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Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover

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Abstract

The Karner blue butterfly *Lycaeides melissa samuelis* is an endangered species residing in the Great Lakes and northeastern regions of the United States. Increased canopy cover is a major factor implicated in the decline of the Karner blue at many locales. Therefore, we examined how the butterfly's behavior varied with canopy cover. Adult males at Indiana Dunes National Lakeshore used habitat under canopy openings for nearly 90% of their activities; females used openings and shaded areas more equally. The frequency of oviposition on the sole host plant, wild lupine *Lupinus perennis*, was highest under 30–60% canopy cover even though lupine was more abundant in more open areas. Larvae fed preferentially on larger lupine plants and on lupines in denser patches. However, lupines were generally larger in the shade. Therefore, shade-related trade-offs existed between lupine abundance and distribution of larval feeding and oviposition. Also, heterogeneity of shading by sub-canopy woody vegetation was greater at oviposition sites than at sites where lupine did not grow. Given the importance of shade heterogeneity, a mixture of canopy openings and shade, on a scale similar to daily adult movement range, should be beneficial for this butterfly. Published by Elsevier Science Ltd. All rights reserved

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1. Introduction

The Karner blue butterfly *Lycaeides melissa samuelis* Nabokov (Lycaenidae) lives in savannas and barrens mainly in the Great Lakes region of North America and in eastern New York state. Nineteenth century records noted large populations and high densities at this sub-species' type locality of Karner, near Albany, New York (Dirig, 1994). Today, however, the Karner blue is listed as endangered in the United States and was extirpated in 1991 in Canada (Captive Breeding Specialist Group, 1992; Andow et al., 1994a; Dirig, 1994; Packer, 1994). As is true for many other butterflies, especially monophagous species, researchers associate the decline of the Karner blue with habitat conversion to human use and with the disruption of historic disturbance regimes (New, 1991, 1993; Clough, 1992; Morris et al., 1994). Indeed, the decline of the Karner blue butterfly in the Midwestern United States coincided with the

succession of much of its remaining oak savanna habitat to denser woodland owing to the cessation of fires historically set by Native Americans and to the contemporary suppression of wildfires (Curtis, 1959; Nuzzo, 1986; Lorimer, 1993).

The distribution of the Karner blue butterfly is considerably restricted compared with the range of its larval host plant, wild lupine *Lupinus perennis* (Dirig, 1994). Therefore, additional significant factors, besides presence of the host plant, may characterize the butterfly's preferred habitat. Understanding the interactions among lupine abundance, habitat structure, and Karner blue behavior and fitness is fundamental for preventing further declines and for setting habitat restoration goals. For example, Packer, 1994 implicated lack of detailed knowledge of habitat requirements, and a resulting lack of effective land management, in the recent extirpation of the Karner blue in Ontario, Canada during a series of droughts.

Our study addresses the question of quality habitat for the Karner blue butterfly. We pay particular attention to the effect of shade from trees which can be

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detrimental to lupine and Karner blue abundance (Boyonoski, 1992; Andow et al., 1994b). By studying the preferred levels of sun and shade for this species, goals for restoration of savanna at forested and scrubby sites can be better defined in Karner blue conservation efforts.

2. Methods

2.1. Study organism and sites

The Karner blue butterfly overwinters as eggs that hatch in April and May. After passing through four larval instars and pupating, adults of the first brood emerge in May and June. Eggs oviposited by first brood females hatch in June and July. Second brood adults emerge from July through September. Eggs from these second brood adults overwinter.

We studied the Karner blue in black oak Quercus velutina savanna communities at Indiana Dunes National Lakeshore, at the southern tip of Lake Michigan (41° 36·5′ N, 87° 13′ W) (Wilhelm, 1990). This savanna community exists on a series of sand dune complexes left by the retreating lake during the past 14500 years (Chrzastowski and Thompson, 1992). Four sites (areas = 200, 20, 70, and 110 ha including interspersed marshes) were selected where nearly all mature trees are black oak.

