The Great Lakes Entomologist

Volume 31
Number 1 - Spring 1998 *Number 1 - Spring 1998*

Article 7

April 1998

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1998 THE GREAT LAKES ENTOMOLOGIST 59

DENSITY-DEPENDENT AND -INDEPENDENT BEHAVIORS OF THE ADULT KARNER BLUE (*LYCAEIDES MELISSA SAMUELIS*) (LEPIDOPTERA: LYCAENIDAE)

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ABSTRACT

At 146 pine-oak barrens in central and northwestern Wisconsin USA during 1988–96, 3973 Karner blues (*Lycaeides melissa samuelis* Nabokov) were found in 95.4 hr of transect surveys during spring and 6896 individuals in 134.8 hr during summer. Of these, 9346 (86%) individuals were first observed copulating, feeding, flushing, flying, or involved in a non-copulatory intraspecific interaction. All these behaviors except copulation showed density-independent influences; all these behaviors also had density-dependent influences. The most frequently significant density-independent variables affecting occurrence of these behaviors were temperature, brood (spring vs. summer), and crepuscularity (time since noon). Male (rather than female or overall) Karner blue density more often significantly related to Karner blue behavior. Males showed density dependence in feeding (positive), flushing (negative), and flying (positive threshold) while females did not. Both sexes showed strong positive density dependence in non-copulatory intraspecific interactions and copulation. Flying and intraspecific interactions showed similar influences in relation to several variables, while flying and flushing had markedly opposite patterns. Males and females were also opposite in their relative tendency to be observed flushing or flying, with females more likely to be flushing, males flying. Males also showed a greater tendency to engage in non-copulatory intraspecific interactions.

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. This butterfly has two complete life cycles per year, feeds only on wild lupine (*Lupinus perennis* L.) (Fabaceae) as a larva rangewide, overwinters as an egg, and has a rather narrow generally east-west historical 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 density-dependent and -independent factors affecting the frequencies of copulation, feeding, flushing, flying, and non-copulatory intraspecific interactions by Karner blues observed on transect surveys. The density-independent factors included survey timing (both daily and seasonal) and weather variables. Such factors have already

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been significantly related to Karner blue numbers observed on surveys (Swengel and Swengel 1996) and are well known to affect both detectability and behavior of butterflies generally (Shreeve 1992, Pollard and Yates 1993: 26–32). We tested for density-dependent influences on Karner blue behaviors by relating them to relative Karner blue density, calculated both by sex and for all individuals (whether sexed or not), on the surveys. Likewise, the behaviors were analyzed both by sex and for all individuals to test for gender differences in behavior patterns. These results are useful for understanding this butterfly's behavior, as well as for designing survey protocols and interpreting results for monitoring this species.

METHODS

Surveys occurred at 146 pine-oak barrens in central and northwestern Wisconsin (43.7°–45.9° N, 89.9°–92.7° W) during 1988–1996. It was not possible to visit each site each year, but most sites were surveyed multiple times both within a year and among years. We conducted transect butterfly surveys along like routes within each site each visit (Pollard 1977, Swengel and Swengel 1996). Karner blue individuals were sexed, if possible, and their behavior when first seen was recorded, as well as any additional notable behaviors after the first (primarily feeding and social interactions). A new survey unit was designated whenever the habitat along the route varied by management and/or vegetation type. For each unit, we recorded temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying. Data from each unit were kept separate.

Behaviors were studied as rates (percents) of occurrence within each survey unit: the percent of all (whether sexed or not), female, and male individuals doing the behavior out of the total number of all, female, and male individuals, respectively, observed in the unit survey. These percentages, expressed as decimals, were directly analyzed with nonparametric statistics (Mann-Whitney U test, Spearman rank correlation) but were natural log-transformed for parametric testing by analysis of variance (ANOVA). Behaviors analyzed here were copulation, feeding, flushing, flying, and non-copulatory intraspecific interactions. Since the numbers of individuals feeding and interacting were recorded both as first behavior and all observed instances, the rates of individuals observed in all feeding and interacting behaviors were analyzed as a comparison to the results for rates of feeding and interacting upon first detection. All copulations were included, whether the pair was first observed in copula or in precopulatory courtship. Observed sex ratio was also analyzed as percent males observed out of all sexed individuals.

