RESEARCH ARTICLE

Factors Affecting Host-plant Quality and Nectar Use for the Karner Blue Butterfly: Implications for Oak Savanna Restoration

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ABSTRACT: In the Midwestern United States, more than 99.99% of pre-settlement oak (*Quercus*) savanna has been lost due to agriculture and fire suppression. Thus, the restoration of this ecosystem is imperative to secure the biodiversity, which depends on oak savanna. In this study, we characterized factors affecting the host-plant quality and nectar use of the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) in Ohio. Past research has shown butterfly abundance to be correlated with host-plant quantity, habitat area, and nectar plant abundance. However, there is growing recognition that host-plant quality is important at small spatial scales. We measured host-plant quality by quantifying leaf nitrogen content for the first larval brood and a PCA analysis of nitrogen and water content for the second larval brood. Additionally, observations quantified adult female foraging rates. Our results for the first brood larval stage found no significant difference in leaf nitrogen between burned, mowed, and unmanaged treatments. We used Akaike's Information Criteria (AIC) to determine that host-plant quality for the second brood was primarily explained by herbaceous vegetation density followed by canopy cover and aspect. Greater herbaceous vegetation density, greater canopy cover, and flat/north aspects were associated with higher quality host-plants. Lower host-plant nitrogen for the second brood was accompanied by a greater adult foraging rate. Management of Karner blue habitats should include restoring areas with a compatible herbaceous structure and increasing historically abundant forbs, which provide nectar to second brood Karner blues. This ecosystem-based management should positively impact many species in this rare oak savanna community.

Index terms: AIC, host-plant, *Lycaeides melissa samuelis,* nitrogen, senescence

INTRODUCTION

Agriculture and fire suppression have lead to the loss of over 99% of Midwestern United States oak (*Quercus*) savanna (Nuzzo 1986), and the remaining savanna requires active land management and extensive restoration in order to be sustained (Leach and Givinish 1999; Peterson and Reich 2001). The success of restoration projects is often measured by the establishment of native plant species and the eradication of exotic plant species (e.g., Smith et al. 2004; Rayfield et al. 2005; Ruprecht 2006). However, vegetation structure and composition are also crucial for the habitat suitability of many animals. The majority of research assessing the response of animals to restoration is focused on bird species composition and reproductive success (Davis et al 2000; Brawn 2006; Thomas et al. 2006). Oak savannas have a diverse assemblage of animals of conservation concern, including rare invertebrates such as persius dusky wing (*Erynnis persius* Scudder), frosted elfin (*Incisalia irus* Godart), Edward's hairstreak (*Satyrium edwardsii* Grote & Robinson), and the Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov**).** Additionally, butterflies can be useful indicator species for the state of the environment (Ehrlich 2003; Ockinger et al. 2006) and species richness (Fleishman et al. 2005). Butterflies can also be indicators of early successional communities, which are often vulnerable to poor management practices. Therefore, there remains a great need to determine characteristics of high quality habitat for this taxonomic group while restoration projects proceed.

The federally endangered Karner blue butterfly (Karner blue)(Family Lycaenidae) has recently been reintroduced into the globally rare black oak/lupine (*Quercus/Lupinus*) savanna of Ohio, but the success of the reintroduction depends on the availability of suitable habitat, whose characteristics are not fully understood. Habitat studies of butterflies often correlate butterfly abundance with host-plant abundance (Fred and Brommer 2003), nectar species abundance (Schultz and Dlugosch 1999), and area of habitat (Moilaen and Hanski 1998; Bergman and Kindvall 2004). However, there is a growing recognition that other factors affect the habitat quality of butterfly species (Ellis 2003; Fred and Brommer 2003), and these factors are generally found at a small scale (Moilanen and Hanski 1998). One such factor is host-plant nutritional quality, but this variable has rarely been quantified under natural conditions. In particular, host-plant nitrogen levels have been identified to increase larvae growth rates (Tabashnik 1982; Mevi-Schutz et al. 2003), correlate

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Natural Areas Journal 28:210–217

with larvae survival (Lincoln et al. 1982; Ravenscroft 1994), increase egg production (Boggs 2003), and increase the number of host-ants protecting larvae of Lepidoptera (Baylis and Pierce 1991; Billick et al. 2005). Host-plant water content is similarly associated with positive relationships in larvae growth rates (Lincoln et al. 1982; Tabashnik 1982; Mevi-Schutz et al. 2003). Water availability is also related to the microclimate of host-plants. In addition to host-plant quality, nectar sources are important for increasing butterfly lifespan and fecundity (Fischer and Fiedler 2001), and further studies of nectar plant use in the field are required to improve our understanding of this resource.

In this study, we quantified high quality habitat for the Karner blue by examining factors affecting host-plant quality and quantifying the use of nectar resources in a restored oak savanna. In a lab setting, Grundel et al. (1998a) showed that Karner blue larvae growth is significantly faster on host-plants with higher leaf nitrogen, and they suggest leaf water content improves the ability of Karner blues to consume nutrients. Several studies focus on the impact of canopy cover on Karner blues and their host-plant (Grundel et al. 1998a, b; Maxwell 1998; Lane and Andow 2003), but other environmental variables related to the management of the Karner blue have not been tested. The objectives of our study were: (1) to directly compare the influence of herbaceous vegetation density, canopy cover, aspect, and prescribed burning on the host-plant quality of the Karner blue; and (2) to determine if the two distinct broods differed in their adult foraging rate or the amount of nitrogen available in host-plant leaves.