Larvae begin feeding on lupine leaves about two weeks after the plants appear in April. Flowering starts about two weeks later (Dirig, 1994; Swengel, 1995). Reproductive plants are usually in flower then go to seed and begin senescing during the second brood larval period. We refer to discrete clumps of lupines as plants although these clumps may contain more than one genet (Boyonoski, 1992; Grigore, 1992).

2.2. Data collection and analysis

We collected data on adult Karner blue activities, from May through August 1993 between the hours of 0930 and 1600. After sighting a butterfly, observers waited 30 s before beginning time budget observations and noted wing wear patterns to reduce repeat observations of an individual. Observers then recorded behaviors, at 1 min intervals for 10 min, in the following categories: (1) butterfly resting on a plant or substrate other than lupine (REST), (2) butterfly flying or hovering near the level of herbaceous vegetation (FLY), (3) a butterfly inserting its proboscis into a flower was classified as nectaring (NECTAR), (4) butterfly on lupine (LUPINE), and (5) all other activities (MISC). We also recorded the distance moved during each minute as <0·5, 0·5–2, 2–10, 10–25, or >25 m. For females observed ovipositing, or crawling over lupines, we

extended observations beyond 10 min until oviposition-related behaviors ended. However, for preparing a time budget, we only used observations during the first 10 min. Using this technique of observation some types of behavior were probably under-recorded. For example, males were more active fliers and were more likely to be lost by the observer. Sequential observations of behavior are typically not independent (Hejl et al., 1990). Therefore, for some analyses below we use only the first behavioral observation within the 10 min period plus any observations different from the observation made at the previous minute.

To distinguish lupines selected for feeding from those not selected we measured size and density characteristics for 75 plants fed upon by late instar larvae and the nearest plant without larval feeding damage. Average distance between plant pairs was 0·92 m, a distance we often observed larvae to move.

We evaluated the effect of canopy cover on lupine abundance using two methods. In 1993 we ran sets of five parallel 50 m transect lines, separated by 5–10 m, across study sites. These transects were centered in areas where lupine and Karner blue butterflies were common and ran into more heavily wooded areas where both were scarce (number of sets = 12, 2, 4, 2 for sites 1–4, respectively). Under each meter segment of each transect line we recorded whether lupine was present or absent and then assigned the segment to one of five conditions: (1) no overhead canopy cover (0%) in an area larger (>10 m radius) than the circumference of the canopy of a mature black oak tree ('large opening'), (2) no overhead canopy cover in an area c. 5–10 m in radius ('small opening'), (3) 1–49% overhead canopy cover present within 5 m, (4) overhead canopy cover 50–90%, and (5) overhead canopy cover >90%.These data also allowed us to estimate canopy cover distribution across our study sites.

In June 1994, we again evaluated the effect of canopy cover on lupine abundance (number of transects = 14, 7, 6, 4 for sites 1–4, respectively). Transects, 25–100 m long, were placed across a lupine and Karner blue area. At 5 m intervals along each transect, we measured canopy cover in the four cardinal directions using a spherical densiometer (Lemmon, 1956) and averaged the four readings. For each 1 m segment, lupine presence was recorded within 1 m on each side of the transect to give an index of abundance (0–10) for each 5 m interval.

Shading of herbaceous vegetation can come from canopy trees and from sub-canopy woody vegetation. To evaluate the importance of the sub-canopy woody vegetation we measured woody vegetation within pairs of 10 m radius plots, one centered at a known oviposition point and one in the nearest lupine-free area. We counted the total number of woody stems <2·5 cm dbh within a 4 m radius subplot and the number of black oak sprouts <2·5 cm arising directly from a living or

dead tree within the entire 10 m radius plot. Counts of both types of < 2·5 cm dbh stems were standardized to a per ha basis and summed to yield an overall density of small woody stems.

To estimate expected canopy cover over nectaring sites across the whole study area, we weighted the percentage of each of the five canopy categories, at each site, by the percent of all nectaring observations made at that site and then summed these weighted percentages across sites. Finally, in mid-July, we assessed the effect of canopy cover on larval feeding on lupines in shaded areas and in openings. Presence or absence of feeding damage, and whether feeding damage was from early or late instars, was recorded for each lupine stem examined.