The Mann-Whitney U test was used to analyze for differences in frequency of a behavior by brood (spring vs. summer), a density-independent timing variable. The Spearman rank correlation was used to test for correlation of the frequency of a behavior with density-independent (timing, weather) and -dependent variables. The timing variables were crepuscularity (the difference between 12:00 CST and the time when the survey started), time of day (when the survey started), and date within brood (spring or summer). The weather variables were sunshine (percent time the sun was shining during the survey), temperature (average of the lowest and highest temperature on the survey), and wind (average of the lowest and highest wind speed on the survey). The three density variables were calculated as all (including unsexed), female, and male Karner blue individuals observed per hour in each unit survey. Unit surveys were included for analysis if >2 indi-

viduals of the sample analyzed (all individuals, females, males; all sexed individuals for sex ratio) were observed on the survey.

Univariate ANOVA was used to test for nonlinear patterns of effect for two variables: year and density. Unit surveys were categorized by density into these four groups (regardless of whether the individuals were sexed or not): >0 and <15 observed per hour, ≥15 and <35, ≥35 and <65, and ≥65. Unit surveys were included for analysis if >1 individual of the sample analyzed was observed on the survey.

Analysis was done with ABstat 7.20 software (1994, Anderson-Bell Corp., Parker, Colorado), with statistical significance set at $p<0.05$. Since significant results occurred overall much more frequently than would be expected due to Type I statistical error, we did not lower the p value further, as many more Type II errors would then be created than Type I errors eliminated.

RESULTS

During the spring brood, we counted 3973 Karner blue individuals in 107.0 hr and 173.2 km of transect surveys in 351 units from 22 May to 26 June, and 6896 individuals in 134.8 hr and 259.9 km in 465 units during summer from 5 July to 6 September (Table 1). We recorded 9346 individuals (86.0% of all observed) first behaving in one of the categories analyzed in this study, with an additional 272 individuals recorded as feeding or in non-copulatory intraspecific interactions after their first observed behavior (Table 1). The remaining 14.0% of behaviors, such as basking, roosting, perching, oviposition, and interspecific interactions, were not analyzed in this study. All analyzed behaviors except copulation related significantly to density-independent factors (Tables 2–4), while all these behaviors were also significantly influenced by density dependence (Tables 5–7). Males dominated the census results (69.6% of sexed individuals), and results for males and all individuals were similar. However, males and females differed markedly in frequency of some behaviors and in factors affecting the occurrence of these behaviors.

In the Mann-Whitney U tests and Spearman rank correlations, all vari-

Table 1. Number of Karner blue individuals recorded in each behavior category, by sex and brood.

	Spring Brood				Summer Brood				Both
	female	male	unsex.	all	female	male	unsex.	all	all
First seen copulating	9	9	0	18	37	37	0	74	92
First seen feeding	67	243	9	319	502	797	177	1476	1795
First seen flushing	358	475	34	867	502	830	66	1398	2265
First seen flying	462	1484	103	2049	605	1723	115	2443	4492
First seen interacting	52	275	10	337	87	273	5	365	702
Subtotal	**948**	**2486**	**156**	**3590**	**1733**	**3660**	**363**	**5756**	**9346**
First seen in other behaviors	95	256	32	383	315	666	159	1140	1523
All individuals seen	1043	2742	188	3973	2048	4326	522	6896	10869
All feeding seen	79	296	9	384	548	868	177	1593	1977
All interacting seen	56	306	10	372	96	318	6	420	792

Table 2. Mean ± SD of the percent Karner blue individuals observed in each behavior, by brood (spring or summer). The two-tailed p value from the Mann-Whitney U test is rounded to three decimal places, with significant values ($p<0.05$) boldfaced. Minimum sample of unit surveys for analyses of spring data: 178 (all), 157 (males), 98 (females); for summer: 244 (all), 143 (females), 199 (males). Sample sizes varied slightly due to a few missing values.