METHODS

Species of Interest

The Karner blue's host-plant, wild blue lupine (*Lupinus perennis* L.), is a perennial plant, which lives in partially shaded to open areas, nutrient poor soils, and thrives in disturbed areas (U.S. Fish and Wildlife Service 2003). Lupine produces blue to purple inflorescences in May, seed pods by June, and then leaves can become senescent. First brood Karner blue larvae feed on lupine during early May, pupate, and then emerge as first brood adults in May to mid-June. The second brood of the year hatches 5 to10 days after oviposition, larvae feed 3 to 4 weeks, pupate, and emerge as second brood adults throughout July. The second brood oviposits eggs which overwinter for nine months.

Study Area and Management

In 2005, Karner blues in Ohio occupied four sites located at The Nature Conservancy's Kitty Todd Preserve located in Lucas County, Ohio (41º 37' N, 083º47' W). This area reports a mean total precipitation of 840 mm per year, and mean temperatures range from –4.5 ºC in January to 22 ºC in July (NOAA 2005). Elevation ranges from 154-254 m, and soils are generally well-drained and sandy. The ecological community is globally rare black oak/lupine savanna, and dominant woody vegetation includes *Quercus velutina, Q. ellipsoidalis,* and *Q. alba* (NatureServe 2006). Herbaceous cover includes the grasses *Schizachyrium scoparium* and *Andropogon gerardii* and a large diversity of forb species.

Land managers divided each of the four Ohio Karner blue sites into thirds, with each third approximately equivalent in the number of lupine stems (totaling 12 individual treatment areas). Each third was then managed on a rotating annual cycle within each site. The cycle rotated treatments in the order of prescribed burning, mowing, and leaving areas unmanaged. Therefore, individual treatment areas were burned approximately every three years. In this particular year of study, mowed management treatments had been burned 1-2 years previously. The three unmanaged treatments had been burned four years ago, and one unmanaged treatment had not been burned in seven years due to low fuel loads. Prescribed burning was always performed during the winter dormant season, including November 2004 and March 2005 before our study. Mowing occurred in the spring season (March 2005).

Sampling Methods

In order to quantify the host-plant quality for Karner blues, we sampled the percent lupine leaf nitrogen for the first and second brood larval stages using a randomized block experimental design. Since the second brood larvae stage is suggested to be water-limited due to early lupine senescence in June and July (Maxwell 1998), we sampled leaf water content for the second brood larval stage. We also performed behavior observations in order to compare the foraging rates of the two broods.

We collected lupine leaf samples on 10 and 11 May 2005. Based on previous Karner blue emergence dates and weather conditions, 10 May was estimated as when larvae were likely to be abundant, and larvae and their feeding marks were visible at this time. All samples were taken between 11:30 and 18:00. Rain did fall as the last samples were taken from one site, but all other samples were taken during mild temperatures, 21-27 ºC, and when weather was dry for two or more days before sampling. Lupine tissue samples were chosen by generating random numbers in Microsoft Excel 2000 (Microsoft, Redmond, WA), which were used as indicators of compass degrees and the number of paces from the center of a management treatment (e.g., burned, mowed, unmanaged). Four leaf samples were taken from each management treatment at each of the four sites for a total of 48 samples. Ten grams of leaf material were needed for analysis of nitrogen content. To prevent lupine mortality, only lupine plants that covered >15% of a 1 m^2 quadrat were sampled. Samples were placed in paper bags and sent overnight to Brookside Laboratories, Inc. (New Knoxville, OH) to determine the percent weight of lupine leaf nitrogen. The laboratory utilized the AOAC 990.03 total combustion method (Gavlak et al. 2003) (combustion chamber: Carlo Erba 1500, oxidation at 1020 ºC, reduction, 650 ºC), and the percent nitrogen was measured by a thermal conductivity detector. In northwest Ohio, oak trees did not have leaves during early May, so there was no canopy cover during the first brood larval stage. Herbaceous vegetation was also minimal

at this time.

During the estimated peak of the second brood larval stage, 22 June 2005, we sampled leaf nitrogen using the same techniques as the first brood sampling, except that we chose samples based on differing aspects and canopy cover as well as management treatment. For each management treatment, we randomly selected samples on north/northwest and south/southeast aspects. These slopes ranged from 9-36 degrees. We also selected at least one sample from a flat area for each management treatment. From these leaf nitrogen sample locations, lupine leaves were also analyzed for leaf water content using methods similar to Grundel et al. (1998a). Water content samples were taken on 20 June between 13:00 and 15:30. Field weight of lupine samples were between 0.5 and 2.9 grams of leaf matter, which represented approximately 3-6 leaves. Leaves were immediately placed in pre-weighed airtight containers and held in a cooler until all samples were processed. Upon returning from the field, leaf samples were immediately weighed with their container, and put into a drying oven (Cenco, forced circulation incubator, 400 watts), at approximately 40 ºC for 48 hours. Samples were then weighed again in their containers to obtain a dry weight, and we used the formula from Grundel et al. (1998a) as follows: 100*(1 – (dry weight/field weight)) = % leaf water content.

A vegetation survey of these second brood sample locations occurred 24-25 June and included measurements of herbaceous vegetation density and canopy cover. A Robel pole was used to measure the structure of the herbaceous layer (Robel et al. 1970). The plastic pole was 2.3 cm in diameter, and we marked each half decimeter in height. The Robel pole measurement is taken at the greatest height at which a half decimeter mark can still be observed, and we averaged the measurements from the east and west of each sample location. This measurement represents the visual obstruction of vegetation (Robel et al. 1970), and previous studies have used this measurement for estimating the herbaceous structure of wildlife habitats (Dieni and Jones 2003; Durham and Afton 2003; Pitman et al. 2005). In our study, the Robel pole measured the amount of visual and solar obstruction due to the density of herbaceous vegetation surrounding lupine. Canopy cover was estimated visually within a 7 m radius of plant samples. Only one sampling point had greater than 75% canopy cover, so we classified samples as either open (0-15% cover) or shaded (16-100% cover). This is modified from Lane and Andow (2003), who used a third class between 76-100% cover.