Independence of frequencies of observations across variables was evaluated by χ^2 tests. *F*- or *t*-tests were used to determine significance of differences among population means. Data are presented as means ± 1 SE.

3. Results

3.1. Adult time budget and habitat use

The proportions of adult behaviors spent in REST, FLY, NECTAR, and LUPINE differed significantly between sexes and between broods (Fig. 1). Males flew more frequently than females and females visited lupine and nectared more frequently than males. Both sexes visited lupine and nectar plants more frequently in the first brood. The patterns of behavior did not vary significantly (χ^2, $p > 0.05$) as a function of shading (full shade, intermediate, full sun), butterfly wing condition (fresh, moderate wear, major breaks), cloud cover (clear, partly cloudy, overcast), wind speed, time o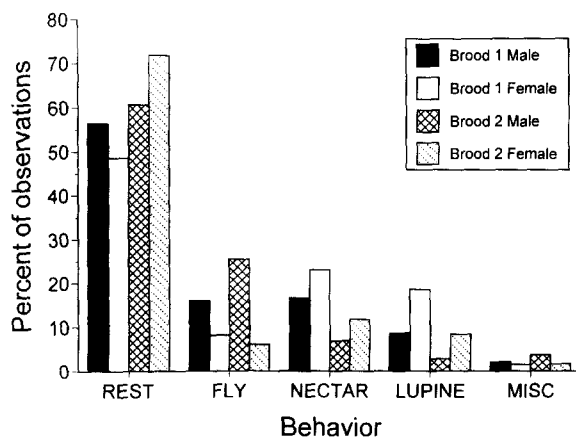f day and temperature (*F*, $p > 0.05$). Of course, wind and temperature do affect adult butterfly behavior. However, we attempted to observe only under conditions of low wind and warm temperatures. The results indicate that limiting observations to such conditions did help to prevent wind and temperature from dictating behavioral patterns.

Adult males moved more often than females and over significantly greater distances during 1 min observation periods ($\chi_3^2 = 273·0$, $p < 0.001$). For example, 45·8% of male movements ($n = 763$) were > 10 m, including 14·3% > 25 m, but only 8·4% of female movements ($n = 573$) were > 10 m.

Second brood males and females differed significantly in use of different categories of tree canopy (Fig. 2). Although the four sites differed in the distribution of the five categories of tree canopy cover ($\chi_{12}^2 = 518·3$, $p < 0.001$), males and females still differed consistently in their preferences for these categories. At each site, both sexes used openings in the canopy significantly more than expected in relation to their availability. Also, at each site females used shaded areas more frequently than did males, and males used openings more frequently than did females (χ^2, $p < 0.05$). Overall, female use of different canopy categories was related to lupine abundance (Spearman rank correlation $r_s = 0.9$, $p = 0.037$) but male use was not ($r_s = 0.7$, $p = 0.188$).

Canopy cover over nectar sites differed significantly from expected for both males ($\chi_4^2 = 82·6$, $p < 0.001$) and females ($\chi_4^2 = 27·1$, $p < 0.001$). Although significant differences existed between the sexes, both sexes preferentially nectared in openings (Fig. 3).

3.2. Characteristics of oviposition sites

All ovipositions were single eggs although a female did occasionally place eggs at different locations on a
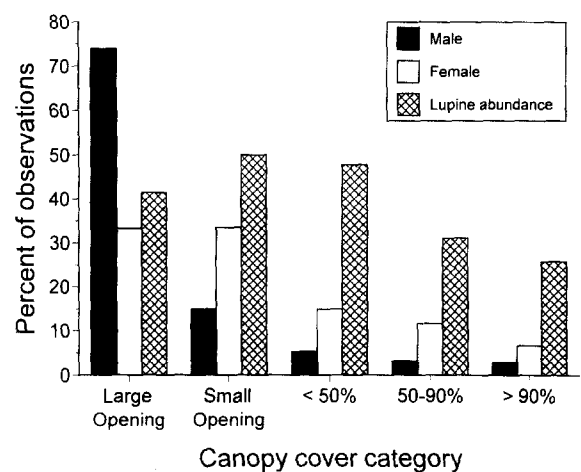

Fig. 1. Time budget of adult Karner blue butterflies ($n = 598, 490, 941$, and 1344 min for Brood 1 male, female, Brood 2 male, female; $n = 415$ butterflies). Differences were significant between sexes ($\chi_3^2 = 53·0$, $p < 0.001$) and between broods ($\chi_3^2 = 13·8$, $p = 0.003$).