	Spring	Summer	*P* value
% copulating	0.3 ± 2.4	0.6 ± 2.3	0.268
% males	71.1 ± 22.1	65.7 ± 21.6	**0.004**
First flushing			
% all individuals	27.2 ± 22.3	25.9 ± 24.1	0.234
% females	34.7 ± 26.4	26.3 ± 22.5	**0.015**
% males	22.6 ± 24.0	23.1± 23.0	0.650
First flying			
% all individuals	50.9 ± 23.5	38.0 ± 25.3	**0.000**
% females	45.5 ± 25.9	34.7 ± 24.3	**0.000**
% males	53.5 ± 25.7	43.1 ± 26.1	**0.000**
First feeding			
% all individuals	8.6 ± 15.3	20.2 ± 23.6	**0.000**
% females	7.3 ± 13.7	23.7 ± 24.4	**0.000**
% males	9.8 ± 17.1	18.6 ± 22.0	**0.000**
All feeding			
% all individuals	11.1 ± 17.0	22.8 ± 25.6	**0.000**
% females	8.4 ± 15.4	26.7 ± 26.3	**0.000**
% males	13.0 ± 19.0	21.1 ± 23.2	**0.001**
First interacting			
% all individuals	6.5 ± 10.5	4.1 ± 8.7	0.061
% females	4.9 ± 9.9	3.8 ± 8.6	0.927
% males	7.9 ± 12.5	5.1 ± 9.8	0.150
All interacting			
% all individuals	7.4 ± 12.0	5.3 ± 10.4	0.160
% females	5.6 ± 10.4	4.3 ± 9.1	0.734
% males	9.3 ± 14.5	6.8 ± 12.2	0.396

ables produced at least one significant result (Tables 2–5). In these analyses, excluding those for sex ratio and all observed feedings and interactions, the most frequently significant timing variables were brood and crepuscularity (7/13 for both), followed by time of day (6/13), with date within brood rarely significant (Tables 2–3). The most frequently significant weather variable was temperature (8/13), followed by sunshine and wind (5/13 for both) (Table 4). Of the density-dependent variables, observation rate of male Karner blues per hour was significant most often (8/13), followed by rate of all individuals and females (6/13 for both) (Table 5).

In ANOVA, density had more significant results (9/20 tests) than year (Table 6). Except for flushing, year was rarely significant; it showed no relationship to feeding at all, despite the plausibility of annual variability in availability and quality of particular food resources.

Copulation. We observed 46 mating pairs (Table 1), between 0937 and 1814 hr CST, 18–33°C, 31 May (1994) to 25 June (1996) in the spring brood and 12 July (1991) to 12 August (1996) in the summer brood. This suggests that successful courtship occurs throughout much of the day and flight period. No density-independent factors related significantly to rate of copula-

Table 3. Spearman rank correlations of percent Karner blue individuals observed in each behavior with timing variables: crepuscularity (see Methods), time of day, and date within brood (spring or summer). Significant coefficients are followed by * ($p<0.05$) or ** ($p<0.01$). Minimum sample of unit surveys for correlations: 422 (179 in spring, 244 in summer) for all, 243 (100, 143) for females, 357 (159, 198) for males. Sample sizes varied slightly due to a few missing values.

	Crepuscularity	Time of day	Spring date	Summer date
% copulating	–0.007	+0.081	+0.034	–0.078
% males	–0.118*	–0.050	–0.339**	–0.351**
First flushing				
% all individuals	+0.175**	–0.134**	+0.011	+0.038
% females	+0.090	–0.097	+0.069	+0.058
% males	+0.194**	–0.152**	+0.051	+0.022
First flying				
% all individuals	–0.110*	+0.084	+0.051	+0.017
% females	+0.007	+0.075	–0.033	+0.267**
% males	–0.118*	+0.015	–0.065	+0.020
First feeding				
% all individuals	–0.249**	+0.105*	–0.118	+0.074
% females	–0.148*	+0.045	–0.124	–0.130
% males	–0.201**	+0.080	–0.133	+0.006
All feeding				
% all individuals	–0.247**	+0.080	–0.145*	+0.075
% females	–0.158*	+0.037	–0.138	–0.123
% males	–0.173**	+0.049	–0.135	–0.005
First interacting				
% all individuals	+0.026	+0.250**	+0.251**	+0.018
% females	+0.094	+0.233**	+0.162	–0.058
% males	+0.024	+0.296**	+0.295**	+0.081
All interacting				
% all individuals	–0.008	+0.237**	+0.252**	+0.032
% females	–0.080	+0.201**	+0.151	–0.056
% males	–0.018	0.278**	+0.310**	+0.111

tion (Tables 2–4), but all density-dependent factors did so positively (Table 5). ANOVA indicated no year effect, but strong density dependence (Table 6), with copulation increasing steadily in the first three density categories, then dropping somewhat again in the highest-density category (Table 7).

