994b).

Karner blues exhibit a general adult preference for canopy openings (Lane 1994; Grundel et al. in press). As noted, however, females preferentially oviposit on lupines growing in moderately shaded areas. Lupine abundance is greatest in more open areas (Grundel et al. in press). Here we examine whether habitat-induced differences in host plant quality can explain this disparity between resource availability and use. We also investigate other potential habitat and phenological correlates of host plant quality. In doing so we ask whether a relationship between habitat structure and host plant quality may be central to oviposition preferences and to the Karner blue decline (Haack 1993; Lane 1994).

Materials and methods

We studied Karner blue butterflies at Indiana Dunes National Lakeshore, at the southern tip of Lake Michigan. Karner blues live there in a savanna community where black oaks (*Quercus velutina*) make up nearly the entire canopy (Wilhelm 1990). Karner blues overwinter as eggs that begin hatching in mid-April. After passing through four larval instars and pupating, adults of the first brood emerge in May and June. Eggs oviposited by the first-brood females hatch in June and July and second-brood adults arise in late July and August. Eggs from these second-brood adults overwinter. Wild lupine emerges before egg hatching in the spring and flowers from midway through the first larval brood through midway into the second larval brood. Often, many of these lupines are senescent by the end of the second larval brood (Dirig 1994; Swengel 1995). Larvae can crawl at least several meters to feed on different lupine plants (personal observation).

Under permit from the U.S. Fish and Wildlife Service, we netted seven female adult Karner blues. We placed each female into a plastic container along with lupine and nectaring plant stalks onto which she laid eggs (mean = 37.7 eggs per 2 days). Groups of three eggs were transferred to capped 35-ml plastic cups that were placed into a plastic bag with a damp paper towel. Eggs were disc shaped, 875 ± 8.9 (SE) μm (n = 10) in diameter by 487 ± 19.2 μm in height. Most eggs (76.7%, n = 267) hatched during the 6th day after laying (range 4–8 days); 95.1% of all eggs hatched (Herms et al. 1996). We transferred each larva into a sealed 200-ml plastic cup containing one large to three small lupine leaves gathered from sites within Indiana Dunes National Lakeshore. All containers were maintained at room temperature (ca. 22°C) and placed by a south-facing window starting on 13 June 1994.

Every 3rd day, lupine leaves were collected and pressed. We measured larval length and transferred larvae to clean containers with freshly collected leaves. After day 10, larvae were also weighed. After collecting the leaves we measured the area eaten in each hole in each leaf. Once pupation began, we checked cups twice daily for pupae and measured pupal length and weight. Once adult emergence began, we checked cups at least twice daily for adults. Overall, 67.5% of the initial larval population (n = 118) was released as adults.

In 1993, we measured mesophyll thickness of two leaflets from 136 lupines. We also measured several characteristics of the environment surrounding those lupines and used this information to determine what factors might affect mesophyll thickness.

Larvae were fed leaves from lupines growing under one of ten different conditions (Table 1). Since delineating individual lupine plants is difficult (Grigore and Tramer 1996), we selected lupine foliage based on characteristics of a distinct lupine clump or characteristics of the habitat surrounding a clump. In the ten feeding treatments, lupines varied in three broad factors, plant phenological stage, canopy cover, and miscellaneous variables affecting lupine or larval growth. We defined five lupine phenological stages. (1) Plants that were in their 1st year of growth (treatment A), having arisen from native seeds planted the previous fall. (2) Plants that did not flower in the year of the study (B). (3) Plants that were in flower or that had recently flowered (C). Since flowering plants were initially mainly available in the sunny areas and later mainly in the shaded areas, we took leaves from sun and shade plants. Near the end of the experiment, however, no more flowering lupines were found. We then selected lupines with green and succulent pods since they were most recently still in flower. (4) Plants that were in seed and had the greatest percentage of unburst pods at the time of leaf collection (D). (5) Plants that were senescent (E). Senescent plants had released all of their seeds and exhibited significant deterioration of leaf tissue.

Second of the factors was the canopy cover under which the lupines grew. We defined two categories: (1) lupines growing under large openings in the canopy (sun plants – most treatments) and (2) lupines growing under nearly complete overhead canopy cover from black oak trees or sprouts (shade plants – treatment F).