Fig. 2. Male ($n = 204$ individuals, 672 new observations) and female ($n = 200$ and 1036) habitat use and percent lupine cover ($n = 911, 545, 608, 1256, 1394$ m transect intervals) as a function of canopy cover. Males and females differed significantly in use of canopy categories ($\chi_4^2 = 271·1$, $p < 0.001$).

single plant (n = 111 from 34 butterflies). All 24 ovipositions by first brood females were on L. perennis leaves, petioles, or stems. For 79 ovipositions by second brood females, only 19 (24·1%) were on lupines and 45 were on grassblades, five on dead twigs, one on leaf litter, and nine on non-lupine plants. However, second brood females always visited a nearby lupine, or lupine fragment, before ovipositing elsewhere (distance to the nearest lupine = 46·6 mm ± 4·0; n = 37). Placing eggs away

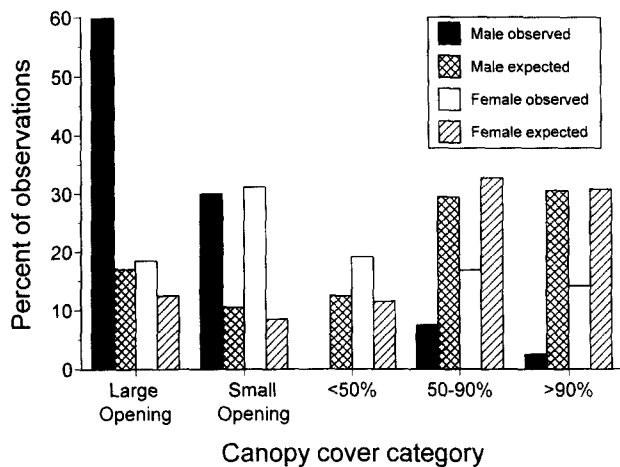Fig. 3. Relationship of canopy cover over observed nectar sites to expected use (males n = 80; females n = 260). Male and female distributions differed significantly ($\chi^2_4 = 53·0, p < 0·001$).
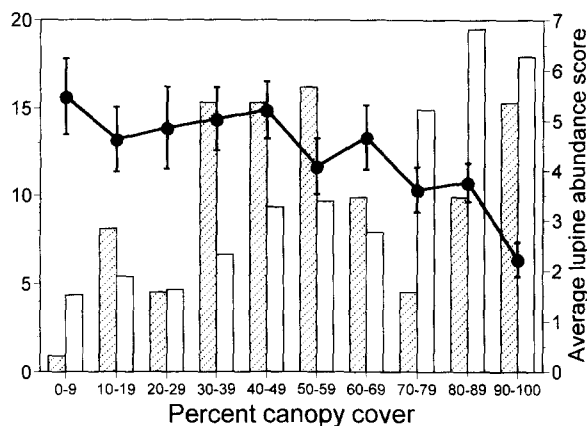

Fig. 4. Distribution of oviposition sites (n = 111) (stipled bars) and mean (± SE) lupine abundance score (line) as a function of overhead canopy cover (n = 27, 37, 26, 32, 43, 46, 36, 55, 77, and 73 in order of increasing canopy cover). Open bars represent expected use which differs significantly from actual use ($\chi^2_9 = 20·3, p = 0·017$).

from the host plant agrees with the general trend of site selection for overwintering butterfly eggs observed by Wiklund (1984).