For both broods, we had one to three trained observers systematically search all lupine areas when the weather was appropriate for surveys (Pollard and Yates 1993). When a Karner blue female was observed, we performed a 15-minute behavior observation. However, 16 of 121 second-brood observations were performed for only 10 minutes, since we originally anticipated a larger population of butterflies at this time. During behavior observations, we recorded the time spent foraging. If the Karner blue foraged at any time during a minute, the minute was counted as "foraging." This method accounted for brief lapses in foraging behavior, since Karner blues often spend a few seconds in-between floral resources, making it unusual that foraging occurred at exactly the 1-minute interval. Foraging was defined as when a butterfly was directly on a flower head and the proboscis was extended for any period of time. On the rare occasion that female Karner blues alighted on lupine flowers, we did not observe proboscis extension. To detect any correlation between foraging rate and temperature, a temperature data logger (HOBO, Onset Computer Corporation, Bourne, MA) was placed in an open, sunny area. The vast majority of Karner blues were found in open, sunny areas, so we were not concerned with the effect of canopy cover on temperature.

Analysis

SAS 8.01 was used for all data analysis (SAS Institute 2000). First brood percent nitrogen and herbaceous vegetation structure were analyzed using a factorial ANOVA with sites and management treatments as main effects. No interactions were included with herbaceous vegetation density measurements, since only four samples per management treatment were taken.

To analyze host-plant quality for second-brood larvae, we used Principal Components Analysis to find the best Eigenvector (PCA1) between lupine leaf nitrogen and water content. Candidate models included canopy cover (shaded or open), herbaceous vegetation density, aspect, and whether the management treatment was burned the year of our study. We combined north and flat aspects because we had relatively few flat samples. Since Grigore and Tramer (1996) found lupine had higher nitrogen in burned areas, we included burned treatments in the model as 0 or 1. Candidate models also included two interaction variables when the individual variables were included. We used Akaike's Information Criteria (AIC), corrected for small sample sizes (AIC_c), to find the best explanatory models (see, Dennis and Otten 2000; Gibson et al. 2004; Grossman et al. 2006). This maximum log-likelihood method of model selection quantifies model uncertainty and analyzes all possible interacting variables (Burnham and Anderson 2002). The lowest AIC_c value represents the best model, and all other models are considered relative to the best model. Akaike's weights give the plausibility that an individual model is the best, given the candidate model set (Burnham and Anderson 2002).

For the foraging analysis, we used a Generalized Linear Model (GLM) with a Poisson distribution and type III Wald tests to test whether the first and second brood differed in foraging rate. Under-dispersion in the Poisson model was corrected by using the SAS quasi-likelihood function to adjust the scale parameter based on the Pearson χ^2 (Quinn and Keough 2002).

RESULTS

All nitrogen and water content data had normal distributions, so no data transformations were performed. For the first brood leaf nitrogen sampling, we found no significant difference between management treatments (2-Factor ANOVA, df = 2, F = 0.27, p = 0.77; mean percent nitrogen ±

SE, burned = 4.64 ± 0.06, mowed = 4.71 ± 0.08, unmanaged = 4.72 ± 0.10), sites (df = 3, F = 2.73, p = 0.058) or the interaction of site and management treatment (df = 6, F = 0.80, p = 0.58).

For the second brood, a correlation analysis of water and nitrogen identified two outliers, which were well outside the 95% confidence interval and outside the general range of nitrogen and water values. These outliers were likely caused from processing errors, so these values were eliminated from all analyses. The Pearson's correlation between water and nitrogen was highly significant (n = 52, p < 0.0001, r = 0.55) and positive (Figure 1). The Principal Components Analysis of leaf water and nitrogen content showed an Eigenvalue for the first axis (Eigenvector) of 1.55, which explained 78% of the variance and corresponded to a factor loading of r = 0.71 for both variables.

The results of AIC_c analysis showed the two best models for explaining lupine nutritional quality during the second brood larval stage included herbaceous vegetation density, canopy cover, and aspect (n = 52, r^2 = 0.48 and 0.50) (Table 1). The best individual model also included the interaction of the three variables. These two best models had considerable support with a combined Akaike's weight of 0.67. Herbaceous vegetation density was positively associated with lupine nutritional quality and explained 37% of the variation by itself. Partial canopy cover increased the quality of lupine, and when added to herbaceous vegetation density, 45% of the variance was explained. South slope and the interaction effect combined to explain 50% of the variation, and south slopes had a negative effect. Burned management treatments were not included in the best AIC_c models (AIC_c < 2.0 from the best model), and explained only 2% of the variance by itself. A Pearson's correlation revealed herbaceous vegetation density was not correlated with aspect (n = 62, r = -0.23, p = 0.07) or canopy cover (n = 62, r = 0.14, p = 0.29). Herbaceous vegetation density did not differ between management treatments (2-Factor ANOVA, df = 2, F = 1.09, p = 0.34) or sites (df = 3, F = 1.06, p = 0.37) (Figure 2). There was significantly less host-plant nitrogen content for the second brood compared to the first brood larval stage (t-test, df = 105, t-statistic = 8.29, p < 0.0001) (Figure 3).