The third factor included four miscellaneous variables, three of which potentially affected plant growth and a fourth that potentially affected larval growth. These four variables asked the following questions. (1) Were the lupines water stressed (G)? Water-stressed plants had not released seeds and exhibited significant wilting and drooping of leaves. Plant tissue was not obviously deteriorating. (2) Were the plants infected with a powdery mildew (H)? This common infection most frequently infected plants late in the growing season (Dirig 1994). (3) Were the plants growing in a soil with O and A horizons (I)? At Indiana Dunes, as in many sand savannas, wild lupine typically grew on a soil that contains 1–2 cm of organic-rich soil above the sandy substrate. However, lupines also grew on dune slopes and eroded areas lacking the O and A horizons. (4) In this treatment, three *Lasius neoniger* ants tended larvae (J). *L. neoniger* were the ants most frequently observed tending Karner blue larvae during 1994 at Indiana Dunes (B. Edinger, personal communication). The lupine leaves used in this treatment were sun-grown leaves, mainly plants in seed, but included some stems that did not flower. We added a little dilute honey solution to the bottom of the cups in this treatment as supplemental food for the ants.

To test the effects of leaf nitrogen content on larval growth, we selected single, uneaten leaflets from leaves eaten by six 7- to 8-day-

old and six 12- to 13-day-old larvae within each treatment and dried the foliage to constant weight. We then measured leaflet total nitrogen content, by percent weight, by combustion in a LECO FP428 instrument. This instrument combusts the sample in a pure oxygen atmosphere at 850°C and then measures percent nitrogen by a thermal conductivity cell.

In mid-July, near the end of the larval phase, we gathered leaves from the field for each treatment. These leaves were transported to the laboratory in airtight boxes containing moist paper towels. Leaves were weighed, dried to constant weight, and then re-weighed. We calculated the ratio 1− (dry weight/wet weight) to estimate leaf field water content.

In data analysis, following significant ($P < 0.05$) analysis of variance, groups were compared using Tukey's multiple-comparison test (Norusis 1992). Following significant Kruskal-Wallis tests, groups were compared using a nonparametric multiple-comparison test (Zar 1984). Mean values of data are expressed ±1 SE.

Results

Larval growth is summarized in Fig. 1. Weight (mg) and length (mm) were related by the general equation:

$$\ln(\text{weight}) = \beta_0 + \beta_1 \ln(\text{length})$$

Slopes (β_1) differed significantly among treatments ($F_{9,438} = 3.16$, $P < 0.001$) with larvae from treatments B (nonflowering) and J (ants) gaining weight relatively more rapidly than length (higher β_1) in comparison to treatment G (water stressed) (Table 2).

Larval duration, or number of days from egg hatching to pupation, varied significantly as a function of feeding treatment ($F_{9,79} = 15.43$, $P < 0.0001$) (Fig. 2). More than 70% of larvae survived to pupation in all treatments except A (first year) (55%) and E (senescent) (46%) (heading to Table 1).

Sexual differences can confound the results in Fig. 2. Therefore, we used multiple-classification analysis of variance (Norusis 1992) to calculate deviations from the overall mean larval duration associated with feeding treatment and larval sex. Both feeding treatment

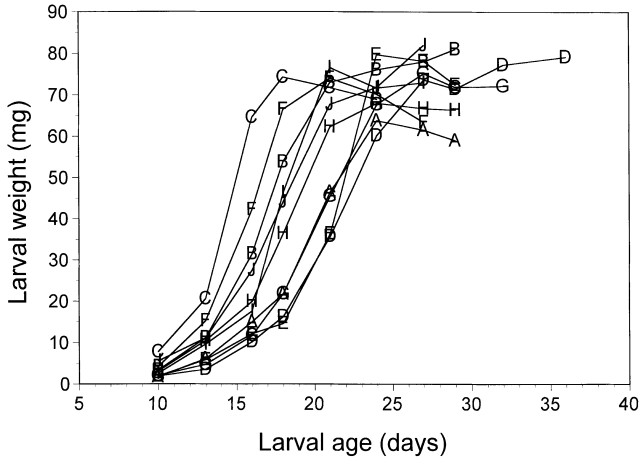

Fig. 1 Larval weight (mg) as a function of larval age posthatching (days). *Letters* on growth curves are feeding treatments (see Table 1)

Table 1 Lupine types fed to Karner blue larvae. Initial $n = 12$ for all treatments except *J* for which $n = 10$. Number of larvae surviving to pupation: *A* 6, *B* 11, *C* 9, *D* 11, *E* 5, *F* 11, *G* 10, *H* 10, *I* 9, *J* 7

