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Ann B. Swengel

Scott R. Swengel

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FACTORS AFFECTING ABUNDANCE OF ADULT KARNER BLUES
(*LYCAEIDES MELISSA SAMUELIS*) (LEPIDOPTERA: LYCAENIDAE)
IN WISCONSIN SURVEYS 1987-95

Ann B. Swengel and Scott R. Swengel¹

ABSTRACT

At 141 pine-oak barrens in central and northwestern Wisconsin, 3,702 Karner blues (*Lycaeides melissa samuelis* Nabokov) were found in 81.1 hr of transect surveys during spring and 6,094 individuals in 116.6 hr during summer. Adults of five other closely related lycaenids occurred with Karner blues. The percentage of Karner blue males (of sexed individuals) correlated negatively with advancing date within brood, exceeded 50% on peak date within brood, but showed wide variability on a given date. Karner blues occasionally occurred up to 800 m from the nearest larval host, or in tiny, isolated host stands. However, all individuals were within 3-5 km of other larger Karner blue populations. Karner blue abundance significantly increased with decreasing latitude, increasing temperature, nearness to midpoint within brood, decreasing site canopy, increasing larval host abundance, and in summer compared to spring. Long-term monitoring sites showed dramatic but relatively similar fluctuations among broods (median of 2.8-fold change among ten brood pairs) that apparently varied by individual brood rather than season or year. Extensive dense host patches and dense Karner blues were in sites representing a diversity of management histories.

Restricted to eastern North America, the Karner blue (*Lycaeides melissa samuelis* Nabokov) is federally listed as endangered in the USA and considered extirpated in Canada (Andow et al. 1994). This butterfly has two full life cycles per year, feeds only on wild lupine (*Lupinus perennis* L.) (Fabaceae) as larvae range-wide, and overwinters as an egg. It has a rather narrow, generally east-west range at the northern end of lupine range, from eastern Minnesota through the Great Lakes states and southern Ontario to New England (Iftner et al. 1992, Bleser 1993, Dirig 1994, Packer 1994, Savignano 1994). In this paper, we present analyses of factors affecting Karner blue abundance on transect surveys. These results are useful for designing survey protocols and interpreting monitoring data.

METHODS

Transect surveys. Surveys occurred at 141 pine-oak barren sites in central and northwestern Wisconsin (43.5-46.8°N, 89.8-92.7°W). Sites were sam-

¹ 909 Birch Street, Baraboo, WI 53913.

pled because of their potential to support barrens-specialized butterflies. These sites represented a diversity of ownerships and land uses including government or private conservation reserves; government-owned forest reserves for timber harvest, some burned by wildfire and some used as recreation lands for off-road vehicle trails; rights-of-way for highways and powerlines; and military reservation.

We conducted transect butterfly surveys similar to the butterfly walk along like routes within each site each time (Pollard 1977, Swengel 1995, 1996a). Nomenclature here follows Miller and Brown (1981), with English names after NABA (1995). All observed butterflies were counted and identified to species, if possible. Karner blues were sexed, if possible, and their behavior when first seen was recorded. A new survey unit was designated (to the degree practical) whenever the habitat along the route varied by (1) management (type and/or years since last treatment), (2) vegetation type (wet, mesic, dry, "extra dry" sand; all pine-oak barrens were "extra dry" sand type), (3) vegetative quality based on diversity and abundance of native and exotic flora (undegraded, semi-degraded, highly degraded), and/or (4) estimated macrostrate canopy of under- and overstory (grassland <10%, open savanna 10–24%, closed savanna 25–49%, forest opening 50–75%; most but not all barrens had >9% canopy). A unit's management was coded based on the entire history of management observed or evident during the study, including combinations (e.g., burn+mow). A unit was in a "diverse" site if it contained contiguous non-forested and uncultivated habitats both wetter and drier than mesic; otherwise the site was rated "uniform." For each unit, we recorded temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying.