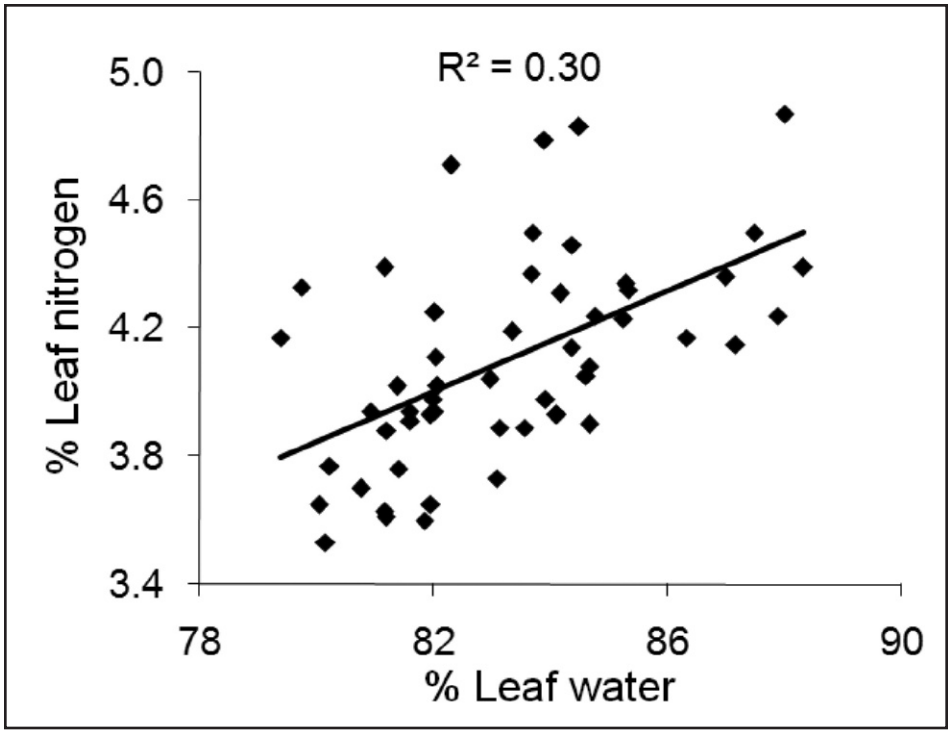

Figure 1. Pearson correlation of lupine leaf nitrogen, as percent weight, and lupine leaf water content, as percent weight.

We conducted 57 behavior observations (805.5 minutes) during the first brood and 116 observations (1643 minutes) during the second brood. Karner blues never foraged for greater than seven minutes during the first brood, but several Karner blues were observed foraging for the entire 15-minute observation during the second brood. The foraging rate of the second brood was significantly higher than the first brood (GLM, df = 1, χ^2 = 6.7, p < 0.010) (Figure 4) with sites as a covariate in the model. Foraging rate did not change with temperature (GLM, df = 1, χ^2 = 0.11, p = 0.74) when brood and sites were covariates in the model.

DISCUSSION

By examining factors affecting host-plant quality and quantifying nectar use of the Karner blue, we were able to identify important ecological variables, which can assist in ecosystem management and restoration for this endangered species. This study links experimental studies of host-plant nitrogen with small scale environmental variables, and generally demonstrates the importance of measuring localized vegetative attributes. Our study of environmental factors associated with host-plant quality complements studies showing how *L. perennis* abundance changes with environmental variation (Grigore and Tramer 1996; Smallidge et al. 1996) and, thereby, further characterizes high-quality habitat for the species. In particular, the management and restoration of ecosystems occupied by the Karner blue should aim at recreating the historical structure and composition of both the canopy and herbaceous layers of the community.

For our first objective, we found that herbaceous vegetation density was the primary correlate of host-plant quality for the second brood, while canopy cover and aspect contributed a relatively minor proportion of the variance. Prescribed burning had no effect on Karner blue host-plant quality for either brood, which contradicts previous findings (Grigore and Tramer 1996). However, our study concentrated solely on leaf nitrogen, while Grigore and

Table 1. Akaike's Information Criteria (AIC_c) results of second brood host-plant quality (n=52). Weight is Akaike's weight. Variables include herbaceous vegetation density (veg density), canopy cover (canopy), aspect, and two interaction effects denoted by an asterisk between the variables. ***Beta coefficients showed host-plant quality was positively associated with herbaceous vegetation density and canopy cover; south slopes had a negative impact on host-plant quality. Host-plant quality was determined through a PCA analysis of leaf nitrogen and water content.***

r^2	AIC_c	ΔAIC_c	Weight	Variables in Model
0.50	-9.6	0	0.35	veg density + canopy + aspect + aspect* veg density *canopy
0.48	-9.4	0.2	0.32	veg density + canopy + aspect
0.45	-7.8	1.8	0.14	veg density + canopy
0.45	-6.5	3.1	0.07	veg density + canopy + veg density *canopy
0.45	-6.5	3.1	0.07	veg density + canopy + burned
0.40	-2.7	6.9	0.01	veg density + aspect
0.41	-2.2	7.4	0.01	veg density + aspect + burned
0.37	-1.9	7.7	0.01	veg density
0.38	-1	8.6	0	veg density + burned
0.19	13.9	23.5	0	canopy + aspect + burned
0.17	14.1	23.7	0	canopy + aspect
0.09	17.5	27.1	0	canopy
0.11	17.5	27.1	0	aspect + burned
0.10	18.2	27.8	0	canopy + burned
0.07	18.5	28.1	0	aspect
0.02	21.1	30.7	0	burned

Tramer (1996) tested whole *L. perennis* plants, and plots had been unburned for an indefinite period. In our study, any increase in host-plant nitrogen due to burning may have been cancelled out by the lack of herbaceous vegetation density in some burned treatments, although this trend was not significant (Figure 2). We also recognize that burning can benefit *L. perennis* by increasing its biomass (Grigore and Tramer 1996), regardless of changes in host-plant quality.