Treatment	Phenological stage					Canopy cover		Other treatments			
	First year	Non-flowering	Flowering	Seed	Senescent	Sun	Shade	Water stressed	Mildew infection	Sandy soil	Ants
A First year	X					X	X				
B Nonflowering		X				X					
C Flower			X			X	X				
D Sun/seed				X		X					
E Senescent					X	X					
F Shade/seed				X			X				
G Water stressed		X		X		X		X			
H Mildew				X		X			X		
I Sand		X		X		X				X	
J Ants		X		X		X					X

Table 2 Slope (β_1) and intercept (β_0) of lines describing the relationship between ln(larval weight) in milligrams and ln(larval length) in millimeters. Significance: *slopes for treatments with the same letter* do not differ from each other (Tukey's test, $P < 0.05$). Differences in *n* from Table 1 reflect the fact that a few larvae that died just before pupation are included here. Larval length range: 2.0–14.2 mm

Treatment	β_1	β_0	*R*	Number of larvae	Significance
A First year	2.718	−2.641	0.974	8	a, b
B Nonflowering	3.099	−3.547	0.980	11	a
C Flower	2.882	−3.074	0.976	10	a, b
D Sun/seed	2.845	−3.027	0.985	10	a, b
E Senescent	2.991	−3.341	0.981	6	a, b
F Shade/seed	3.019	−3.294	0.967	11	a, b
G Water stressed	2.656	−2.586	0.979	10	b
H Mildew	2.745	−2.732	0.982	11	a, b
I Sand	2.847	−2.966	0.985	10	a, b
J Ants	3.169	−3.611	0.948	9	a

($F_{9,59} = 22.6$, $P < 0.001$) and sex ($F_{1,59} = 20.6$, $P < 0.001$) were significant factors in the analysis of variance. Treatment by sex interaction was not significant ($F_{8,59} = 0.46$, $P = 0.879$). After adjusting for the effect of sex, the order of effect of feeding treatment on larval duration remained the same as in Fig. 2 (data not shown). After adjusting for the effect of feeding treatment, mean larval duration for males was 2.8 days less than for females. Overall, mean number of days from egg laying to adult emergence was 41.5 ± 0.4 (SE) ($n = 76$, range 35–49). This corresponds well to field observations of time spans between peaks of first and second broods of adults: 37–41 days in 1995 and 44–52 days in 1996 (R. Knutson, personal communication). We derive these data from mark-release-recapture studies of the Karner blue at several sites at Indiana Dunes National Lakeshore.

Significant differences occurred among feeding treatments in the ratio of final larval weight (weight gain) to area of leaf eaten over the entire larval period (Kruskal-Wallis $\chi^2_9 = 44.5$, $P < 0.0001$) (Fig. 3a). Significant differences also occurred in total leaf area eaten by larvae (Kruskal-Wallis $\chi^2_9 = 45.6$, $P < 0.0001$) (Fig. 3b). Larval duration was not correlated ($P > 0.05$) with either the weight gain per leaf area eaten or the total leaf area eaten while a larva (Table 3).

Because mesophyll thickness can affect the total amount of food plant material ingested per area of leaf eaten, we also examined whether mesophyll thickness varied systematically with habitat or plant characteristics. No correlations were significant ($P > 0.05$, $n = 136$) between average mesophyll thickness and percent canopy cover over the plant, number of leaves per plant, leaf diameter, lupine density, depth of soil O and A horizon, stem diameter, or stem length. Mesophyll thickness also did not differ significantly ($t = 0.15$, $P = 0.88$) between plants infected with powdery mildew (0.576 ± 0.012 mm, $n = 37$) and not infected (0.574 ± 0.010 mm, $n = 90$). The absence of significant habitat or plant effects on mesophyll thick-

