Timing of Karner Blue (Lepidoptera: Lycaenidae) Larvae in Spring and Adults in Spring and Summer in Wisconsin During 1991-1998

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TIMING OF KARNER BLUE (LEPIDOPTERA: LYCAENIDAE) LARVAE IN SPRING AND ADULTS IN SPRING AND SUMMER IN WISCONSIN DURING 1991–1998

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ABSTRACT

During 1991–1998, formal surveys and incidental observations of the Karner blue (*Lycaeides melissa samuelis*) (Lepidoptera: Lycaenidae) occurred on 2–8 dates each year for spring larvae and on 5–10 dates in each adult generation at 148 pine-oak barrens in ten counties of central and northwestern Wisconsin. A total of 493 spring larvae were recorded, as well as 16,039 adults (6755 in spring and 9284 in summer) in 375.5 hours of formal adult survey effort. Adult Karner blue timing varied among years by about 2–5 weeks in spring and 2.5–6 weeks in summer. The mean span between spring and summer adult generations was about 46 to 50 days for all sites pooled. In some years, Karner blue phenology appeared to "speed up" or "slow down" relative to this average span between generations. At six sites surveyed for spring and summer adults in the same 5 years, the mean date of maximum adults differed among sites by about 9.5 days in spring and 6 days in summer. These sites varied in the consistency of their relative phenology (early, average, or late) between spring and summer. Consistent sites changed relatively little in shading from spring to summer because canopy was sparse or primarily evergreen. Variable sites changed in degree of insolation between spring and summer, because of the leafing out of deciduous canopy or the higher angle of the summer sun rising above the surrounding forest more. Four kinds of variability should be considered in assessments of Karner blue phenology: (1) intergenerational fluctuations in abundance, (2) phenological differences among years and (3) among sites, and (4) interannual variation in span between spring and summer generations.

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 throughout its range, 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).

Surveying and monitoring are necessary components of conservation programs for rare or declining butterfly species (Pollard 1977, Thomas 1983, New 1993, Pollard and Yates 1993). As a result, much effort in the U.S.A.

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and Canada is devoted to surveying and monitoring Karner blues (e.g., many chapters in Andow et al. 1994, Brown and Boyce 1998). But depending on seasonal progress, the timing of butterfly life stages—and thus, appropriate timing for field surveys—may vary among years (Warren 1992, Glassberg 1993, Pollard and Yates 1993).

In this paper, we analyze the date on which we observed various phenological events for Karner blue larvae in spring, and adults in spring and summer, for each year during 1991–1998 in Wisconsin. We provide the means and ranges for these dates as well as the means and ranges for the differences in days between pairs of these dates. We also identify patterns of variation in the timing of Karner blue generations. Such information should prove useful for designing survey procedures to monitor populations of this butterfly.

METHODS

Study sites and surveys. Formal surveys and incidental observations of larvae and adults occurred during 1991–1998 at 148 pine-oak barrens in nine counties (Clark, Eau Claire, Green Lake, Jackson, Juneau, Monroe, Portage, Waushara, Wood) in central Wisconsin and one county (Burnett) in northwestern Wisconsin (43.7–46.0° N, 89.1–92.7° W). It was not possible to visit each site each year, but most sites were surveyed multiple times both within a year and among years. Numerous sites in both central and northwestern Wisconsin were surveyed each year.

Although the Burnett County study area is 175 km northwest of the central Wisconsin study area, these two areas seemed to have similar average phenologies during the study. According to Curtis (1959), the two counties are similarly situated in relation to the "tension zone" between vegetative communities characteristic of southern and northern Wisconsin; this tension zone relates to growing season climate. Thus, data from both regions were pooled for analysis here. However, in some individual years, Burnett County might have an earlier phenology than in central Wisconsin (e.g., 1998), or vice versa.

Systematic surveys and casual observations of spring larvae occurred on 2–8 days each year during 1991–1998 (Table 1), as described in Swengel (1995), who analyzed data from 1991–1994. We found larvae both by searching a random number of lupine plants and by searching plants with obvious feeding signs characteristic of the taxon, as demonstrated in Swengel (1995). The length of each larva was measured in the field to the nearest 0.5 mm with a ruler held near but not touching the larva in order to obtain an easily replicated measure of size without disturbing the larva. Summer larvae were noted in casual observations too few and unsystematic for this analysis.

We conducted transect surveys of adult butterflies along like routes within each site each visit, as described in Swengel and Swengel (1996). All species found were counted, but survey times and locations were selected especially to study barrens-specific butterflies, including the Karner blue (Swengel 1998). Karner blue adults were recorded on 5–10 dates in each generation during 1991–1998 (Tables 2–3). Surveys also occurred on at least two dates 1–13 days prior to the first observed spring adult (Table 2). Karner blue individuals were sexed, if possible, and wing wear was informally noted when relevant (e.g., to distinguish a worn spring-generation individual from a fresh summer-generation individual). For each survey, we recorded temperature, wind speed, percent cloud cover, percent time the sun was shining, route distance, and time spent surveying. A few pertinent observations from casual visits in the study areas are also included in this analysis.