Sex ratio. The percentage of males (out of sexed individuals) correlated negatively with date within brood (Table 3), as found previously for this butterfly (Leach 1993; Swengel and Swengel 1996) and as is typical for adult butterfly observation generally (Rutowski 1984, Scott 1986:26, Shreeve 1992). Percentage of males also differed by brood, with higher male ratios in spring (Table 2). Of the other significant density-independent patterns, sunshine and wind related positively and crepuscularity negatively to the proportion of males vs. females (Table 4). The two density-dependent patterns were logical (Table 5). The stronger was a negative relationship of percent males to female density. The observation rate of female Karner blues tends to increase as the brood progresses, as more adult females eclose. Thus the relative proportion of observed females increases. The second was a positive correlation of percent males with male density. This contrasts somewhat with

Table 4. Spearman rank correlations of percent Karner blue individuals observed in each behavior with weather variables: % sunshine, temperature, and wind speed. Significant coefficients are followed by * ($p<0.05$) or ** ($p<0.01$). Sample sizes are as in Table 3.

	Sunshine	Temperature	Wind
% copulating	–0.037	+0.081	+0.043
% males	+0.134**	+0.010	+0.192**
First flushing			
% all individuals	–0.053	–0.189**	–0.108*
% females	–0.037	–0.073	–0.118*
% males	–0.069	–0.222**	–0.103
First flying			
% all individuals	+0.217**	+0.205**	+0.113*
% females	+0.079	–0.019	+0.118*
% males	+0.204**	+0.188**	+0.110*
First feeding			
% all individuals	–0.165**	+0.116*	+0.064
% females	–0.149**	+0.042	+0.061
% males	–0.159**	+0.066	+0.040
All feeding			
% all individuals	–0.148**	+0.083	+0.067
% females	–0.185**	+0.015	+0.053
% males	–0.132*	+0.046	+0.037
First interacting			
% all individuals	+0.042	+0.202**	+0.007
% females	+0.038	+0.208**	–0.007
% males	+0.031	+0.215**	–0.120
All interacting			
% all individuals	+0.056	+0.228**	0.000
% females	+0.071	+0.190**	–0.054
% males	+0.040	+0.243**	–0.031

the linear decline in percent males with increasing date in a brood since highest male densities do not occur at the beginning of the flight period, but rather somewhere in the middle. Thus, highest male sex ratios tended to occur both at the beginning of the brood (before peak numbers) and at high male relative densities (which occurs sometime in the middle of the brood, but not all sites and years produce such densities). ANOVA detected no density-dependent patterns (Table 6), although only density of all individuals was tested.

Feeding. Brood, crepuscularity, and sunshine related significantly to all measures of feeding frequency (by sex and for all individuals; as first and as any observed behavior), with relatively more feeding in the summer brood, nearer noontime, and with less sunshine (Tables 2–4). First observed feeding by all individuals also covaried with increasing time of day and temperature (Tables 3–4). Rate of feeding by all and male individuals showed many positive density-dependent patterns, especially as the first observed behavior, while female feeding never showed density dependence (Table 5). In ANOVA, only the rate of males first seen feeding showed significant density dependence (Table 6), which was positively progressive (Table 7). No feeding measures showed a year effect (Table 6). Rates of feeding at first observation

Table 5. Spearman rank correlations of percent Karner blue individuals observed in each behavior with density variables: all, female, and male Karner blue individuals observed per hour per unit survey. Significant coefficients are followed by * ($p<0.05$) or ** ($p<0.01$). Sample sizes are as in Table 3.