Statistical analysis. Analysis was done with ABstat 7.20 software (1994, Anderson-Bell Corp., Parker, Colorado). Statistical significance was set at $p < 0.05$. Before analysis, based on plant development (timing of leafout, above-ground sprouting, flowering, and seeding), we adjusted the survey dates to about similar phenology as follows: 1987 +10, 1988 & 1991 +14, 1989 0, 1990 -4, 1992 -14, 1993 -14 (through July) & -7 (after July), 1994 +4 (through June), 1994 0 (after June), 1995 -16 (through June) & -9 (after June). In comparisons **within** unit over time (monitoring abundance fluctuations), the peak raw number observed per flight period (or "brood") was used, if during main flight period, since survey route within unit was held constant. To allow valid comparisons **among** units, the survey totals were standardized into observation rates per hour per unit (i.e., an index of relative density). Units with Karner Blues were then categorized by rate into these four levels of density: >0/hr and <15/hr, ≥ 15 and <35, ≥ 35 and <65, and ≥ 65 .

For the parametric tests including Pearson Product-Moment Correlation Matrix, analysis of variance (ANOVA), and stepwise linear regression, the tested values (dependent variable) were log-transformed first to meet parametric assumptions better. ANOVA was used when valid analysis required only one or several independent variables. Stepwise linear regression allowed extensive multivariate analysis but assumed a progressive (correlative) effect for each independent variable. With most variables, this assumption was plausible (e.g., temperature, wind), while others could be manipulated to become a logical continuum (described below). But these continua are not necessarily the only valid ordination and regression would not necessarily detect a significant effect for bimodal or intermediate peaks.

The first regression included these types of variables: **geography** (latitude, longitude), **survey** (N surveyors - usually 2 but occasionally the first author alone, beginning time, time difference between beginning time and 12:00 CST, calendar and phenological date), **unit** (quality, canopy, site diversity),

weather (percent sunshine, average temperature, average wind speed), **flight period** (difference between survey date and midpoint of flight period observed in entire study as calendar and phenological dates; season - spring or summer); **year** (calendar, ranking of annual fluctuation - explained below), and **management** (unintrusiveness - explained below). The annual fluctuation variable ranked the years of survey data (if >2 units) based on mean unweighted observation rate in all units that year. Management types were ordered with consecutive codes along this continuum of intrusiveness: nothing long-term, recreation (vehicle trailsides), mowing, timber cutting, wildfire, rotational fire. Mixed managements (e.g., burn+mow) were placed between both types.

The second regression added two lupine variables: **lupine "core"** (3=unit in large landscape context of abundant lupines with numerous other lupine patches within 2 km; 2=on edge of such a core or in a smaller landscape area of lupine, with several lupine patches within 2 km; 1=isolated lupine patch) and **relative lupine abundance** based on these categories and arithmetic ratios: superabundant (100,000), abundant (10,000), common (1000), uncommon (100), rare (10), and absent. Some sites were categorized based on descriptions in Bleser (1993) and Leach (1993); values were unavailable for some sites.

The third regression added two management variables: **age class** (years since last treatment, if known) and an **intensity index** calculated as the unintrusiveness code x (age class+1). Age classes were coded as 0 (treatment since last growing season), 1, 2, and so on. For rotational fire, age classes >4 were lumped as 5+. Wildfire age classes ranged from 4 to 18, with >14 lumped as 15+. "Nothing" was coded as 20+, with no age class exceeding that. The third regression also added two lupine variables: **lupine patch size** and **volume** (relative abundance x patch size). It was difficult to define discrete sites (and therefore their size and lupine characteristics). The full extent of some lupine patches was inadequately demarcated because of their large size and spotty occurrence. The fourth regression added one lupine variable: **lupine uniformity** (1=very patchy to 4=very uniform).

RESULTS

During spring, we counted 3702 Karner blue individuals (2581 males, 941 females, 180 unsexed) in 81.1 hr and 141.5 km of transect surveys at 293 units and 6094 individuals (3929 males, 1846 females, 487 unsexed) in 116.6 hr and 225.3 km at 386 units during summer. Both actual (raw) survey totals and observation rates were valuable indicators of population size, as these correlated very strongly ($r=0.906$, $N=679$, $p=0.0000$). In regression, the number of surveyors showed a highly significant but unsurprising positive covariance with Karner blue rates (Table 1).