Table 1. Observation dates (MDD) of spring generation larvae in April and May, by year. No attempts were made earlier than the earliest date listed for each year.

Year	Dates
1991	502 510 514 515
1992	505 506 518 520 521 526 527 528
1993	504 505 511 519 527
1994	510 511 516 517 520 522 523 526
1995	426 502 509 516 518 520 525 603
1996	507 513 514 520 521 523 606 610 612
1997	506 523 528 601 604
1998	428 506

Table 2. Survey dates (MDD) for spring–generation adults in each study year, including the nearest two survey dates prior to observation of first adults each year.

Year	Dates
1991	515 520 523 528 529 602 607
1992	520 521 526 527 601 602 610
1993	519 527 601 603 605 606 622
1994	517 520 522 523 526 529 531 601 604 606 613 615
1995	529 530 531 603 606 612 614
1996	529 530 601 605 606 610 612 625 626
1997	523 526 527 528 601 603 604 611 612 623 711
1998	510 512 513 519 522 526 602 603 622

Table 3. Survey dates (MDD) for summer-generation adults in each study year, excluding dates after observation of last adult in that year. No adults were observed in 1996 on 712 and 722 and in 1998 on 825. Adults were also observed in 1994 on 906, in 1995 on 905, and in 1997 on 902 and 903.

Year	Dates
1991	712 715 717 719 724 725
1992	727 729 804 805 821
1993	726 728 803 804 820
1994	708 718 720 723 727 803 809 819 822
1995	719 721 726 802 803 812 827
1996	712 722 724 730 731 812 827
1997	711 716 721 723 729 806 827
1998	622 701 708 713 714 715 720 722 728 812

Table 4. List of Karner blue phenological events analyzed in this study, both for all sites pooled and individually for 15 frequently surveyed sites. For individual sites, if a date for the beginning of the flight was unavailable, a date for "none" was used only if it was plausible given the history of phenology at the site among years (i.e., an early, average, or late site) and given that year's overall Karner blue phenology (i.e., an early, average, or late year). For individual sites, a date for the beginning of the flight was used if it was the first date adults were observed at any site, if the site had been visited within a few days before ("none"), or if the date was plausible given the site's and year's phenology.

Spring larval greatest length	
≥3 mm	first date any larva ≥3 mm and <7 mm long was observed
≥7 mm	first date any larva ≥7 mm and <13 mm long was observed
≥13 mm	first date any larva ≥13 mm long was observed
≥15 mm	first date any larva ≥15 mm long was observed
Spring larval mean length (only if >1 larva observed that date)	
$\bar{x} = 5$ mm	first date all larvae observed averaged 5 mm and <10 mm
$\bar{x} = 10$ mm	first date all larvae observed averaged 10 mm
Spring adult flight	
none	last date of no adults observed before beginning of spring flight, if <7 days before date of beginning of spring generation of adults
beginning	date first adult was observed in spring generation, if only 1–5 individuals observed (fewer in a small population, up to the larger range in a large population) as long as weather was not inclement
flight peak	date of highest mean density in spring generation, only if >1 site surveyed that date (not applicable to individual site analysis)
site maximum	date of highest density on one site survey in spring generation
Summer adult flight	
none	last date of no adults observed before beginning of summer flight, if <7 days before date of beginning of summer generation of adults
beginning	date first adult was observed in summer generation, if only 1–5 individuals observed, as long as weather was not inclement
flight peak	date of highest mean density in summer generation, only if >1 site surveyed that date (not applicable to individual site analysis)
site maximum	date of highest density on one site survey in summer generation

Phenological events. The phenological events analyzed in this study (Table 4) seemed readily identifiable in our dataset, replicable by others, and comparable to information available in the literature. These events were dated, if possible, for each year from 1991 to 1998, both for all sites pooled and separately for 15 sites in Jackson and Wood Counties most often surveyed both within and among years for both larvae and adults. Only one of these sites had a date for both spring and summer adult site maxima in each year. No site had a date for any other spring or summer adult event, or any spring larval event, for each year in the study. Pooling sites drew on the most sampling days per generation, thus minimizing sampling error. Analysis by individual site portrayed the variation in timing among sites within a year.