	All	Female	Male
% copulating	+0.184**	+0.125**	+0.211**
% males	–0.045	–0.651**	+0.332**
First flushing			
% all individuals	–0.172**	–0.042	–0.184**
% females	–0.118	–0.121	–0.115
% males	–0.127*	–0.078	–0.108
First flying			
% all individuals	+0.090	–0.035	+0.139**
% females	–0.047	–0.013	–0.028
% males	+0.013	–0.048	+0.037
First feeding			
% all individuals	+0.198**	+0.211**	+0.156**
% females	+0.119	+0.094	+0.106
% males	+0.206**	+0.203**	+0.190**
All feeding			
% all individuals	+0.129**	+0.161**	+0.098
% females	+0.105	+0.075	+0.100
% males	+0.089	+0.143**	+0.062
First interacting			
% all individuals	+0.332**	+0.241**	+0.335**
% females	+0.239**	+0.195*	+0.217**
% males	+0.263**	+0.229**	+0.251**
All interacting			
% all individuals	+0.319**	+0.215**	+0.329**
% females	+0.240**	+0.150*	+0.236**
% males	+0.252**	+0.214**	+0.245**

were roughly similar between the sexes in each brood (6.4% for females and 8.9% for males in spring, 24.5% and 18.4% respectively in summer, 16.5% for all individuals in both broods, calculated from Table 1), and were much higher in summer than spring. The overall rate of feeding when first observed (mostly nectaring but also some feeding on moist dirt and feces) of all spring individuals was similar between our data (8.0% of all individuals first observed feeding) and Leach's (1993) nectaring rate at Fort McCoy (10.6%). The summer rate at Fort McCoy (8.6%) was similar to the spring rate there, but we found proportionately more feeding in the summer (21.4%).

Flushing. Brood significantly related only to females, with more flushing in spring (Table 2). Negatively significant density-independent factors included time of day and temperature (flushing by all and male individuals) and wind (all and female) (Tables 3–4). The one positive density-independent factor was crepuscularity (all and male) (Table 3). Flushing by all and male individuals negatively correlated with all and/or male density, while female flushing showed no density dependence (Table 5). In ANOVA, rate of flushing by all and male individuals showed year and density effects (Table 6), with a threshold of significantly more flushing in the lowest-density category compared to all other categories (Tables 7). Rate of flushing was higher for fe-

Table 6. Results of ANOVAs analyzing percent Karner blue individuals observed in certain behaviors (copulating, feeding, flushing, flying, and non–copulatory intraspecific interactions) and percent males of sexed individuals (sex ratio) by year, density category (grouped by rates of observations of all Karner blue individuals/hr per unit survey), or site (16 disjunct units in 15 sites), for females, males, and all individuals (whether sexed or not). Significant p values (<0.05) are boldfaced. See Tables 7–8 for Duncan's post–hoc tests for significant ANOVAs.

	Year			Density		
	df	F	P	df	F	P
% all copulating			>0.1	3,493	4.206	**0.0059**
% males			>0.1			>0.1
First flushing						
% all individuals	5,483	3.554	**0.0036**	3,430	13.559	**0.0000**
% females			>0.1			0.0741
% males	5,434	3.652	**0.0030**	3,431	10.783	**0.0000**
First flying						
% all individuals			0.0784	3,480	3.309	**0.0020**
% females	5,309	2.687	**0.0214**			>0.1
% males			>0.1	3,431	4.281	**0.0054**
First feeding						
% all individuals			>0.1			>0.1
% females			>0.1			>0.1
% males			>0.1	3,433	2.716	**0.0443**
All feeding						
% all individuals			>0.1			>0.1
% females			>0.1			>0.1
% males			>0.1			>0.1
First interacting						
% all individuals			>0.1	3,417	4.634	**0.0034**
% females			>0.1			>0.1
% males			0.0991	3,351	2.747	**0.0429**
All interacting						
% all individuals			>0.1	3,417	2.832	**0.0385**
% females			>0.1			>0.1
% males	5,353	2.199	**0.0426**			>0.1

males than males (34.3% for females and 17.3% for males in spring, 29.0% and 22.7% respectively in summer, 20.8% for all individuals in both broods, calculated from Table 1).

Flying. Brood and wind significantly related to all measures of flying frequency (by sex and for all individuals), with relatively more flying in the spring brood and in stronger wind (Tables 2,4). Rates of all and male flying negatively correlated with crepuscularity and positively with sunshine and temperature, while female flying correlated positively with date in summer (Tables 3–4). Rate of flying by all individuals showed the only density-dependent correlation (positive with male density) (Table 5). In ANOVA, flying by all and male individuals showed density dependence (Table 6), with a threshold effect of significantly less flying in the lowest-density category (Table 7). Females also showed a significant year effect (Tables 6,8). Rates of flying at first observation were higher for males than females, and in spring compared to summer (44.3% for females and 54.1% for males in spring, 29.5% and

Table 7. Results of Duncan's post–hoc test for significant ANOVAs, with density (rate of observation of all Karner blue individuals/hr per unit survey) as the independent variable (Table 6). Within column, mean log–transformed percentages (expressed as decimals) lacking similar letter(s) after them are significantly different ($p<0.05$).