Average canopy cover at oviposition sites was 54·8% ± 2·3 (n = 111) (Fig. 4). Cover over oviposition sites in the second brood was significantly higher (60·3% ± 2·5, n = 87) than in the first brood (34·7% ± 3·4, n = 24) ($t = 6·1, p \not> 0·001$). Oviposition was infrequent in the most open areas and exceeded expected frequency most consistently between 30–60% canopy cover. Lupine abundance declined with increasing canopy cover ($r = -0·23, n = 452, p < 0·001$).

Canopy cover at a subset of oviposition sites was significantly lower than at nearby lupineless sites (Table 1). Total number of small woody stems < 2·5 cm dbh for lupineless plots and oviposition plots did not differ significantly. However, these woody stems often grew in clumps such as when a black oak tree sprouted basally. The average number of stems per clump was significantly higher in oviposition plots than in lupineless plots.

3.3. Larval use of lupine plants

Plants with feeding damage were larger (longer, thicker stems and larger leaves) and were locally more abundant than undamaged plants ($p < 0·05$, t-test). Leaf size, in turn, was negatively related to sun exposure, the largest leaf of randomly selected lupines growing on northern exposures of dunes being significantly larger (78·8 mm ± 2·0, n = 37) than those on the southern, sun-exposed side (70·8 ± 2·2, n = 39) ($t = 2·6, p = 0·01$).

Lupines growing in large openings had the lowest percent of stems with feeding damage, followed by lupines in the shade, and in small openings (Table 2). Lupines in large openings also had the lowest percent of late instar feeding damage, followed by lupines in small openings, and in the shade.

4. Discussion

Wiklund (1977) proposed that butterflies require at least three types of habitats—for mating, for breeding or oviposition, and for foraging or nectaring. These behavior-specific habitats can be spatially separate and structurally different. The Karner blue butterfly exhibited such behavioral separation of habitat use in relation to

Table 1

Comparisons of woody cover surrounding oviposition sites and nearby sites lacking lupine. Stems are woody stems of all species < 2·5 cm dbh. Significance based on paired t-test (n = 23, except for per cent black oaks sprouting, n = 21)

	Oviposition plots	Lupineless plots	t	p
Per cent canopy cover	55·8 ± 4·7	69·4 ± 4·7	2·8	0·01
No. stems / ha	12 471 ± 2207	12 917 ± 1648	0·2	0·86
Per cent black oak trees sprouting	38·8 ± 0·9	15·0 ± 0·6	3·3	0·003
Mean no. stems/clump	2·30 ± 0·11	1·53 ± 0·06	6·2	< 0·001

canopy cover. Males consistently used openings, especially large openings, implying that large openings served as primary mating and nectaring habitat (Figs. 2 and 3). Males were more likely than females to spend their time flying across these openings (Fig. 1) although these males spent most of their time resting on vegetation, not patrolling their habitat (Scott, 1975, 1982). Females spread their time more evenly across canopy covers concentrating oviposition in moderately shaded areas, especially in the second brood (Fig. 4).

The larval preference for larger lupines, with higher local density, is similar to that documented for some other butterfly larvae (Damman and Feeny, 1988; Bourn and Thomas, 1993). The preference for larger plants can help explain the use of shaded areas for oviposition by Karner blues since lupine leaves that received less direct sunlight were larger. However, lupine density decreased with shading. Similarly, although oviposition and larval feeding were relatively high on shade-grown plants, lupine abundance was negatively correlated with canopy cover (Fig. 4, Table 2). In at least two ways, therefore, a trade-off exists between lupine quality and quantity. This is much as Rausher (1979) described for three Aristolochia-feeding swallowtail butterflies. He too concluded that swallowtails could find sun-grown plants more readily than shade-grown plants. The greater opportunity for egg laying on sun-grown Aristolochia outweighed lower larval growth rates or survivorship on those plants. In comparison with the swallowtails, Karner blue females balanced the trade-off between lupine quantity and quality by more frequently selecting shade-grown plants. The sandy soils at Indiana Dunes might accentuate the effect of sun and, by increasing levels of water stress with heating, negatively affect plant quality and account for the trade-off selected by the Karner blue. As a counter against this effect of sun and soil, Karner blue oviposition across the shade gradient will provide lupines over a range of phenological stages for their larvae, much as has been described for the checkerspot butterfly Euphydryas editha in the western United States (Singer and Ehrlich, 1979; Weiss et al., 1988). For example, in hot years, many lupines in the largest openings will be senescent before many second brood larvae pupate. Lupines in the shade, which are typically behind sun-grown plants phenologically, might, on the other hand, still be in flower or in seed and would be higher quality food for the larvae.