Larval events (Table 4) were based on larval length rather than instar, as the former requires less expertise than the latter. Larval events were dated both on the basis of any observed larva reaching the specified length and on means of multiple individuals. The latter would be less prone to sampling error (as it requires a sample of multiple individuals), but the former may be more comparable among research teams. Given daily mortality, smaller larvae are more abundant than larger ones in a given generation, but larger larvae are much easier to find (Swengel 1995). Thus, means may be more affected by differential ability among surveyors, as the value of the mean depends on how many of the smaller larvae present are found. Larval lengths of 3 mm, 7 mm, and 13 mm should all represent different instars, but the lengths of 13 mm and 15 mm should both be final instars (Swengel 1995). The greatest larval length observed in this study was 15 mm, except for two individuals measuring 16 mm and 17 mm in 1994 (Swengel 1995), so we included the 15 mm length as the measure of fully mature larvae. But 15 mm larvae were not observed every spring of this study, while 13 mm ones were, so the 13 mm length was included to increase sample size.

The dates for site maximum and flight peak in spring and summer (Table 4) were included only if plausibly within a few days of peak. This was a stricter definition than used previously for population monitoring in Figure 2 of Swengel and Swengel (1996), which only required the peak survey to occur within the main flight period. The definition of flight peak in this analysis (Table 4) also differs a bit from that used in Table 2 of Swengel and Swengel (1996), which used the date on which the most individuals were observed, regardless of survey effort. As a result, a few differences occur between Swengel and Swengel (1996) and this study in date of adult peak for a given generation.

We calculated the mean and range of dates for these phenological events, and the mean and range of the span in days between pairs of events, both for the pool of all sites and for the 15 individual sites. To facilitate these calculations, each calendar date was first converted to a Julian date, a sequential integer numbering of each date in the year (1 for 1 January and 365 for 31 December). But we adjusted for leap year (when 31 December is 366) so that each calendar date (e.g., 1 June: 152 in non-leap years and 153 in leap years) had the same Julian date (e.g., 152) in all years. To provide the most control in comparisons of variation among years, the mean and range of dates and spans were also calculated only for the six sites with values for spring and summer adult site maximums in the same years (1992, 1994–1995, 1997–1998); data were insufficient for the other years (1991, 1993) and for all other events. Analysis was done with ABstat 7.20 software (1994, Anderson-Bell Corp., Parker, Colorado).

RESULTS

The total numbers of Karner blue larvae and adults observed, as well as hours of formal survey effort for adults, are listed by generation in Table 5. Since larval survey effort was often unmeasured (in terms of time, distance, or area), it was not possible to assess variation in larval density among years. However, the adults varied considerably in abundance among years, based on the crude measure of total number of individuals per survey effort in each generation (Table 5).

Variation in date. For the pool of all sites, the dates on which each phenological event occurred varied greatly among years (Table 6). For example, mature larvae (13+ mm length) were found on 28 April 1998, while no larvae

Table 5. Total number of Karner blue larvae observed in spring, and for adults, the total hours of formal survey effort and total number of Karner blue individuals observed, for all sites pooled. The total for survey effort includes the nearest two dates prior to observation of first adults in spring (applicable in all years) through the first date after observation of the last adult in summer (only applicable in 1998). For the two dates (in 1997 and 1998) when both spring and summer adults were apparently observed, the individuals are included in the total for the appropriate brood but the survey effort is all allocated to the summer brood.

	1991	1992	1993	1994	1995	1996	1997	1998	All years
Spring									
N larvae observed	15	186	84	76	52	19	18	43	493
N hours of adult surveys	12.3	14.3	11.9	42.0	28.2	23.2	37.0	24.0	192.9
N adults observed	520	1237	264	1448	346	276	979	1685	6755
Adults/survey effort	42.3	86.5	22.2	34.5	12.3	11.9	26.5	70.2	35.0
Summer									
N hours of adult surveys	16.6	21.9	16.1	30.9	28.6	19.3	24.8	24.4	182.6
N adults observed	877	1377	585	2319	884	620	1366	1256	9284
Adults/survey effort	52.8	62.9	36.3	75.0	30.9	32.1	55.1	51.5	50.8

Table 6. Date (MDD) for each phenological event (defined in Table 4) by year, for all sites pooled. Mean rank for each year is calculated based on the ranks for all events for which a date is available in each year (see Table 10). Dates in parentheses are not included in analyses, as these are believed to be less precise than in the other years.

	Spring larval length (mm)						Spring adult				Summer adult				Year rank
year	≥3	≥7	≥13	≥15	$\bar{x}=5$	$\bar{x}=10$	none	beg.	peak	max.	none	beg.	peak	max.	mean±SD
1991		502	514		502	510	520	523	529	529			712	712	2.4 ± 1.4
1992	505		518	518		518	521	526	610	602			805	805	5.6 ± 1.9
1993	504		511	519	511	519	527	601	(622)	(622)			803	804	6.6 ± 1.3
1994			510			510	520	522	606	606		708	727	727	3.3 ± 1.0
1995	426	502	516	518	509	516	530	531	612	612		719	802	726	5.4 ± 0.5
1996	507	514	520		513	520	530	601	(625)	(612)	722	724	812	731	7.3 ± 1.0
1997			506			506	526	527	612	604		711	729	721	3.4 ± 1.5
1998			428		428	506	512	513	522	526		622	714	713	1.3 ± 0.5