Many butterfly species are affected by the timing of host-plant senescence (Cappuccino and Kareiva 1985; Weiss et al. 1988; Peterson 1997), and our PCA analysis represents a novel method to quantify senescence. Both leaf nitrogen and water content relate to the condition of plant tissue, but reflect different temporal influences on the plant. For instance, dehydration can cause plant leaves to temporarily curl, while nitrogen is a factor indicative of environmental conditions over the growing season. Phenology of individual plants (Grundel et al. 1998a) and water deficits can inhibit nitrogen-fixing of legumes (Engin and Sprent 1973). We discarded soil nitrogen as a confounding factor in our analysis, since *L. perennis* leaf nitrogen rises only slightly with fertilization (Reich et al. 2003) or with more organic soils (Grundel et al. 1998a). Instead, our results are consistent with microclimate effects, such as shade (Grundel et al. 1998a; Boughton 1999) and flat/north aspects (Fleishman et al. 1997) reducing water loss and, therefore, slowing senescence. Although the summer of 2005 displayed a period of drought conditions in Ohio, our methodology simultaneously compared the relative impact of several variables. Our results are also supported by Grundel et al. (1998a), who reported *L. perennis* under canopy cover to have a higher nitrogen content than other lupine plants.

Although moderate grazing is regarded as beneficial to early successional butterflies (WallisDeVries and Raemakers 2001), increased herbaceous vegetation density has also been positively correlated with butterfly density (Ellis 2003). Of course, early successional plants, such as *L. perennis,* need reduced woody plant cover in order to thrive (Smallidge et al. 1996), but the impact of an herbaceous layer on invertebrate species has rarely been tested. We cannot distinguish between the impact of microclimate and other possible correlates in our study (e.g., soil characteristics), but shade from herbaceous vegetation density certainly has the potential to prevent water loss in associated host-plants and soils. Little bluestem (*Schizachyrium scoparium*), dewberry (*Rubus villosus*), and bracken fern (*Pteridium aquilinum)* were the most common species providing herbaceous cover to host-plants in our study (Figure 5). However, *R. villosus* competes with lupine without active management (G. Haas 2006, The Nature Conservancy, pers. comm.), and *P. aquilinum* was observed to displace lupine in 2006. The importance of the herbaceous structure on host-plant quality warrants further investigation into which plant species positively and negatively impact lupine abundance and reproduction. Smallidge et al. (1996) did find large *L. perennis* populations to be associated with sweet fern (*Comptonia peregrina*) in transmission line right-of-ways, and *S. scoparium* is also abundant in remnant lupine populations in New York (B. Pickens, pers. observation). In Ohio oak savannas, *S. scoparium* and *C. peregrina* were historically abundant (Moseley 1928), but *C. peregrina* is now rare in the region. The decline of this robust, early successional, nitrogen-fixing species is just one example of how herbaceous vegetation has changed after nearly a century of fire suppression. Restoration and management of oak savanna, or pine barrens, should aim to maintain an herbaceous layer, which provides shade, but does not displace *L. perennis*. This management for host-plant quality should complement prescribed burning and the reduction of woody vegetation in order to increase host-plant quantity (Grigore and Tramer 1996; Smallidge et

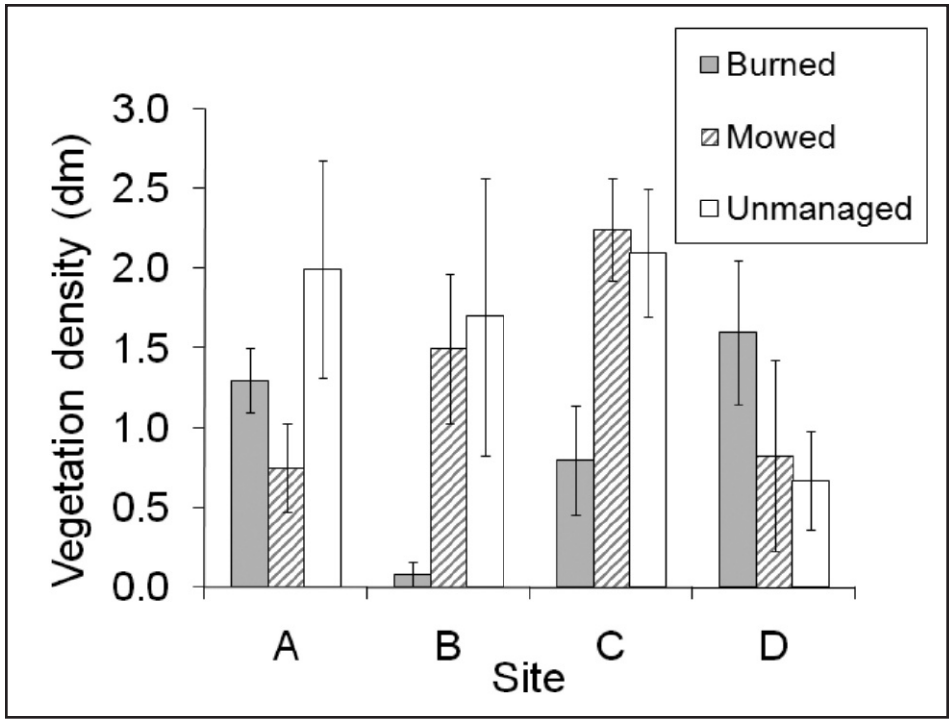

Figure 2. Herbaceous vegetation density, in decimeters, by management treatment. Error bars represent ±1 standard error.

al. 1996).