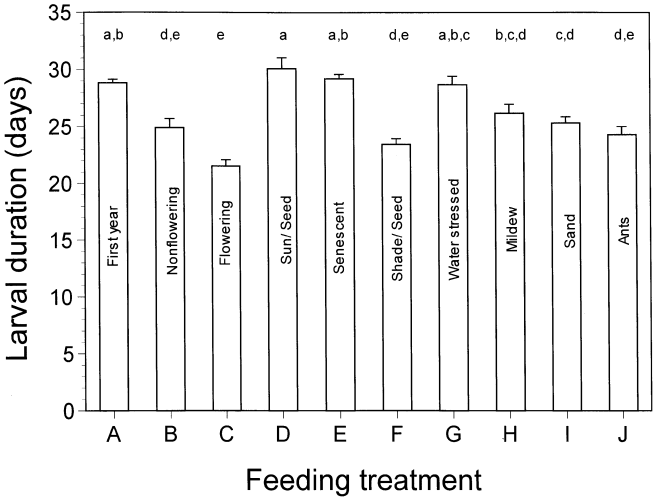

Fig. 2 Larval duration (±1 SE) (days) as a function of feeding treatment. *Treatments with the same letter above the bar* are not significantly different from each other (see Table 1 for *n*)

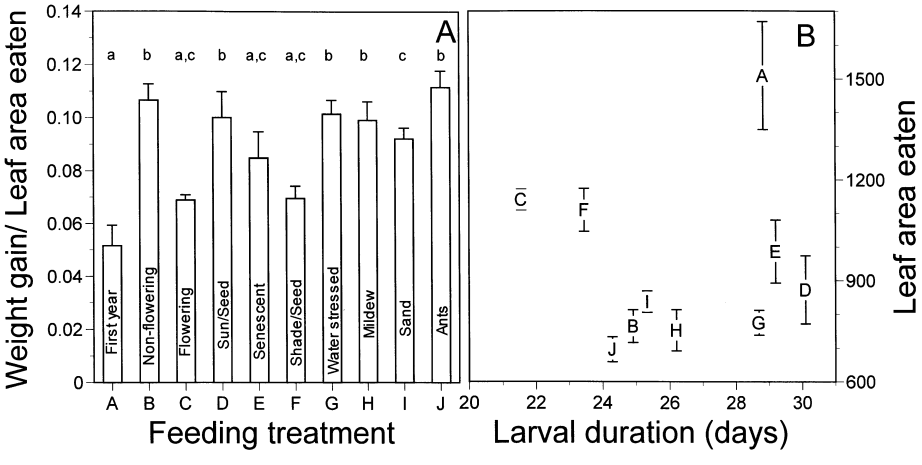

Fig. 3 a Ratio of final larval weight (mg) to total leaf area eaten as a larva (mm^2) (±1 SE). *Treatments with the same letter above the bar* did not differ significantly. **b** Total lupine leaf area (mm^2 ± 1 SE) eaten during the larval phase versus larval duration (days). Treatments that were not significantly different from each other were: (A, C, D, E, F, I); (B, D, E, G, H, I, J). See Table 1 for *n*

Table 3 Pearson correlations (*r*) among lupine leaf characteristics, larval characteristics, and feeding patterns ($n = 10$). Data were averaged within a feeding treatment before correlations were calculated

First variable	Second variable	*r*	*P*
Larval duration (days)	Leaf area eaten by larva (mm^2)	0.05	0.89
	Number of holes eaten in lupine by larva	0.35	0.32
	Average hole size eaten in lupine (mm^2)	−0.15	0.68
	Lupine leaf total nitrogen content (%)	−0.76	0.01
	Larval weight gain/leaf area eaten (mg/mm^2)	0.09	0.82
	Lupine leaf water percent	−0.27	0.46
Leaf area eaten as larva (mm^2)	Lupine leaf total nitrogen content (%)	0.02	0.96
	Lupine leaf water percent	0.63	0.05

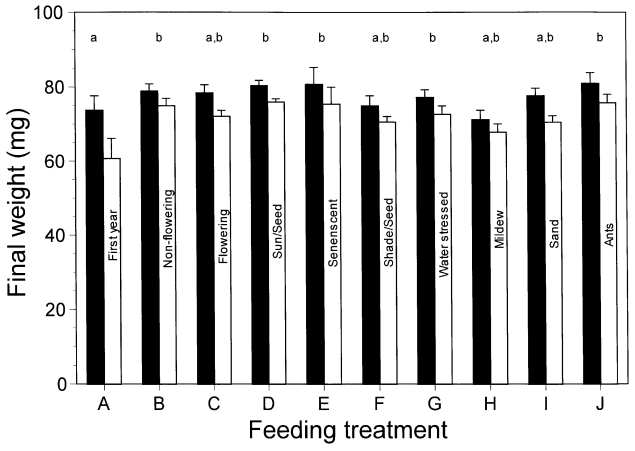

Fig. 4 Effect of feeding treatment on final larval weight (*filled bars*) and final pupal weight (*open bars*) (±1 SE). *Treatments with the same letter above the bar* did not differ significantly in final pupal weight; no significant differences occurred for final larval weight