were ≥7 mm on later dates in May in 1992, 1993, and 1996. Dates for flight peak and site maximum of spring adults in 1991 and 1998 were earlier than the last date of no adults being recorded prior to the spring adult generation in 1995 and 1996. Likewise, dates for flight peak and site maximum of summer adults in 1991 and 1998 occurred before the date of first summer adults being recorded in 1995 and 1996. In three of six analyzable spring generations and five of eight summer generations, the flight peak and site maximum occurred on different dates (Table 6). That is, the date on which a single particularly high-density site achieved its maximum count was often different from when the pool of sites peaked.

At the six consistently surveyed sites, the mean date of adult site maximum differed among sites by about 9.5 days in spring and 6 days in summer (Table 7). These sites were variable in the consistency of their rankings between spring and summer (Table 7). Dike 17 ranked first (earliest) in both seasons, while two other sites were rather similar in rank between spring and summer: Stanton was fourth and third (intermediate) in rank and Highway X (main) sixth and fifth (late), respectively. These three sites had relatively little change in canopy from spring to summer, because either they have little canopy from shrubs and trees (Dike 17), or the canopy includes a considerable proportion of evergreen pines (Stanton, Highway X main). The other three sites varied considerably in rank between seasons; i.e., they tended to be relatively earlier or later in one season than the other. The two sites that became relatively later in summer than spring (North Brockway east and Wildcat northeast) had a considerable proportion of deciduous canopy, so that their shading increased considerably between spring and summer upon leafing out. Highway X (east-west) tended to be relatively later in spring than summer. At this east-west powerline right-of-way through mature forest, insolation increases greatly from spring to summer, as the sun becomes higher in the sky and rises above the surrounding forest for more of the day.

The mean dates for all sites pooled tended to be slightly earlier than the corresponding mean dates for the 15 individual sites (Table 8). Since the dating of most events for the pool of sites is based on the first date for that event at any site, most of these dates (except flight peak and site maximum) are biased toward the earliest site(s).

The tendency was strong for the standard deviation around the mean for a spring adult date to be consistently smaller than the standard deviation around the mean for the comparable summer adult date (counting only events with >1 date to average in this comparison). That is, the various dates measuring the development of the summer adult generation were more variable than the comparable dates in spring. This was consistently the case for the pool of all sites and the sample of 15 individual sites (Table 8) and for the six sites sampled for both spring and summer adults in the same five years (Table 7). This pattern did not hold, however, when these six sites were pooled for analysis by year (Table 7), as the spring generation was more variable (i.e., had higher standard deviations) than the summer generation in some years.

The variation among years in date for each spring adult event spanned 17–21 days (depending on the particular event) for the pool of all sites and 28–37 days for the 15 individual sites (Table 8). The spring adult site maximum varied among years by 11–20 days within each of the six consistently surveyed sites, and by 26 days between the earliest and latest site maximum among these sites (Table 7). The range in date for summer adult events was consistently larger: 24–32 days for the pool of all sites and 30–41 days for the 15 individual sites (Table 8); 18–25 days within each of the six sites and 29

Table 7. Mean ± SD and range of Julian dates for spring and summer adult site maximums (defined in Table 4), and mean ± SD and range of the difference in days between these two maximums, for six sites with dates available for these events in each of the same 5 years (1992, 1994, 1995, 1997, 1998), in order of mean spring adult maximum.

Site	Spring adult site maximum (Julian date)		Summer adult site maximum (Julian date)		Difference (days) between maximums	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
By site						
Dike 17	151.2 ± 7.1	139–157	204.2 ± 9.7	189–214	53.0 ± 5.0	49–61
North Brockway (east)	152.0 ± 4.1	146–157	208.6 ± 8.2	195–216	56.6 ± 5.3	49–64
Wildcat (northeast)	155.4 ± 7.7	146–165	210.2 ± 9.3	195–218	54.8 ± 6.2	49–64
Stanton	155.6 ± 7.8	146–165	208.0 ± 8.7	195–216	52.4 ± 6.1	48–63
Highway X (east-west)	155.8 ± 7.0	146–163	205.4 ± 9.6	195–217	49.6 ± 9.1	40–64
Highway X (main)	160.8 ± 4.5	153–164	209.8 ± 6.8	199–217	49.0 ± 8.7	35–56
By year						
1998	146.0 ± 4.4	139–153	196.3 ± 6.7	189–209	50.3 ± 2.8	49–56
1992	154.0 ± 3.5	152–161	216.0 ± 1.1	214–217	62.0 ± 3.2	56–64
1994	154.3 ± 4.9	151–164	203.2 ± 4.2	199–208	48.8 ± 8.3	35–57
1997	159.7 ± 4.0	154–163	210.0 ± 5.1	202–218	50.3 ± 6.5	40–56
1995	161.7 ± 3.7	157–165	213.0 ± 3.0	207–215	51.3 ± 2.9	49–57
Mean for these sites	155.1 ± 6.8	139–165	207.7 ± 8.3	189–218	52.6 ± 6.9	35–64

Table 8. Mean ± SD and range of dates in N years of available data, for various events of larval and adult timing (defined in Table 4), presented both as Julian and rounded calendar dates.