Flight period and sex ratio. The most strongly significant variable concerning adult timing was nearness to flight period midpoint in calendar date (Table 1), indicating a strong spike in numbers mid-flight. Season was significant in three of four regressions, with the rate tending to be higher in summer (Table 1), as shown in Shapiro (1974). Combining our survey data from years of more thorough date coverage with those from other sources, the spring flight has varied among the years in start date between 18 May and 1 June (Table 2), with peak date between 29 May and 14 June, and end date between 18 and 30 June (Table 2). During summer, the start date was 4-27 July, peak date 24 July-5 August, and end date 18 August-6 September (Table 2). Span within brood was 26-35 days in spring (summer 25-60), with the dura-

Table 1. Results of stepwise linear regressions of Karner blue observation rates (per hour, log-transformed) by 18 survey and site variables plus (1) one management variable, (2) one management and two lupine variables, (3) three management variables and four lupine variables, and (4) three management and five lupine variables. See "Methods" for specific variables. Variables with no significant results are not listed.

Regression	First Regression			Second Regression			Third Regression			Fourth Regression		
	N	r	p	N	r	p	N	r	p	N	r	p
	657	0.586	0.000	627	0.586	0.000	406	0.668	0.000	236	0.643	0.000
	Step	r	p	Step	r	p	Step	r	p	Step	r	p
Latitude	1	-0.479	0.000	1	-0.435	0.000	1	-0.613	0.000	1	-0.357	0.000
N surveyors	2	+0.285	0.000	2	+0.304	0.000	4	+0.251	0.000	4	+0.284	0.000
Annual fluctuation	3	+0.282	0.000	3	+0.289	0.000	2	+0.320	0.000	2	+0.356	0.000
Temperature	4	+0.210	0.000	4	+0.226	0.000	3	+0.209	0.000	7	+0.204	0.000
Peak-calendar date	5	+0.231	0.000	5	+0.238	0.000	7	+0.280	0.000	5	+0.228	0.000
Season	6	+0.638	0.000	6	+0.660	0.000	9	+0.577	0.000			
Canopy	7	-0.155	0.000	7	-0.164	0.000	5	-0.289	0.000	3	-0.329	0.000
Month-day	8	-0.481	0.000	8	-0.493	0.000	10	-0.413	0.000			
Year	9	+0.097	0.004	10	+0.093	0.009	6	+0.190	0.000			
Lupine core		—		9	+0.120	0.003						
Wind	10	+0.067	0.069	11	+0.082	0.025	8	+0.093	0.034			
Vegetative quality	11	+0.066	0.073									
Lupine abundance		—					11	+0.100	0.014			
Time of day	12	+0.063	0.075				12	+0.073	0.077			
% sunshine										6	-0.208	0.000
Habitat diversity										8	+0.092	0.094

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Table 2. Flight period details observed for the Karner blue: closest 1--2 survey dates in habitat and range before and after flight period, first and last dates adults were observed (a second date, marked *, is provided from Bleser [1993] if it increased the span of the flight period), first and last dates mating pairs were observed, peak date (when the most adults were seen), mean ± SD of percent males (m) out of sexed individuals on peak date, span of flight period, and years of markedly advanced (fast) and retarded (slow) phenology.

	surveys before flight	first date	first mating pair	peak date	peak date mean % m ± SD	last mating pair	last date	flight span (days)	surveys after flight	phen- ology
Spring										
1990	24 May	6 Jun 28 May*								
1991	15 May 20 May	23 May		29 May	77.2±13.2		28 Jun* 7 Jun 18 Jun*	31 15 26		fast
1992	20 May 21 May	26 May	2 Jun	2 Jun	74.1±16.1		10 Jun 30 Jun*	15 35		slow
1993	19 May 27 May	1 Jun		22 Jun	60.0±17.9	22 Jun	22 Jun	21		slow
1994	17 May 20 May	22 May	31 May	6 Jun	66.0±16.2	6 Jun	15 Jun	24		fast
1995	29 May 30 May	31 May		14 Jun	76.4±21.2		14 Jun	14		slow
all		22 May	31 May	2 Jun	70.8±18.8	22 Jun	30 Jun*	39		
Summer										
1989		5 Jul					18 Aug	44		
1990	28 Jun	20 Jul		1 Aug	53.4±15.8		1 Aug 10 Aug*	12 21		
1991		12 Jul 4 Jul*	12 Jul	24 Jul	51.2±14.7	24 Jul	24 Jul 19 Aug*	32 46		fast
1992		27 Jul	4 Aug	5 Aug	68.1±29.0	5 Aug	21 Aug	25		slow
1993		26 Jul	26 Jul	3 Aug	79.8±20.9	4 Aug	4 Aug	9		slow
1994		8 Jul	18 Jul	27 Jul	59.1±15.8	3 Aug	6 Sep	60	19 Sep	fast
1995		19 Jul	21 Jul	2 Aug	56.0±21.3	2 Aug	22 Aug	34	5 Sep	slow
all		4 Jul*	12 Jul	27 Jul	61.1±17.9	5 Aug	6 Sep	64		