Table 2
Percent of lupine stems with feeding damage as a function of shading

	All feeding damage	Late instar damage	n
Large openings	4·87	1·49	3821
Small openings	6·05	2·26	5280
Shade	5·80	2·37	3585

The oak savanna habitat of this region has changed significantly in the 150 years since extensive settlement by Europeans began. Auclair (1976) documented a typical situation in southern Wisconsin where about three-quarters of the total savanna acreage was converted to agriculture, one-quarter developed into forests due to decreased fire frequency, and almost no area remained as savanna. Nuzzo (1986) estimated a typical 20–40 year period for conversion of oak savanna to closed oak forest in the absence of fire. The subsequent loss of open and heterogeneous canopy has been postulated to be deleterious for the Karner blue butterfly. The evidence here supports that hypothesis.

Shade heterogeneity can be present at many strata. In this study we have emphasized shade provided by canopy trees. However, black oaks can vigorously resprout after burning; trees that die or are injured from other causes often do not resprout (Henderson and Long, 1984). This resprouting can result in post-fire habitats that are open, or heterogeneous, in the canopy but shaded by the smaller woody vegetation. Comparisons between areas where oviposition occurred and nearby areas where lupine did not grow indicated that shade heterogeneity at lower strata may also affect habitat quality for the Karner blue (Table 1). The oviposition sites not only had more open canopies than the lupineless sites but the smaller woody vegetation differed between the sites as well. The total density of the smaller woody vegetation was similar between the oviposition and lupineless plots but that vegetation was present in fewer, larger clumps at oviposition sites, mainly due to basal sprouting of standing black oaks. The overlap in foliage caused by clumping means that more light should reach the ground and there should be larger patches of shade and sun in the oviposition areas. Thus we have evidence for a benefit of, or preference for, shade heterogeneity at two strata within woodland habitats. Herbaceous vegetation is a third shade-producing stratum. It may be the key component in those few locales where significant Karner blue populations are surviving in homogeneous, open habitats such as mowing-maintained airport fields (Andow et al., 1994b).

Woodland management policies that do not promote opening of canopies often negatively affect butterflies exploiting seral stages within the successional progression from grassland to woodland (Warren, 1985; Greatorex-Davies et al., 1992; Morris et al., 1994; Sparks et al., 1994). The usual reason given for the decline in butterfly diversity in areas with canopy closure is that most temperate butterflies are sun loving or shade intolerant (Greatorex-Davies et al., 1993). The Karner blue should not be categorized as strictly shade tolerant or shade intolerant; in fact, this species benefits from the canopy heterogeneity that defines the oak savanna (Packard, 1993). Questions still remain, however, concerning the necessary scale for that

heterogeneity. Based on mark-release-recapture studies of the Karner blue we do know that >90% of individuals at Indiana Dunes moved >200 m between captures (R. Knutson pers. comm.). Maximum distance between capture locations was <400 m for >90% of butterflies in a Wisconsin study (Bidwell, 1995). Although the Karner blue's range may vary with habitat structure, providing canopy heterogeneity within <200 m of population centers is a prudent conservation measure. Conservation management for this species should aim to provide a landscape with large canopy openings, 25 m or more in diameter for adult males, and areas with 30–60% canopy cover for ovipositing females. Canopy openings will enhance habitat suitability for nectaring in both sexes. For locales that depend on prescribed fires as the main management tool, burn heterogeneity must be incorporated, if topography itself does not produce heterogeneity, to achieve a landscape of openings and shade. Multiple fires over a span of one to two decades are probably needed to return a forest to a savanna.

Acknowledgements

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