	N	Julian mean ± SD	Calendar mean	Julian range	Calendar range
All sites pooled					
Spring larval greatest length					
≥3 mm	4	123.0 ± 4.8	3 May	116–127	26 Apr–7 May
≥7 mm	3	126.0 ± 6.9	6 May	122–134	2 May–14 May
≥13 mm	8	131.6 ± 7.1	12 May	118–140	28 Apr–20 May
≥15 mm	4	136.3 ± 4.2	16 May	130–139	10 May–19 May
Spring larval mean length					
x̄ = 5 mm	5	126.6 ± 6.3	7 May	118–133	28 Apr–13 May
x̄ = 10 mm	8	133.1 ± 5.8	13 May	126–140	6 May–20 May
Spring adult flight					
before flight	8	143.3 ± 6.2	23 May	132–150	12 May–30 May
beginning	8	145.8 ± 6.5	26 May	133–152	13 May–1 June
flight peak	6	155.8 ± 8.6	5 June	142–163	22 May–12 June
site maximum	6	153.8 ± 6.0	3 June	146–163	26 May–12 June
Summer adult flight					
before flight	1	203.0	22 July		
beginning	5	191.8 ± 12.3	11 July	173–205	22 June–24 July
flight peak	8	209.5 ± 10.7	29 July	193–224	12 July–12 August
site maximum	8	206.1 ± 9.2	25 July	193–217	12 July–5 August
By individual site					
Spring larval greatest length					
≥3 mm	12	124.0 ± 2.9	4 May	116–127	26 April–7 May
≥7 mm	12	128.3 ± 6.2	8 May	118–140	28 April–20 May
≥13 mm	28	134.9 ± 6.1	15 May	118–142	28 April–22 May
≥15 mm	15	137.6 ± 4.4	18 May	130–142	10 May–22 May
Spring larval mean length					
x̄ = 5 mm	13	127.0 ± 5.8	7 May	118–134	28 April–14 May
x̄ = 10 mm	20	136.6 ± 5.0	17 May	126–142	6 May–22 May
Spring adult flight					
before flight	37	147.0 ± 7.9	27 May	133–161	13 May–10 June
beginning	22	151.4 ± 8.1	31 May	133–165	13 May–14 June
site maximum	65	157.3 ± 8.3	6 June	139–176	19 May–25 June
Summer adult flight					
before flight	5	201.4 ± 14.7	20 July	182–212	1 July–31 July
beginning	12	201.0 ± 12.3	20 July	173–214	22 June–2 August
site maximum	66	210.4 ± 9.4	29 July	189–224	8 July–12 August

days between the earliest and latest summer site maximum among these six sites (Table 7). Thus, individual sites showed more variation in timing than the overall pool of sites did.

Variation in spans between dates. The spans between the same pairs of phenological events, averaged over all the study years, were rather similar for the pool of all sites compared to the corresponding mean spans for the 15 individual sites (Table 9, counting only means based on more than one span of dates per pair of events). Each year from 1991 to 1998 could be ranked

Table 10. Rank of each year for each phenological event for which a date was available for each year during 1991–1998 (Table 6). Years in parentheses correspond to dates in parentheses in Table 6.

	Larval length		Spring adult			Summer adult	
rank	≥13 mm	$\bar{x}$ = 10 mm	beginning	peak	maximum	peak	maximum
1	1998	1998,1997	1998	1998	1998	1991	1991
2	1997		1994	1991	1991	1998	1998
3	1994	1991,1994	1991	1994	1992	1994	1997
4	1993		1992	1992	1997	1997	1994
5	1991	1995	1997	1995, 1997	1994	1995	1995
6	1995	1992	1995		1995, (1996)	1993	1996
7	1992	1993	1993, 1996	(1993)		1992	1993
8	1996	1996		(1996)	(1993)	1996	1992

(from earliest to latest) for each of the seven events (Table 10) that were dated in all these years for the pool of all sites (Table 6). Two years—1998 (which ranked first overall) and 1995 (fifth out of eight)—had very similar ranks for each of these events, based on the very low standard deviations of their mean ranks (Table 6). The two years (1992, 1997) with the highest standard deviations around their mean ranks showed two marked reversals in ranking during the course of the growing season. The rank for 1992 changed from being relatively later for spring larvae, then relatively earlier for spring adults, then relatively later again for summer adults. By contrast, the rank for 1997 was earlier for spring larvae, then later for spring adults, then earlier again for summer adults. Two years showed progressive changes in rank: 1991 became progressively earlier, while 1993 became progressively later.