For our second objective, we found evidence that the first brood larvae have more host-plant nitrogen available, while the second brood dramatically increases their adult foraging rate. Lower host-plant nitrogen in the second brood is consistent with lower nitrogen levels found in *L. perennis* leaves after seed set (Grundel et al. 1998a). Experimental research shows that butterflies rely more on nectar sources when host-plant nutrition is low (Mevi-Schutz et al. 2003), and this is one hypothesis for the differential in Karner blue adult foraging rates. The second brood also seems to emerge when floral resources are at a peak for the season. Our foraging results contradict Grundel et al. (1998b), and this could be a result of differing methodologies, study years, or study locations. Our analysis did not support the possibility of temperature directly affecting Karner blue foraging rates. Regardless of the specific reason for the observed foraging rate differences, the high amount of nectar use during the second brood warrants management for nectar species at this particular time.

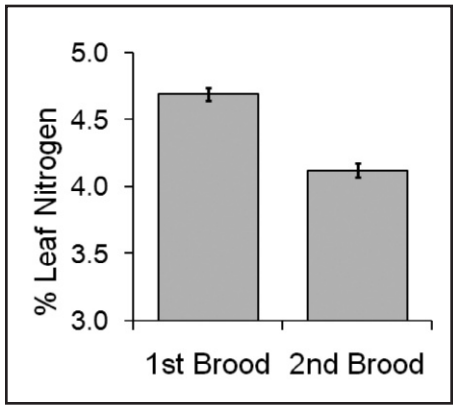

Figure 3. Lupine leaf nitrogen, as percent weight, versus Karner blue brood. Error bars represent ±1 standard error.

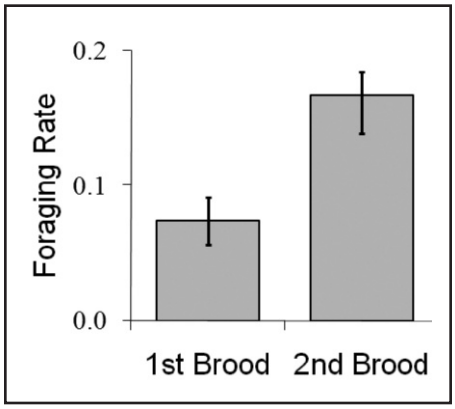

Figure 4. Foraging rate of female Karner blues, expressed by the proportion of time spent foraging (minutes foraging / total minutes observed), versus Karner blue brood. Error bars represent ±1 standard error.

CONCLUSION

Our study of host-plant quality and butterfly behavior complements traditional approaches of habitat studies by directly measuring small-scale variables. The comparison of multiple environmental variables found that herbaceous vegetation density, canopy cover, and aspect to all play important roles in determining host-plant quality for the Karner blue. Our results indicate that management and restoration of Karner blue habitat should include more than the addition of host-plants alone. This conclusion supports the current shift towards ecosystem-based management. Managing for the proper structure and composition of the natural community will likely benefit the many rare plants and animals found in this endangered ecosystem.

ACKNOWLEDGMENTS

The Ohio Department of Natural Resources, Division of Wildlife provided funding support for this project through a State Wildlife Grant; an additional small grant was provided by the Ohio Biological Survey. We are thankful for the many people and organizations that were supportive of this project: G. Haase (The Nature Conservancy), P. Tolson, and C. Ellsworth (Toledo Zoo) were especially helpful. We are grateful for the data collection efforts of E. Knurek, R. Kip, and M. Ricci; J. Bouzat and H. Michaels (Bowling Green State University) provided valuable insights and comments for this project. We thank C. Johnston, H. Harms, and two anonymous reviewers for their constructive comments which improved this manuscript. Endangered species permits from the U.S. Fish and Wildlife Service were obtained through the Ohio Division of Wildlife.

Bradley A. Pickens received a Master's of Science degree at Bowling Green State University and is currently a Research Associate at Louisiana State University. At