	First feeding		First flushing				First flying			
Individuals/hr	% males		% all indiv.		% males		% all indiv.		% males	
> 0 < 15	0.071	A	0.334	A	0.329	A	0.284	A	0.279	A
≥ 15 < 35	0.101	AB	0.227	B	0.207	B	0.348	B	0.364	B
≥ 35 < 65	0.122	B	0.209	B	0.184	B	0.342	B	0.380	B
≥ 65	0.135	B	0.189	B	0.167	B	0.368	B	0.384	B

	First interacting				All interacting		Copulating	
Individuals/hr	% all indiv.		% males		% all indiv.		% all indiv.	
> 0 < 15	0.009	A	0.005	A	0.019	A	0.000	A
≥ 15 < 35	0.052	B	0.039	B	0.048	AB	0.001	A
≥ 35 < 65	0.068	B	0.054	B	0.063	B	0.008	B
≥ 65	0.059	B	0.055	B	0.064	B	0.005	AB

Table 8. Results of Duncan's post–hoc test for significant ANOVAs, with year as the independent variable (Table 6). Within column, mean log-transformed percentages (expressed as decimals) lacking similar letter(s) after them are significantly different ($p<0.05$).

	First flushing				First flying		All interacting	
Year.	% all individuals		% males		% females		% males	
1990							0.095	A
1991	0.172	A	0.132	A	0.246	A	0.053	A
1992	0.195	AB	0.161	AB	0.330	AB	0.081	A
1993	0.248	BC	0.227	BC	0.291	AB	0.072	A
1994	0.224	AB	0.205	ABC	0.320	AB	0.048	A
1995	0.236	AB	0.219	BC	0.241	A	0.082	A
1996	0.304	C	0.277	C	0.359	B	0.111	A

39.9% respectively in summer, 41.3% for all individuals in both broods, calculated from Table 1).

Intraspecific interactions. Time of day and temperature correlated positively with all measures of non-copulatory intraspecific interactions (by sex and for all individuals; as first and as any observed behavior); all and male interactions also correlated positively with date in spring (Tables 3–4). Furthermore, all measures of these interactions correlated positively with all density variables (Table 5). In ANOVA, rate of males and all individuals first observed in interactions, as well as all observed interactions by all individuals, showed density dependence (Table 6), as a threshold effect, with significantly less interaction in the lowest-density category (Table 7). Males in all observed interactions also had a year effect (Tables 6,8). As with flying, rates

of intraspecific interaction at first observation were higher for males than females (5.4% for females and 10.0% for males in spring, 4.2% and 6.3% respectively in summer, 6.5% for all individuals in both broods, calculated from Table 1).

Corresponding behaviors. Flushing and flying showed opposite tendencies with respect to crepuscularity, temperature, and wind (Tables 3–4). Likewise, all density-dependent effects were negative for flushing but positive for flying (Tables 5–7). However, these two behaviors were similar relative to brood (i.e. both more flushing and flying in spring than summer) (Table 2). Males and females were also opposite in their relative tendency to be observed flushing or flying, with females more likely to be flushing, males flying (based on rates calculated from Table 1).

Copulation and non-copulatory intraspecific interaction might be expected to show similar patterns, but copulation had no significant density-independent results, while interaction had many (Tables 3–4). Nonetheless, these two behaviors were both strongly and positively density dependent (Tables 5–7).

Flying and intraspecific interactions showed some similarity as well. Both flying and interaction were positively influenced by temperature (Table 4) and by density dependence (Table 5), although the latter was much more frequent and marked for interactions than flying. Otherwise, brood, crepuscularity, sunshine, and wind were significant for flying but not interaction, while time of day had opposite effects on the two behaviors (Tables 2–4). In ANOVA, both behaviors showed a threshold effect, with significantly less of the behavior in the lowest-density category (Table 7). Males showed a greater tendency than females both to fly and to interact intraspecifically (based on rates calculated from Table 1).