DISCUSSION

Comparisons with other studies. The larval measurements we obtained in the field could not be precise, given the obscured or bent positions of the larvae and their sensitivity to disturbance (Swengel 1995). Herms et al. (1996) reported that even with laboratory conditions and equipment, larval length was difficult to measure because the larvae were often moving, appearing more elongate than when stationary. Although larvae were usually not moving when we measured them, they could still be actively engaged (e.g., feeding, being tended by ants). This may explain why our measurements tended to be longer than theirs; our greatest length was 15 mm (except for one 16 mm and 17 mm larva), while theirs was 12.5 mm.

Herms et al. (1996) reported that for laboratory rearing at 24–26° C of Michigan larvae in summer 1994 (i.e., eggs laid by spring females), development from the first to final instar required a mean±SE of 13.1±0.4 days (range 11–16 days, n=15 larvae). They measured this span more exactly than we could, and our measurements occurred under the vagaries of spring weather in the field. Yet, rather remarkably, our span between 3 mm (early instar) larvae and 13 mm (last instar) larvae was quite similar, with a mean±SE of 13.3±2.7 days for all sites pooled and 13.3±1.5 for the 15 individual sites (Table 9). Herms et al. (1996) also reported a mean±SE of 26.0±0.4 days (range 24–29, n=15 individuals) in laboratory rearing from egg laying to summer adult emergence. Although our measurements do not include egg de-

velopment, our mean±SE for the span from 3 mm spring larvae to the first spring adult was similar: 27.3±3.0 (range 21–35) for all sites pooled and 26.0±2.1 (range 21–31) for individual sites (Table 9). By contrast, Grundel et al. (1998) reported a mean±SE in span from egg laying to summer adult emergence of 41.5±0.4 days for 1994 rearing at room temperature (about 22° C) in Indiana. This difference in span between Grundel et al. (1998) and Herms et al. (1996) may be attributable at least in part to the 2–4° C warmer rearing temperature in the latter study.

The mean span of 41.5 days for laboratory rearing from egg laying to summer adult reported by Grundel et al. (1998) is consistent with but slightly faster than the mean span we observed in the field between the same spring and summer adult events, which should approximate the amount of time required for one complete life cycle. Our span was about 46 to 50 days (range 35–64) for the pool of sites, depending on which phenological event was compared between spring and summer (Table 9). The 6 individual sites averaged slightly longer spans, with means varying from 49 to over 56 days, although the range (35–64) was the same as for the pool of all sites (Table 7).

Others' survey data from Wisconsin sites indicated similar spans between comparable phenological events for spring and summer adults. Bleser (1993, 1994) provided beginning and/or peak survey dates for spring and/or summer adults at six Wisconsin sites for 1991–1992: three sites in Necedah National Wildlife Refuge (Juneau County), Wedde Creek Fishery Area (Waushara County), and Hartman Creek State Park and the nearby Welch property (both in Portage County). Maxwell (unpubl. data) provided similar data for 1993–1995 at Fort McCoy (Monroe County, Wisconsin), here treated as a single site. In those surveys, a mean±SD of 43.5±6.4 days (range 37–52 days, n=4) occurred between the beginning of the spring and summer adult generations and 48.8±13.7 days (range 34–78 days, n=13) between the spring and summer adult site maximums. For 27 subsites at Fort McCoy with distinct site maximums (i.e., the highest number of individuals observed occurred on only one date) in spring and summer 1993 (Maxwell unpubl. data), the mean span was 54.7±6.4 days (range 44–69).

Field data from other states tended toward somewhat shorter spans between the spring and summer generations but still within the range found here. Grundel et al. (1998) reported a span between spring and summer adult site maximums of 37–41 days in 1995 but 44–52 days in 1996. Data in Lawrence (1994) from 1989 at Allegan State Game Area, Michigan indicated a span from spring to summer adult site maximums of 41 days. Herms et al. (1996) indicated a difference between the beginning of the spring and summer adult generations of 39–42 days in 1994 in Michigan at Allegan and Huron-Manistee National Forest.

The survey data available for Wisconsin sites in Bleser (1993, 1994) and Maxwell (unpubl. data) indicated similar but slightly longer spans than we found between the first and maximum adults in both generations. In spring we documented a mean±SD of 10.2±3.7 days (range 6–15) for the pool of all sites and 9.3±3.0 (range 5–14) for the 15 individual sites (Table 9), while the others' data averaged 11.6±1.7 days (range 10–14 days, n=5). In summer we observed a span of 12.0±6.3 days (range 7–21) for pooled sites and 10.2±3.7 (range 6–16) for individual sites, while the others' data averaged 13.6±5.0 days (range 9–22, n=5).