Table 3. Summary information on blue flight periods within known Karner blue range in Wisconsin. Dates marked with * come from Kuehn (1983), Nielsen (1984, 1986), and Ferge (1990, 1991).

	first date	peak date	last date	span (days)
Karner blue	18 May*	27 Jul	6 Sep	111
Eastern tailed-blue	10 May	22 Aug	19 Sep	132
Western tailed-blue	22 May*	25 May	3 Jun*	9
Reakirt's blue	29 Jun*	—	17 Jul	19
Silvery blue	9 May*	25 May	3 Jun	25
Spring azure	28 Apr	3 Aug	6 Sep	131

tion from first spring date to last summer date ranging among years from 87 to 107 days (Table 3). The longer flight continuing after peak in summer may explain the significant negative correlation for date (month-day) in regression (Table 1). Although phenologically adjusted variables showed no significant effects in regression (Table 1), beginning, peak, and end dates appeared to vary among years in correspondence to phenological advancement or retardation (Table 2).

Five other blue species occurred in sites with Karner blues, all overlapping in adult flight timing (Table 3). The vagrant Reakirt's blue, *Hemiargus isola* (Reakirt), occurs sporadically in Wisconsin while the resident western tailed-blue, *Everes amyntula* (Boisduval), overlaps with Karner blues in Wisconsin only in their northwestern-most range (Opler and Krizek 1984). Found throughout the Karner blue's Wisconsin range (Opler and Krizek 1984), the silvery blue, *Glaucopsyche lygdamus* (Doubleday), appears scarce in central Wisconsin but regular and widespread in northwestern Wisconsin. The eastern tailed-blue, *Everes comyntas* (Godart), and spring azure, *Celastrina ladon* (Cramer), are frequently encountered and overlap broadly with the Karner blue in space and adult timing (Table 3). Both *C. l. ladon* (Cramer), single-brooded in spring, and *C. l. neglecta* (W. H. Edwards), multiple-brooded later in spring through summer, occur here and may be sister species (Wright 1995), but these two taxa overlapped in flight period and were not distinguished in the field. However, no *C. ladon* individuals were observed after May in two years (1992, 1995), implying that only *C. l. ladon* were found those years. In northeastern Wisconsin, outside the scope of this study, Karner blues have been documented within the range of a sixth species, the northern blue, *Lycaeides argyrognomon nabokovi* Masters (Bleser 1993).

The percentage of males (out of sexed individuals) correlated negatively with both calendar date and phenological date, more strongly with the latter: $r = -0.290$ and -0.355 respectively in spring ($N = 210$ units and 2581 males out of 3522 sexed individuals); $r = -0.335$ and -0.354 in summer ($N = 290$ units and 3929 males out of 5775 sexed individuals); $p = 0.0000$ for all (Fig. 1). Leach (1993) also found that percent males decreased as each brood progresses. Sex ratio varied greatly within a particular date (Fig. 1), always exceeding 50% males on peak date (Table 3). We observed 88 individuals in mating pairs, most on or before the date of peak observed numbers (Table 2).

Brood fluctuation. Regression showed significant effects for the annual fluctuation ranking and year (Table 1), suggesting strong variation among years. Fluctuations observed by independent Wisconsin research teams (Bleser 1993, Welch 1993, this study) displayed, despite high variance among sites, similarly shaped graphs (Fig. 2), with the only marked difference out of