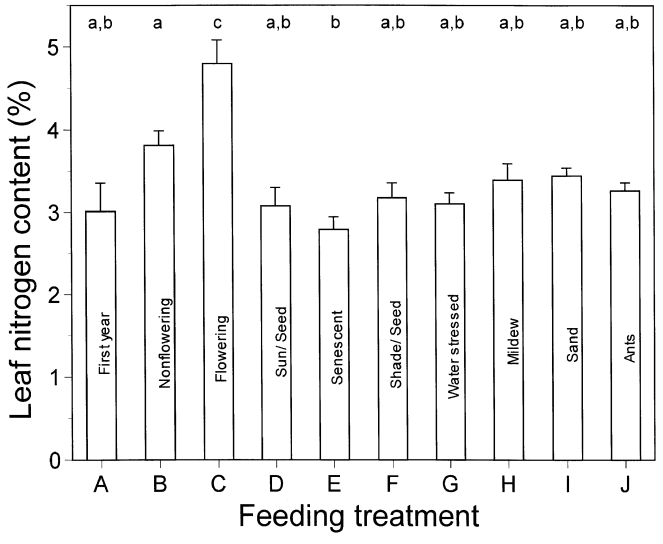

Fig. 5 Differences among feeding treatments in average percent total nitrogen content of leaves (±1 SE). *Treatments with the same letter above the bar* did not differ significantly

ness suggests that leaf area is an adequate estimator of food intake.

No significant differences existed, among feeding treatments, for final larval length ($F_{9,81} = 1.7$, $P = 0.11$) (data not shown) or for final larval weight ($F_{9,81} = 1.7$, $P = 0.11$) (Fig. 4). Larval sex did not significantly affect final larval weight in a two-way analysis of variance ($F_{1,67} = 3.8$, $P = 0.06$ for sex and $F_{9,67} = 1.3$, $P = 0.28$ for feeding treatment). The average final male larval weight (75.8 ± 6.6 mg, $n = 42$) over all feeding treatments was not significantly different ($t = 1.9$, $P = 0.06$) from the average final female larval weight (78.7 ± 7.1, $n = 36$). However, the intersexual weight differences were close to being statistically significant in both analyses.

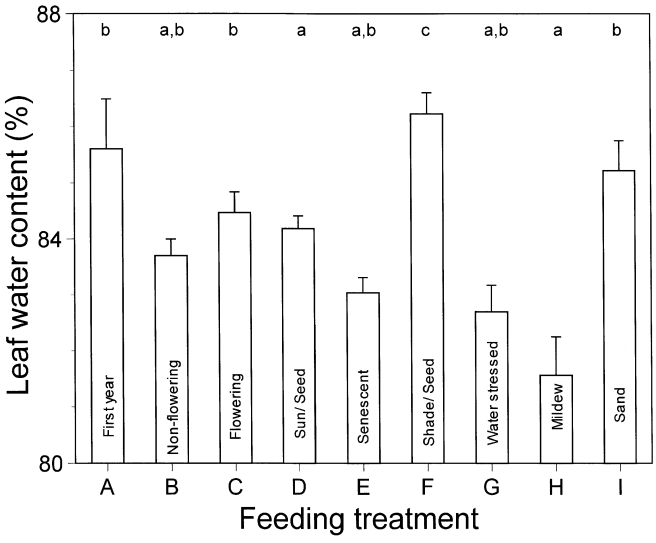

Fig. 6 Differences among feeding treatments in percent leaf water content. At the time of testing, leaves used in treatment J were the same as in treatment B and are omitted. *Treatments with the same letter above the bar* did not differ significantly

Significant differences in pupal weight existed among feeding treatments ($F_{9,74} = 3.3$, $P = 0.002$) but this mainly reflected the significantly lower pupal weight of feeding treatment A, the first-year leaves (Fig. 4). Although significant differences existed among feeding treatments for length of time spent as a pupa ($F_{9,68} = 2.1$, $P = 0.04$), only two feeding treatments, D and J, differed significantly from each other (data not shown).