The actual dates of spring and summer adults showed considerable concordance between our and others' data for Wisconsin sites in the same years. The beginning date of spring adults for the sites in Bleser (1993, 1994) and Fort McCoy (treated as a single site) in Maxwell (unpubl. data) in 1991, 1993, 1994, and 1995, with ours (Table 6) in parentheses following theirs,

were 24–26 May (23 May), 4 June (1 June), 24 May (22 May), and 27 May (31 May), respectively. The spring adult maximum for the sites in Bleser (1993, 1994) in 1991–1992 and the estimated flight peak at Fort McCoy in 1993–1995, with our flight peak (Table 6) following in parentheses, were 2–7 June (29 May), 2–11 June (10 June), 14 June, 3 June (6 June), and 10 June (12 June). Somewhat more variation occurred between their and our data in summer. The beginning date of summer adults in the others' survey data in 1991–1995, with ours (Table 6) following in parentheses, were 4 July, 28 July, 26 July, 30 June (8 July), and 10 July (19 July). Their maximum dates for summer adults in 1991–1995, with our flight peak (Table 6) following in parentheses, were 10–19 July (12 July), 3–19 August (5 August), 9 August (3 August), 22 July (27 July), and 22 July (2 August).

Dates from other states were similar to, but sometimes slightly earlier than, ours. Dirig and Cryan (1976) reported that spring adults at the Albany Pine Bush, New York typically first appeared on or a few days after 20 May. We observed the first spring adult before or within three days after 20 May in only three of eight years (Table 6). Lawrence (1994) reported the spring adult maximum at Allegan, Michigan in 1989 on 8 June, similar to our average flight peak of 5 June during 1991–1998 (Table 8). First spring adults at Allegan and Huron-Manistee, Michigan in Herms et al. (1997) in 1993–1995, with ours (Table 6) following in parentheses, were 25 May (1 June), 19–24 May (22 May), and 22–29 May (31 May). The Michigan dates had a mean±SD of 144.0±3.3 (24 May), compared to 145.8±6.5 (26 May) for our pool of sites and 151.4±8.1 (31 May) for individual sites (Table 8). First summer adults at the two Michigan sites in 1994 (Herms et al. 1996) was 27 June–5 July, compared to 8 July in our surveys (Table 6). Lawrence (1994) reported the summer adult maximum at Allegan, Michigan in 1989 on 19 July, somewhat earlier than our average flight peak during 1991–1998 of 29 July but within our range from 12 July to 12 August (Table 8).

Types of variability. Four kinds of variability should be considered in assessments of Karner blue phenology. The first is fluctuation in abundance. This was rather crudely measured here (Table 5), since sites and timing of survey dates relative to phenological development were not controlled among generations. But the considerable variation in relative abundance was consistent with the pronounced fluctuation reported in Swengel and Swengel (1996) for a set of consistently surveyed Karner blue sites. Observation of few or no individuals in the life stage targeted by a survey may lead to an assumption that the targeted life stage has primarily occurred already or will occur later. But it is also possible that the survey occurred during prime timing for that life stage, but very few individuals were findable because of low fluctuation in abundance. Thus, it is very important to survey with sufficient intensity so as to distinguish between a paucity of observed individuals because of fluctuation or phenology.

A second form of variability relates to phenological differences among years. For British butterflies, this variation has been correlated to climatic factors, with the beginning of flight periods differing by about 2–4 weeks among years (Pollard et al. 1986, Pollard and Yates 1993, Sparks and Yates 1997). Karner blue timing varied by about 2–5 weeks in spring and 2.5–6 weeks in summer, depending on the event measured and spatial scale, as individual sites showed more variation in timing than pooled sites (Tables 8–7).

This phenological variation among years is distinct from the third form of variability: phenological variation among sites. In this study, different sites exhibited persistent differences in phenology, with some consistently "fast" sites relatively earlier in average phenology than "slow" sites (Table 7). Pol-

lard and Yates (1993) also documented strong differences in timing and length of the adult life stage in the same year for the same butterfly species between nearby sites. For phenological variation among *years* (the second form of variability), date and span tended to be slightly more variable in summer than spring (Tables 8–9; see preceding paragraph). But for phenological variation among *sites* averaged over many years (the third form of variability), the mean date of maximum adults at the six consistently surveyed sites tended to be slightly more variable in spring than summer. The difference in mean spring adult site maximum between the earliest and latest sites was about 9.5 days, but about 6 days in summer (Table 7).

This appears contradictory but could be a matter of sampling error or minor differences with no great importance. But these patterns could also validly represent two separate phenomena. First is the range in timing of the adult generations *among* years (the second form of variability), which could be somewhat greater in summer than spring as a result of compounding. An early spring combined with a hot summer could cause the span between spring and summer generations to be shorter, with the summer adult generation relatively earlier compared to the average summer adult timing than the spring adults were relative to average spring adult timing. Conversely, a late spring followed by a cool summer could extend the span between generations, with summer adults relatively later compared to average summer timing than the spring adults were relative to average spring timing.