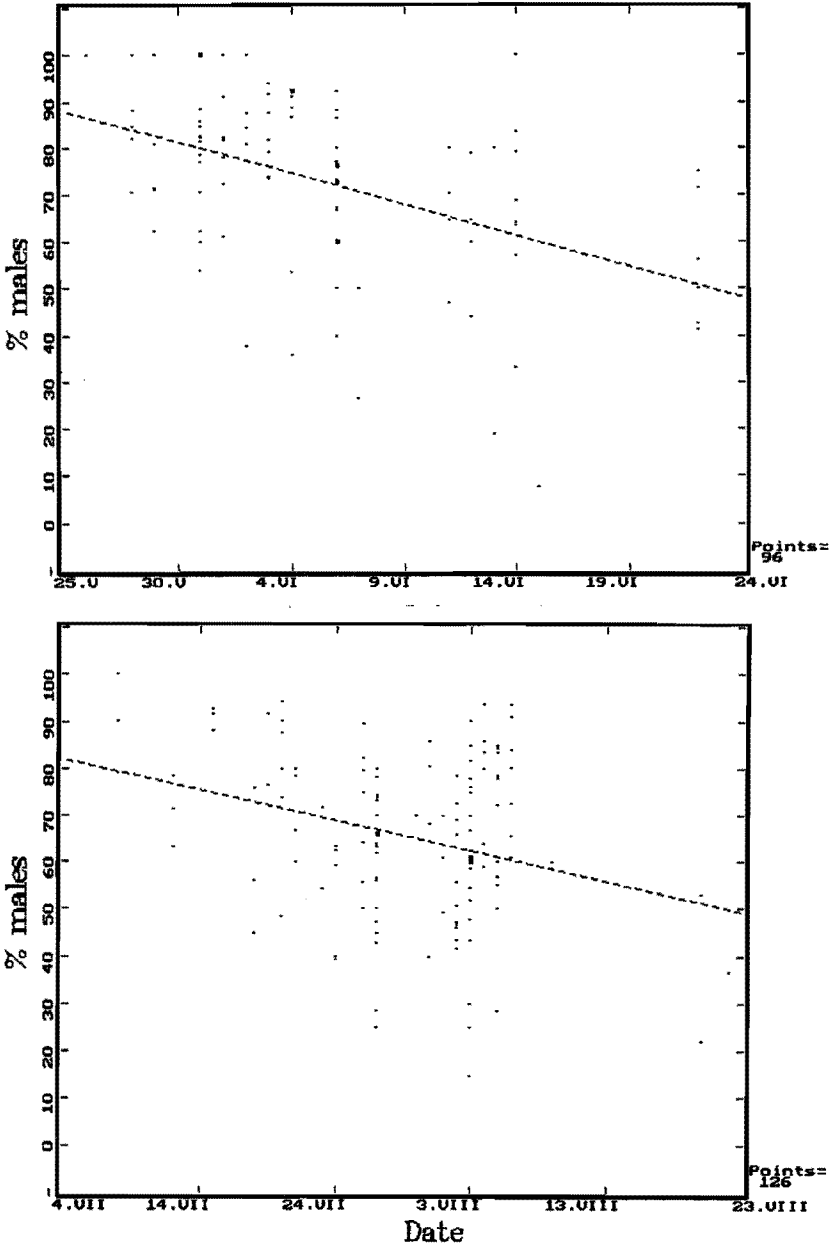


Figure 1. Percent males of sexed Karner blue individuals on all surveys with >9 individuals observed in spring and summer.