DISCUSSION

Density-independent factors. Karner blue behavior strongly related to daily and seasonal timing (Tables 2,3). Symmetrical circadian rhythms in flying and feeding were indicated by significant crepuscular effects, while significant time-of-day effects revealed differences between morning and afternoon in frequency of intraspecific interactions. Flushing showed both effects, with less flushing around midday but also less earlier in the morning than later in the evening. Rate of interaction also showed the most effects of increasing date within brood, but only in spring. The strongest pattern of brood (spring vs. summer) was the significantly greater frequency of flying in spring and feeding in summer. Perhaps it is drier in summer, thus necessitating more hydration, or perhaps more food (nectar) is available, so that more time spent feeding is possible. A few year effects were also apparent for flushing and flying (Table 8).

The effects of weather on Karner Blue behavior were generally unsurprising (Table 4). With increasing temperature and/or sunshine, the butterflies became more active (i.e. flying, interacting) and less likely to remain perched in the vegetation upon our approach so as to be first observed flushing. While rate of feeding increased with increasing temperature, logical in that a butterfly must be active to make visits to food sources, rate of feeding strongly declined with increasing sunshine. This suggests that the butterflies might be more likely to remain perched at a food source upon our approach under less sunny conditions. Increasing wind speed had an interesting association with reduced flushing and increased flying. This may directly reflect behavioral tendencies of the Karner blue or may be a consequence of relative

detectability. In calm conditions, the departure of the butterfly from a perch in the vegetation may be more apparent, so that the butterfly's first behavior would be recorded as flushing, not flying.

Density-dependent factors. Males had density-dependent effects for feeding (positive), flushing (negative), and flying (positive threshold), while females did not (Tables 5–7). Both sexes showed strong positive density dependence for non-copulatory intraspecific interactions and copulation. The greater frequency of density dependence in male than female behaviors suggests that males may seek more sociality than females. Male Karner blue sociality did not appear to have characteristics of a lek, as found in several other butterfly species (Rutowski 1984, Alcock 1987, Cordero and Soberón 1990), since nearly all Karner blues were observed in breeding habitat as defined by proximity of the larval host plant. According to Rutowski (1991), lekking behavior would not be expected in Karner blues because larval resources and female adults are not widely and unpredictably distributed in sparse densities.

Shapiro (1970) reported a positive density-dependence in mudpuddling by male pierid butterflies. In high-density populations, male pierids unsuccessful at courtship earlier in the day aggregated at puddles along the habitat periphery, where aggressive intraspecific behavior was suppressed. Consistent with this, male Karner blue feeding showed positive density dependence (Tables 5–7). However, most Karner blue feeding occurred *within* the breeding habitat (a few instances outside lupine patches are related in Swengel and Swengel 1996) and positively related to female as well as male and total density (Table 5). The positive density dependence of male feeding could be a mate-finding strategy. But females showed no density dependence in feeding frequency, so that increased densities of males at food sources would not lead to proportionately more encounters with females. It is possible that males feed relatively more at higher densities because they exhibit so many density-dependent behaviors, and so may incur greater energy costs at higher densities.

Rutowski (1991) argued that mate-finding by male butterflies should focus on adult female food sources only in species in which both (1) female rematings occur frequently (i.e., the species has a long-lived active adult stage) and (2) adult food resources are patchily distributed in a way that concentrates females. The former condition does not appear to apply to the Karner blue. Only the American copper (*Lycaena phlaeas*, Lycaenidae), of 44 butterfly and seven lycaenid species reviewed, was documented to use nectar resources for mate location (Rutowski 1991).

Our data do not allow analysis at a fine enough scale to test whether a skewed distribution of individuals might be occurring *within* a unit because of congregation at a patchily distributed but preferred food source. Microdistribution of butterflies within an area may significantly relate to type and amount of available nectar (Wiklund 1977, Wiklund and Åhrberg 1978, Loertscher et al. 1995). Our data do suggest, however, that male feeding is affected by female density (and other measures of density), but not vice versa. Thus females did not appear to avoid feeding in areas of denser males and presumably greater male harassment, as found for swallowtails by Grossmueller and Lederhouse (1987). Perhaps because of the Karner blue's seemingly low vagility, females do not venture far from the natal habitat patch, regardless of how densely that patch supports Karner blues. But within a given unit, microdistribution and nectar selection of Karner blue individuals could still have such effects unapparent at the larger spatial scale studied here.