However, *within* a year (whether early, average, or late in phenology), the variation in timing of adults *among* sites (the third form of variability) could vary a bit more in spring than summer as a consequence of the thermal threshold for larval activity and development, apparently about 12-13° C (Swengel 1995). Since diurnal spring weather would be near or below this threshold much more often than summer weather, differences in microclimate among sites would affect larval development in spring more than in summer. Spring immatures in a site consistently just above the threshold temperature would complete development well ahead of those in a site consistently just below the threshold. In summer, phenological variation among sites might not matter nearly as much because virtually all sites would be above the threshold temperature most or all of the time. Thus, among years the prime time for the adult generation could be more volatile in summer (varying from early July in one year to mid-August in another) than spring (from late May to mid-June). But within a given year, regardless of overall phenology (early, average, or late), variation in timing at individual sites could be more volatile in spring than summer. This is consistent with Scott's (1986) report that flight periods in Colorado (as measured for a pool of sites) tended to be longer in spring than summer as a consequence of seasonal differences in weather.

The fourth source of variability concerns the span between pairs of phenological events within a year (i.e., time elapsed between spring and summer generations). While some years were quite consistent in rank throughout the growing season from spring larvae through summer adults, other years showed some relative change in rank (Table 10). Radical differences in Karner blue phenology between the spring and summer generations appear unlikely. That is, a very early summer generation couldn't follow a very late spring generation. But Karner blue timing in some years appeared to "speed up" from a later spring phenology to a not as late summer phenology, or vice versa, and more complex combinations of "speeding up" and "slowing down" were also apparent (Table 10 and see Results). Some of this could result from sampling error, but it also seems plausible that the span between spring and

summer adults, which was quite variable (Table 9), could differ among years as a function of climatic variation.

Thus, it is not possible to predict with much precision the dates for summer timing simply by adding a set number of days to comparable dates for spring timing. However, future analyses relating the dates of phenological events, like those presented here, to weather data such as degree-days offer the possibility of greater predictive power for the timing of Karner blue phenological events later in the same year, as done for many insect pest species (Pruess 1983).

Summary. In this study, field measurements of larvae (in which we avoided touching or otherwise disturbing the larvae) were slightly longer (maximum length 15 mm, except for one 16 mm and one 17 mm) than reported from caliper measurements in the laboratory (maximum 12.5 mm). While measurements are not directly comparable between these two methods, the data reported here should be useful to other researchers when using the same method of measurement in the field.

The span between comparable spring and summer phenological events in this study was typically about 46–56 days (range 35–64), which is similar to spans in others' survey data from Wisconsin. Field data from other states tended toward somewhat shorter spans (37–52 days) which are closer in length to reports from laboratory rearing. We observed slightly shorter but similar spans between first and maximum adults within the same generation (mean 9–12 days, range 5–21) than others have in Wisconsin (mean 11–14 days, range 6–22 days). The actual dates of phenological events for spring and summer adults in Wisconsin varied by 1–9 days in spring and 2–14 days in summer between our and others' data in the same years. In other states, these dates were similar to, but sometimes slightly earlier than, those reported for Wisconsin.

Four kinds of variability affect assessments of Karner blue phenology. The first is fluctuation in abundance among years, which can be pronounced for this butterfly. It is important to be able to interpret whether low observed numbers of the life stage targeted by a survey may be due to phenology (timing of the survey) or low fluctuation (correct survey timing but low numbers in that generation).

The second form of variability relates to phenological differences among years, often attributed to climatic factors. In this study, Karner blue timing varied among years by about 2–5 weeks in spring and 2.5–6 weeks in summer. The third form is variation in phenology among sites, which can be consistently "fast" (relatively earlier in phenology), average, or "slow" (relatively later in phenology). In this study, the mean date of maximum adults at six consistently surveyed sites tended to be slightly more variable in spring (range of 9.5 days) than summer (range of 6 days). Thus, among years (the second form of variability), the prime time for the adult generation appeared more volatile in summer than spring. But within a given year, regardless of that year's overall phenology (early, average, or late), variation in timing among sites (the third form of variability) seemed more volatile in spring than summer.

Fourthly, the span between comparable phenological events in the spring and summer generations can vary among years. In some years, Karner blue phenology was consistently early, average, or late in both the spring and summer generations. But in other years, Karner blue timing appeared to "speed up" from a later spring phenology to a somewhat earlier summer phenology, or vice versa, in apparent correspondence to climatic variation. Thus, it does not appear possible to predict with much precision the dates for sum-

mer timing simply by adding a set number of days to comparable dates for spring timing.

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