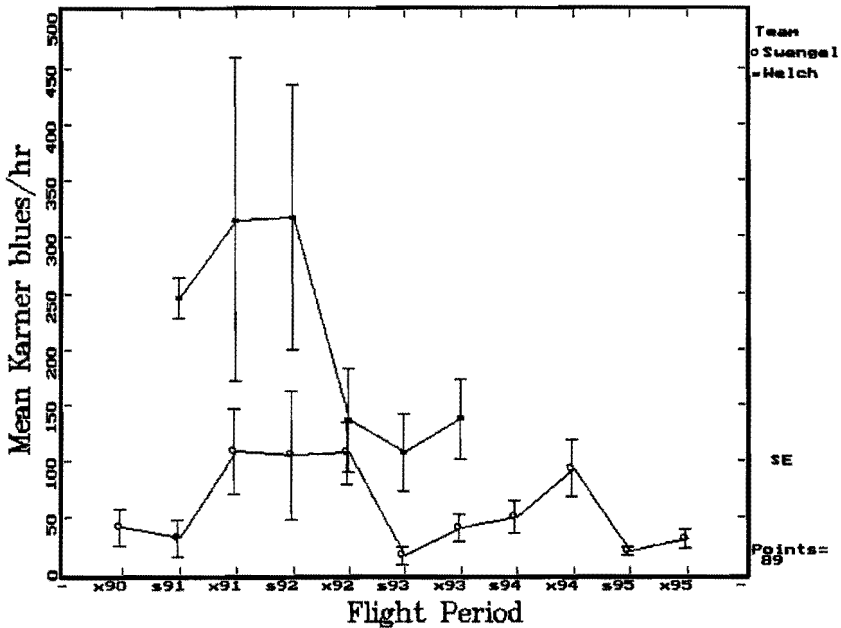


Figure 2. Mean \pm SE of highest survey total for Karner blues observed per brood at sites surveyed each brood. Swengel team: N=3 sites in 1990, 5 in 1991, 8 during 1992-95, all in Jackson and Wood Counties. Welch team: N=2 sites in Portage County, Wisconsin, data from Bleser (1993) and Welch (1993). s=spring, x=summer.

six comparable broods in summer 1992. Twice in the Swengel surveys (Fig. 2), a strong generally upward trend occurred through four broods, from spring 1991 to summer 1992 and from spring 1993 to summer 1994. The tendency in regression for density to be lower in spring than summer is apparent here also, for the two sharpest drops occurred in spring (1993, 1995). However, this pattern is highly variable, for twice, in 1992 and 1994, the spring brood was at similar or slightly greater levels than the previous summer. The fluctuations in the Swengel surveys were highly significant, by season ($p=0.0031$) and year ($p=0.0028$) in two-way ANOVA and by individual brood ($p=0.0012$) in one-way ANOVA. Thus, seasonal, annual, and individual brood effects were all apparent in the brood fluctuations. The bivoltine species graphed in Polard and Yates (1993: 63) showed a stronger pattern of seasonal effect (and relatively less individual brood effect), since the spring index was always lower than the summer during 1976-91 for these three species.

To measure the amount of fluctuation Karner blues exhibited, we used the mean in Fig. 2 (Swengel team) as the brood index. We then calculated how manyfold was the variation between each pair of consecutive broods. In terms of absolute value (regardless of increase or decrease), the median fluctuation was 2.8-fold for all consecutive brood pairs (range 1.7 to 20.9), for spring (rel-

ative to previous summer) 3.7-fold (2.0 to 20.9) and summer (relative to previous spring) 2.8-fold (1.7 to 8.6). By contrast, the overall mean Karner blues observed in all spring surveys was 45.2/hr, in summer 70.6/hr, only a 1.6-fold difference. Including direction of change (increase or decrease), the median fluctuation was 1.7-fold for all consecutive brood pairs (range -20.9 to 7.0), for spring (relative to previous summer) 1.5-fold (-20.9 to 4.0) and summer (relative to previous spring) 1.9-fold (0.65 to 7.0). The spring brood showed a wider range of fluctuation, with enough increases for the median to be positive, but with the declines steeper than the increases. The summer brood varied among the years from relatively small to considerable increases.

One-way ANOVAs testing these amounts of fluctuation showed no effect for site ($p=0.4533$) or season (i.e., spring vs. summer) ($p=0.2650$), a near-significant effect for year ($p=0.0601$), and a highly significant effect for individual brood (independent of year and season) ($p=0.0005$). This indicates that, despite high variability in survey results, the different sites fluctuated overall in generally similar patterns that apparently operated at the level of the individual brood rather than the season or the year.

Weather. Karner blue rates showed a strong positive covariance with temperature in all four regressions (Table 1). The other weather effects were surprising and hard to explain: wind produced a less pronounced but significant positive effect and percent sunshine a significant negative effect. A mildly positive but non-significant covariance with time of day occurred in the first and third regressions. Active Karner blue adults were observed in temperatures ranging from 13 to 35°C and from 06:51 to 18:18 CST.