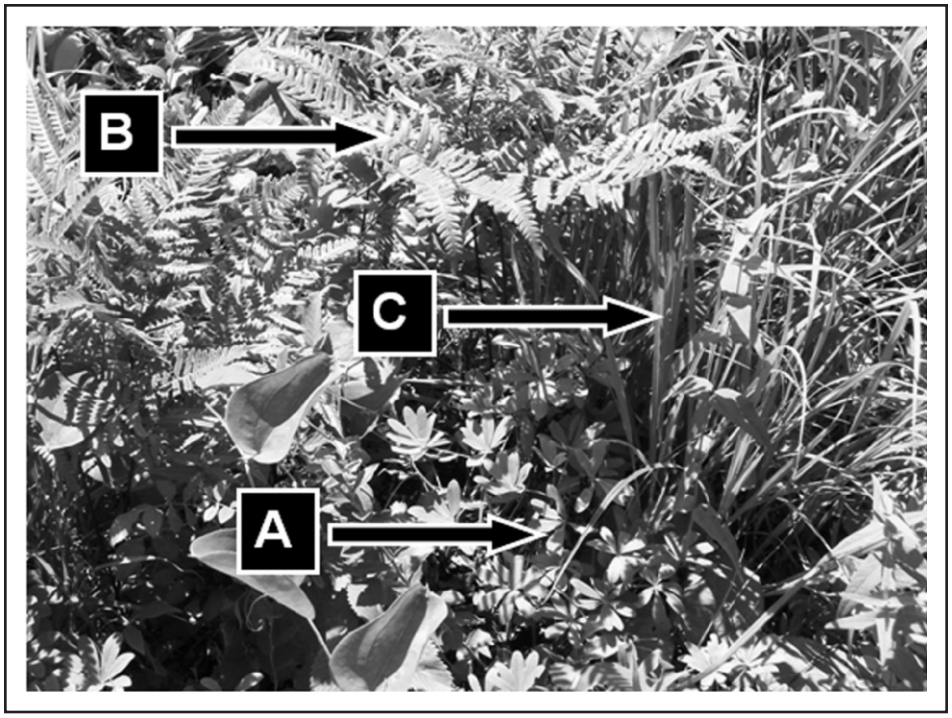

Figure 5. An example of *L. perennis* (A) being shaded by herbaceous vegetation density at Kitty Todd Preserve, Lucas County, Ohio. Plant species such as *Pteridium aquilinum* (B) and *Schizachyrium scoparium* (C) were commonly found alongside *L. perennis.* Photograph by Emily Knurek.

LSU, he continues to pursue his research interests by studying the habitat suitability and landscape ecology of birds in southwest Louisiana.

Karen V. Root is an Associate Professor in the Department of Biological Sciences at Bowling Green State University. Her research focuses on conservation biology for many taxa across a variety of scales, habitat assessment, population viability analysis, and reserve design.

LITERATURE CITED

Baylis, M., and N.E. Pierce. 1991. The effect of host-plant quality on the survival of larvae and oviposition by adults of an ant-tended Lycaenid butterfly *Jalmenus-Evagoras*. Ecological Entomology 16:1-10.

Bergman, K.-O., and O. Kindvall. 2004. Population viability analysis of the butterfly *Lopinga achine* in a changing landscape in Sweden. Ecography 27:49-58.

Billick, I., R. Brown, and J. Reithel. 2005. Importance of fertilization of host plants to ant tending and growth rates in *Glaucopysche lygdamus* (Lepidoptera: Lycaenidae). Annals of the Entomological Society of America 98:491-495.

Boggs, C.L. 2003. Environmental variation, life histories, and allocation. Pp. 185-206 *in* C L. Boggs, W.B. Ward, and P.R. Ehrlich, eds., Butterflies: Ecology and Evolution Taking Flight. The University of Chicago Press, Chicago.

Boughton, D.A. 1999. Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. Ecology 80:2727-2739.

Brawn, J.D. 2006. Effects of restoring oak savannas on bird communities and populations. Conservation Biology 20:460-469.

Burnham, K.P., and D.R. Anderson 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer Science+Business Media, New York.

Cappuccino, N., and P. Kareiva. 1985. Coping with a capricious environment: a population study of a rare Pierid butterfly. Ecology 66:152-161.

Davis, M.A., D.W. Peterson, P.B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas. 2000. Restoring savanna using fire: impact on the breeding bird community. Restoration Ecology 8:30-40.

Dennis, B., and M.R. Otten. 2000. Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. Journal of Wildlife Management 64:388-400.

Dieni, J.S., and S.L. Jones. 2003. Grassland songbird nest site selection patterns in northcentral Montana. The Wilson Bulletin 115:388-396.

Durham, R.S., and A.D. Afton. 2003. Nest-site selection and success of mottled ducks on agricultural lands in southwest Louisiana. Wildlife Society Bulletin 31:433-442.

Ehrlich, P.R. 2003. Butterflies, test systems, and biodiversity. Pp. 1-6 *in* C.L. Boggs, W.B. Ward, and P.R. Ehrlich, eds., Butterflies: Ecology and Evolution Taking Flight. The University of Chicago Press, Chicago.

Ellis, S. 2003. Habitat quality and management for the northern brown argus butterfly *Aricia Artaxerxes* (Lepidoptera: Lycaenidae) in North East England. Biological Conservation 113:285-294.

Engin, M., and J.I. Sprent. 1973. Effects of water stress on growth and nitrogen-fixing activity of *Trifolium repens*. New Phytologist 72:117-126.

Fischer, K., and K. Fiedler. 2001. Effects of adult feeding and temperature regime on fecundity and longevity in the butterfly *Lycaena Hippothoe* (Lycaenidae). Journal of the Leidopterists' Society 54:91-95.

Fleishman, E., A.E. Launer, S.B. Weiss, J.M. Reed, D.D. Murphy, and P.R. Ehrlich. 1997. Effects of microclimate and oviposition timing on prediapause larval survival of the bay checkerspot butterfly, *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae). Journal of Research on the Lepidoptera 36:31-44.

Fleishman, E., J.R. Thomson, R. MacNally, D.D. Murphy, and J.P. Fay. 2005. Using indicator species to predict species richness of multiple taxonomic groups. Conservation Biology 19:1125-1137.

Fred, M.S., and J.E. Brommer. 2003. Influence of habitat quality and patch size on occupancy and persistence in two populations of the Apollo butterfly (*Parnassius apollo*). Journal of Insect Conservation 7:85-98.

Gavlak, R., D. Horneck, R.O. Miller, and J. Kotuby-Amacher 2003. Soil, Plant and Water Reference Methods for the Western Region, 2nd ed. WREP-125, Western Region Extension Publication. Available online <http://cropandsoil.oregonstate.edu/nm/WCC103-manual-2003-table%20of%20Contents-pdf.pdf>. Accessed September 2007.