The various density-dependent effects on flushing (Tables 5–7) indicated

reduced rates of flushing in higher Karner blue densities. This might result from less inclination to flush at all in higher densities or from an inclination to flush sooner, perhaps in response to other individuals already flushed by our approach, resulting in their being first observed in some other behavior such as flying or interacting. By contrast, the density dependence related to flying and interacting was positive (Tables 5–7). Furthermore, the significant positive density dependence of copulation (Tables 5–7) suggests the Allee effect, in which paucity of encounters with suitable mates leads to relatively lower frequency of mating in populations of lower density (cf. Smith and Peacock 1990). Consistent with this, Shapiro (1970) reported significantly higher rates of unmated fresh females in pierid butterflies when in low-density populations.

Survey protocols and interpretation. Variation over time in the location of preferred nectar sources relative to transect route does not appear likely to affect transect counts of Karner blues dramatically, since only a minority of individuals were feeding upon first observation. This was especially so in spring, when 8.0% of all individuals detected were first seen feeding (Table 1). Attention to nectar sources within the transect strip is useful, however, especially in summer, when 21.4% of individuals were first seen feeding (Table 1).

Sex ratio varies within brood over time, being more male skewed earlier in the brood (Leach 1993; Swengel and Swengel 1996), as evidenced in this study by the negative effect of date (Table 3). But the sex ratio within a butterfly brood is usually about equal based on total eclosures, as is the case in captive rearing of this taxon (Herms et al. 1996). The relatively earlier eclosure of males than females (protandry) is theoretically and observationally attributed to male competition for virgin (receptive) females (Rutowski 1984, Brakefield and Shreeve 1992).

Observed sex ratios in the field reflect not just the actual proportion of the sexes present in the site on that day (a function of timing within brood), but also the relative detectability of the sexes (a function of behavior). Theory predicts and observation bears out that male butterflies more actively and frequently court, while females are typically unreceptive to courtship overtures except when virgin or depleted in spermatophore resources (Rutowski 1984, 1991). Females would devote the relatively greater proportion of their time not involved in courtship and mating to maintenance activities (such as feeding), oviposition, and hiding (to avoid the attention of conspecific males as well as predators). Thus, female avoidance of conspecific male attention may explain why the sex ratio skews more toward males as male density increases (Table 5). Furthermore, consistent with theoretical expectations, male Karner blues were more frequently seen upon first observation to be engaging in more active and overt behaviors, such as flying and intraspecific interactions, while females were more frequently first seen flushing, symptomatic of more covert behavior. The pattern for feeding was mixed, with males feeding slightly more than females in spring but vice versa, with more disparity, in summer. But feeding can be either relatively overt or covert. Assumptions of how many of a gender are actually present, versus the number detected on a survey, must take into account how gender-based behavioral differences affect the relative detectability of each sex.

Likewise, assumptions about the mathematical relationship between the number of overall butterfly individuals actually present in the site to the number detected should also be affected by the tendency of these individuals to behave in ways that make them more or less detectable. These behaviors, in turn, are influenced to some degree by timing and weather variables, as would be expected (Tables 2–4). These variables are relatively amenable to

prescription in survey protocols. But these behaviors are also affected by density dependence. For example, density-dependent sociality may enhance Karner blue detection, for one Karner blue may make another more findable by flushing it or engaging it in flight. It is less clear how survey protocols could account for such density-dependent influences. Thus, relative indices for abundance are often recommended and used for measuring *relative* population size and change (Pollard 1977, Thomas 1983, Pollard and Yates 1993), rather than extrapolating actual population sizes from observations of adult butterflies in the field, which may require many assumptions that may be questionable in validity (Gall 1985).

ACKNOWLEDGMENTS

We gratefully acknowledge funding from the U.S. Fish and Wildlife Service via the Wisconsin Department of Natural Resources in 1990–92, directly in 1993–94, and from Drs. William and Elsa Boyce in 1994–95. We thank two reviewers for their numerous helpful comments.

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