Dispersal. Our surveys did not directly study Karner blue dispersal, but some indirect observations are possible. Like others (e.g., Bleser 1993, Leach 1993, Welch 1993), we occasionally observed Karner blues away from lupine: 12 summer adults (11 males, 1 female) mudpuddling and nectaring about 400 m from lupine, three summer males mudpuddling in a mucky trail apparently about 800 m from the nearest lupine patch, and ten summer adults (3 males, 7 females) mudpuddling and nectaring along a dirt road through a wet forest up to 650 m from the nearest lupine. Small numbers of feeding Karner blues of both sexes also occurred on the edges of lupine patches, seemingly following nectar and mud away from the patch. In three places Karner blues occurred in lupine patches too tiny and isolated to support a viable population. One spring male perched along a trail in dense forest near about 300 lupines, with about 50 lupines ca. 80 m to the east, with no other known lupines within 1600 m. Two spring (1 male, 1 female) and eight summer (5 males, 3 females) adults were in tiny lupine clumps about 650 m south of the main lupine patch. One summer male occurred among several dozen lupines along a railroad, with no other known lupines within 1600 m. Most but not all of these observations occurred in 1991-92 and 1994, years of high Karner blue numbers (Fig. 2). Yet in this study all Karner blues occurred within 3-5 km of other Karner blue sites, although areas further away were also surveyed.

Habitat and management. Known Karner blue distribution in Wisconsin (Bleser 1993, this study) forms a generally southeast to northwest band similar in location to but slightly wider than the tension zone for range limits of southern and northern plants (Curtis 1959). Within this range and at sites with the sandy soil required by lupine, Karner blues occurred in a variety of relatively natural and human-disturbed sites. The most significant habitat factor was latitude (negative) (Table 1). It is unclear whether this relates to climate/edge of range or extent of suitable habitat (greater in central vs. northwestern Wisconsin) or habitat/management differences between these two areas. The next most important factor was canopy (negative), consistent with other studies and corresponding to lupine's preference (Dirig 1994, Lane

Table 4. Number of sites containing unit(s) with dense lupine (relative abundance "common" or greater, with ≥ 0.8 ha patch size) and number of units and sites with high-density Karner blues (rate ≥ 65 /hr with survey time ≥ 0.25 hr), by management category. Some sites are double-counted because of differing management among units or among years.

	dense lupine sites	N sites assessed	Karner Blue Transect Surveys			
			High Density		All	
			N units	N sites	N units	N sites
nothing	3	10	7	1	38	10
mowing	7	55	16	4	211	58
mixed cutting	1	14	10	3	52	15
forestry	2	5	0	0	11	7
wildfire	8	19	12	6	143	20
wildfire+other	1	10	8	6	47	22
rotational fire+cut	1	1	0	0	1	1
rotational fire+mow	6	15	1	1	73	15
rotational fire	6	8	10	1	81	8
recreation	1	1	2	1	9	1

1994, Bidwell 1995). Lupine "core" and abundance each produced one highly significant positive effect, consistent with the positive effects of patch proximity and lupine density in other studies (Savignano 1994, Bidwell 1995). Vegetative quality and diversity produced non-significant positive covariances. Savignano (1994) and Bidwell (1995) found lupine patch size to be significant, while this study, with its cruder measure of this factor, did not.

No management variables produced significant effects in regression (Table 1). Extensive dense lupine and Karner blues occurred in sites representing a diversity of management histories (Table 4), as reported elsewhere in Wisconsin (Bleser 1993, Bidwell 1995). Karner blues typically produced favorable numbers at sites treated with rotational fire alone or in combination with other managements (Table 5), even though burning greatly reduces larval numbers (Swengel 1995). These management fires did not burn all lupine stands in an occupied area, usually rotated over 3–4 years or more, and occurred in the context of multiple Karner blue populations in the vicinity. A variety of other managements also produced substantial Karner blue rates (Table 5). In particular, mowing often produced rates similar to those at sites in conservation management (i.e., rotational fire). This was especially apparent for mowed sites with lupine abundance and patch size at least at the minimum values found in the rotationally burned conservation sites.

DISCUSSION

Flight period statistics in this study agree with the flight graphs in Shapiro (1974) and Iftner et al. (1992), except the latter's summer flight ended by mid-August, probably reflecting lower detectability in that study's fewer and smaller populations. The generally longer but more variable span for summer flight suggests the possibility of a partial third brood in years of longer growing seasons, such as 1994 (Table 2), but a partial third cannot be distinguished from a more asynchronous and protracted second brood in this

Table 5. Percent Karner blue individuals ("ind"), percent survey hours during Karner blue flight period, and weighted observation rate (total individuals/survey hours) by management category for Burnett County and Central Wisconsin. GL=good lupine patch (relative abundance uncommon or greater and patch size ≥ 0.8 ha, the minimum characteristics of rotationally burned units).