Gibson, L.A., B.A. Wilson, D.M. Cahill, and J. Hill. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. Journal of Applied Ecology 41:213-223.

Grigore, M.T., and E.J. Tramer. 1996. The short-

term effect of fire on *Lupinus perennis* (L.). Natural Areas Journal 16:41-48.

Grossman, G.D., R.E.J. Ratajczak, J.T. Petty, M.D. Hunter, J.T. Peterson, and G. Grenouillet. 2006. Population dynamics of mottled sculpin (Pisces) in a variable environment: information theoretic approaches. Ecological Monographs 76:217-234.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998a. The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly (*Lycaeides melissa samuelis)*. Oecologia 114:243-250.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998b. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85:47-53.

Lane, C., and D. Andow. 2003. Oak savanna subhabitat variation and population biology of *Lycaeides melissa samuelis (*Lepidoptera: Lycaenidae). Annals of the Entomological Society of America 96:799-809.

Leach, M.K., and T.J. Givinish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. Ecological Monographs 69:353-374.

Lincoln, D.E., T.S. Newton, P.R. Ehrlich, and K.S. Williams. 1982. Coevolution of the checkerspot butterfly *Euphydryas chalecedona* and its larval food plant *Diplacus aurantiacus*. Oecologia 52:216-223.

Maxwell, J.A. 1998. The conservation of the Karner blue butterfly, *Lycaeides melissa samuelis* (Nabokov): ecological studies on habitat creation and management. Ph.D. diss., University of Wisconsin-Madison, Madison.

Mevi-Schutz, J., M. Goverde, and A. Erhardt. 2003. Effects of fertilization and elevated CO2 on larval food and butterfly nectar amino acid preference in *Coenonympha pamphilus* L. Behavioral Ecology and Sociobiology 54:36-43.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503-2515.

Moseley, E. L. 1928. Flora of the Oak Openings. Ohio Academy of Science. Special Paper 20:79-134.

NatureServe. 2006. NatureServe Explorer: an online encyclopedia of life [web application]. Version 4.6. NatureServe, Arlington, Va.

[NOAA] National Oceanic and Atmospheric Administration. 2005. National Weather Service Forecast Office: climate data-Toledo, OH. National Oceanic and Atmospheric Administration, Asheville, N.C.

Nuzzo, V.A. 1986. Extent and status of midwest oak savanna: presettlement and 1985. Natural Areas Journal 6:6-36.

Ockinger, E., O. Hammarstedt, S.G. Nilsson, and H.G. Smith. 2006. The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. Biological Conservation 128:564-573.

Peterson, D.W., and P. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914-927.

Peterson, M.A. 1997. Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. Ecology 78:167-180.

Pitman, J.C., C.A. Hagen, R.J. Robel, T.M. Loughin, and R.D. Applegate. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. Journal of Wildlife Management 69:1259-1269.

Pollard, E., and T.J. Yates 1993. Monitoring Butterflies for Ecology and Conservation. Chapman & Hall, London.

Quinn, G.P., and M.J. Keough 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, New York.

Ravenscroft, N.O.M. 1994. The ecology of the chequered skipper butterfly *Carterocephalus palaemon* in Scotland. II. Foodplant quality and population range. Journal of Applied Ecology 31:623-630.

Rayfield, B., M. Anand, and S. Laurence. 2005. Assessing simple versus complex restoration strategies for industrially disturbed forests. Restoration Ecology 13:639-650.

Reich, P.B., C. Buschena, M.G. Tjoelker, K. Wrage, J. Knops, D. Tilman, and J.L. Machado. 2003. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. New Phytologist 157:617-631.

Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-297.

Ruprecht, E. 2006. Successfully recovered grassland: a promising example from Romanian old-fields. Restoration Ecology 14:473-480.

SAS Institute. 2000. Release: SAS 8.01 Edition. SAS Institute, Cary, N.C.

Schultz, C.B., and K.M. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231-238.

Smallidge, P.J., D.J. Leopold, and C.M. Allen. 1996. Community characteristics and vegetation management of Karner blue butterfly (*Lycaeides melissa samuelis)* habitats on right-of-way in east-central New York, USA. Journal of Applied Ecology 33:1405-1419.

Smith, M.A., C.D. Grant, W.A. Loneragan, and J.M. Koch. 2004. Fire management implications of fuel loads and vegetation structure in jarrah forest restoration on bauxite mines in Western Australia. Forest Ecology and Management 187:247-266.

Tabashnik, B.E. 1982. Responses of pest and non-pest *Colias* butterfly larvae to intraspecific variation in leaf nitrogen and water content. Oecologia 55:389-394.

Thomas, G., A.L. Holmes, S.L. Small, N. Nur, G.R. Geupel, and G.H. Golet. 2006. Abundance patterns of landbirds in restored and remnant riparian forests on the Sacramento River, California, USA. Restoration Ecology 14:391-403.

U.S. Fish and Wildlife Service. 2003. Karner Blue Butterfly Recovery Plan *(Lycaeides melissa samuelis)*. Department of the Interior, U.S. Fish and Wildlife Service, Great Lakes-Big Rivers Region (Region 3), Fort Snelling, Minn.

WallisDeVries, M.F., and I. Raemakers. 2001. Does extensive grazing benefit butterflies in coastal dunes? Restoration Ecology 9:179-188.

Weiss, S.B., D.D. Murphy, and R.R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas Editha*. Ecology 69:1486-1496.