The percent nitrogen content of leaves differed significantly among feeding treatments ($F_{9,68} = 7.8$, $P < 0.0001$) (Fig. 5). Feeding treatments also varied in percent field water content of lupine leaves (Kruskal-Wallis $\chi^2_8 = 47.9$, $P < 0.0001$) (Fig. 6). Larval duration was significantly, and negatively, correlated with percent lupine nitrogen content but not with percent field water content (Table 3). In addition, the leaf area eaten was not correlated with leaf nitrogen content but was significantly correlated with leaf water content.

Discussion

The growing conditions of wild lupine affect the growth rate of Karner blue larvae. This interaction can help explain observed patterns of Karner blue oviposition and larval distribution, especially across gradients of shade in oak savannas. In this study we examined how well lupine leaves from ten common habitat and phenological conditions supported Karner blue larval growth. Larvae feeding on these typical lupine variants exhibited significant differences in larval duration (range of means 21.6–30.1 days) or time from egg hatching to pupation (Fig. 2). Final larval and pupal weights did not generally differ significantly among the feeding treat-

ments (Fig. 4). Thus, faster development, but not increased final size of larvae or pupae, is a likely advantage of eating the most favorable of these ten *L. perennis* variants. More rapid larval development, in turn, should increase larval survivorship due to decreased predation and parasitism. Perhaps a more important advantage of the faster larval development, however, is avoidance of senescent lupines which become common as the second brood progresses (Dirig 1994).

Several key differences in larval growth rates occur among the feeding treatments (Fig. 2). First is the significantly faster growth of larvae eating leaves of shade-grown lupines that had just gone to seed (F) than of larvae feeding on similar sun-grown lupines (D). Lupines in seed are a common variant during most of the second larval brood (Dirig 1994). In the field, however, direct effects of temperature on larval development could offset the intrinsic growth advantage offered by these shade-grown lupines. For example, third-instar solitary caterpillars of the buck moth, *Hemileuca lucina*, exhibited a 34% increase in relative growth rate between 20°C and 25°C and a 70% increase between 25°C and 30°C (Stamp and Bowers 1990). Larvae of the tiger swallowtail, *Papilio glaucus*, developed 15–35% faster in sunny exposures than when not directly exposed to the sun (Grossmueller and Lederhouse 1985). In comparison, the Karner blue larval period was completed 22% more rapidly on shade-grown foliage than on sun-grown foliage. We do not know whether cooler shade temperatures in the field would counteract this 22% growth rate differential. Previously, we showed, however, that the percentage of lupines with late-instar feeding damage was greater for shade-grown plants than for sun-grown plants (Grundel et al., in press). That result is consistent with the intrinsic positive effect of shade host plant quality exceeding a possible negative effect of cooler shade temperatures. Moreover, it is not even certain that higher temperatures consistently exert an intrinsically positive effect on Karner blue larval development. For example, in Michigan, Lawrence (1994) concluded that temperatures in very open, xeric sites were incompatible with successful Karner blue larval development.

In a second important comparison, treatments A–E represent a continuum of lupine phenological age. Within this continuum, duration reached a minimum for larvae fed leaves from flowering plants (C). Larvae on first-year (A) and senescent plants (E) not only grew slowly but also had poorer survivorship (Table 1). In Ontario, Boyonoski (1992) reported that the percentage of *L. perennis* plants in flower peaked in areas of intermediate shading. These areas allowed about 70–80% of maximum light to reach ground level. The percent flowering plants was significantly lower in both very open (100% of maximum light) and shaded (45% of maximum light) sites. Preferentially ovipositing in areas of intermediate canopy cover (Grundel et al., in press) is, therefore, consistent with placing eggs in areas of the highest concentration of the highest-quality phenological variant, flowering plants. In addition, we found flowering plants present later into the season in shaded areas than in openings. As with the faster larval growth on shade-grown lupines (F) than on sun-grown lupines (D), this can be an advantage for oviposition preferentially occurring in shaded areas despite lupine abundance being higher in the most open areas.

In a third set of comparisons, larvae were subject to feeding treatments that we anticipated might slow growth but often did not. For example, postflowering leaves infected with powdery mildew (H) supported more rapid larval development than did comparable, uninfected lupines (D). Non-water-stressed lupines growing on sand (I) were not significantly poorer in supporting larval growth than similar plants growing on soil with an organic O and A horizon (B and D). Because wild lupine is a nitrogen-fixing species, the absence of organic material in the soil will not necessarily affect plant nitrogen levels (Fig. 5), a key correlate of growth rate (Table 3). Nonetheless, the abundance of mature *L. perennis* is low on purely sandy substrates and the germination of seeds and survival of seedlings is poor (N.B. Pavlovic and R. Grundel unpublished data). Thus plant nutrient quality is less a consideration than is plant demography in determining the usefulness of these low-nutrient soils as sites for restoration of Karner blue populations. Also, lupines on sandier soils should be more susceptible to water stress. Larvae feeding on water-stressed plants (G) grew slowly (Fig. 2). Water stress often results in low growth rates due to inhibitory changes in the protein and allelochemic profiles of the plant (Mattson 1980).