	SPRING FLIGHT			SUMMER FLIGHT			BOTH FLIGHTS		
	% Ind	% Hr	Rate	% Ind	% Hr	Rate	% Ind	% Hr	Rate
Burnett County									
forestry				0.6	3.4	2.4			
mixed cut				0.1	1.1	0.0			
mowing				16.4	15.8	13.3			
mowing, GL				5.0	1.4	46.8			
rotational fire				43.2	37.2	14.9			
rotational fire+mow				39.7	42.5	12.0			
Central Wisconsin									
forestry	0.0	0.4	0.0	0.4	0.8	30.0	0.2	0.6	21.6
mixed cut	8.2	13.2	29.7	13.8	13.4	65.1	11.6	13.3	49.3
mowing	27.9	35.0	38.3	24.9	26.1	60.1	26.1	30.1	48.7
mowing, GL	22.8	25.3	43.3	20.5	20.5	62.9	21.4	22.6	53.1
nothing	14.1	7.3	93.2	5.1	6.8	46.5	8.5	7.0	68.1
recreation	1.3	2.5	25.8	3.8	2.5	96.6	2.9	2.5	64.5
rotational fire	22.6	9.5	115.1	21.4	17.6	76.6	21.8	13.9	88.3
rotational fire+cut	0.3	0.6	23.1	-	-	-	0.1	0.3	23.1
wildfire	24.2	26.9	43.2	17.5	19.3	57.0	20.1	22.7	49.7
wildfire+trail	1.4	4.6	14.8	13.1	13.5	61.3	8.6	9.5	51.2

dataset. Many factors potentially affect sex ratio, so that sex ratio does not provide a simple ordination of a given survey's timing relative to peak date.

Our observations related to dispersal agree with typical descriptions of Karner blues as localized near lupines, with dispersal rarely >1 km from their habitat patch, and flying in a weak, low, circling pattern (e.g., Iftner et al. 1992, Bleser 1993, Leach 1993). While Karners can and do move away from their lupine patch and colonize new sites, they apparently do so primarily in low numbers and over relatively short distances (Welch 1993). It is unclear yet whether or how much this dispersal tendency may be affected by the considerable variation in the species' abundance among broods.

Rotational fire is the management preferred by conservation agencies (many papers in Andow et al. 1994). In this study, alternative managements rarely occurred on conservation lands except in combination with rotational fire. Swengel (1996a) identified five factors affecting butterfly response to fire management. For three, the Karner blue has unfavorable characteristics: ecological niche (specialized), vagility (low), and location during fire (above ground as eggs or larvae in litter). For two others, the Karner blue has favorable characteristics: voltinism (>1 generation per year) and response of key plants (established lupines are fire increasers) (Dirig 1994, Grigore and Tramer 1996). Nonetheless, the Karner blue's response to fire management (with case histories described in Swengel 1994) was much more favorable than for many other midwestern butterflies specialized to the herb layer (Swengel 1996a), including the sympatric, lupine-feeding frosted elfin (Swengel 1996b). These results suggest that, given adjacent unburned refugia as

sources for recolonization and several years to re-establish, a favorable plant response and a second generation per growing season contribute greatly to ameliorating the Karner blue's response to fire management.

Opportunities to study management without rotational fire mostly occurred in timber reserves and rights-of-way. Since these treatments were not designed for conservation objectives, they may underestimate their value when designed specifically for conservation. Nonetheless, these alternative managements (especially mowing) show considerable promise for maintaining appropriate habitat occupied densely by Karners. Furthermore, these alternative managements appear more effective at maintaining other sympatric butterfly species of conservation concern than burning (Swengel 1996b, Swengel 1997).

Despite the Karner blue's relatively narrow range and specificity to wild lupine as larval host, this butterfly occurred in a wide variety of sites and managements compatible with lupine's occurrence. Monitoring the status of this butterfly requires wide sampling over many years because of its strong variability in abundance relative to peak date and brood fluctuations, as well as shifts in brood timing and length among years.

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