The presence of ants (J) did not slow the growth rate compared with two control groups (B and D). Not only did ant-tended larvae develop rapidly (Figs. 1, 2) but these larvae also exhibited a relatively steep rise in weight as length increased (Table 2) and a high ratio of weight gain per leaf area eaten (Fig. 3a). More rapid larval growth in the presence of ants has been reported for other lycaenid larvae (Cushman et al. 1994). It represents an advantage of ant tending beyond a previously documented lower disappearance rate for ant-tended Karner blue larvae (Savignano 1994).

Larvae can grow faster by eating more of a given lupine variant per unit time or by receiving more critical nutrients per unit of leaf consumed. A complex combination of these two possibilities can account for the observed differences in larval duration. Larvae with the greatest weight gain per leaf area eaten did not consistently exhibit the shortest larval duration (Fig. 3a, Table 3). Therefore, rate of food intake must also play an important role in determining larval duration. Larval duration though was not significantly correlated with total lupine leaf area eaten (Fig. 3b, Table 3). Duration was negatively correlated, however, with lupine leaf nitrogen concentration (Fig. 5, Table 3), suggesting a central role for nitrogen concentration in the determination of duration, as has been documented for other Lepidoptera (Mattson 1980; Scriber and Slansky 1981;

Scriber 1984). Nonetheless, more than just nitrogen content determined the amount of lupine consumed since the amount eaten was not correlated with the average nitrogen content of the leaves but was positively correlated with field leaf water content (Table 3). This positive relationship between consumption rates of lupine and water content suggests simply that for a caterpillar to obtain sufficient nutrients it must eat more plant material if that plant material has a high water content (Slansky 1993). The fact that water content is positively associated with assimilation efficiency of food may help explain the significantly faster growth of larvae on shade-grown plants (F) than on sun-grown plants (D) despite similar nitrogen concentrations and phenological stage of development. Thus, the ecological milieu and the phenological stage of the host plant undoubtedly act together to influence host plant quality.

The growth advantage of eating shade-grown lupine can help explain the relative overuse of shade-grown lupines both by ovipositing females and feeding larvae in the field. Thus, lupine abundance, which is greatest in open areas, is not the sole arbiter of habitat quality. Instead, a landscape mixture of sun and shade benefits this endangered species by allowing a trade-off between host plant availability and quality. The pace of lupine development will also depend on shading and will affect synchronization between larval stage and the favorable flowering lupine phenological stage, particularly in the second brood. Synchronization between resources and the insect life stages that use those resources is a challenge faced by insects in temporally variable environments (Weiss et al. 1993). Thermal, topographic, and light environments interact with yearly climatic variation to decrease the predictability of resources. Insects respond by spreading themselves or their progeny across thermal, topographic, and light gradients. Therefore, successful conservation planning must provide sufficiently wide segments of these gradients. This seems true for the Karner blue butterfly and canopy cover gradients. We know that openings are important for this species because males prefer such areas and because lupine is most abundant there (Grundel et al., in press). Here we have learned why moderately shaded areas may benefit this species as well. In addition, sandy soils often characterize Karner blue habitat. These sandy soils affect the conservation planning equation by accentuating the effect of canopy openings and hot temperatures on water stress in the lupines. This furthers the benefit of shaded areas.

Today, Karner blue populations are persisting in unshaded habitats (Andow et al. 1994b). Nonetheless, we believe that canopy heterogeneity, or sufficient shade heterogeneity from shorter vegetation, is a key for long-term viability of Karner blue populations, as it is for other butterfly species (Singer and Ehrlich 1979; Weiss et al. 1988; McGarrahan 1997). This shade heterogeneity is critical for the success of larval Karner blues since it regulates the availability of wild lupine variants for a butterfly whose larval stages nearly completely span the yearly growth, flowering, and senescence of a single host plant species growing in sandy soils.

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