Movement Patterns and Population Characteristics of the Karner Blue Butterfly *(Lycaeides melissa samuelis)* at Indiana Dunes National Lakeshore

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ABSTRACT: We conducted a three-year mark-release-recapture study of the endangered Karner blue butterfly *(Lycaeides melissa samuelis* Nabokov) at Indiana Dunes National Lakeshore to describe the butterfly's movement patterns and to assess seasonal changes in the Karner blue's population structure. Estimated mean Karner blue adult life span was less than 3.5 days. Populations exhibited protandry and about a 2:1 male:female sex ratio at population peak within a brood. Ranges, or maximum distances moved by individual butterflies, were typically less than 100 m. Maximum ranges were less than 1 km. These distances are similar to those reported for other lycaenid butterflies and from other studies of the Karner blue in the midwestern United States. At two sites, fewer than 2% of adults had ranges greater than 300 m, while at a third site 4.3% of adults had ranges greater than 300 m. Given typical subpopulation sizes these movement percentages suggest that few adults per generation will move between subpopulations separated by more than 300 m. Movement of individuals between subpopulation sites is important for maintaining genetic diversity within a metapopulation and for recolonizing areas following local extinctions. Therefore, prudent conservation planning should aim for a landscape with habitat patches suitable for Karner blue butterfly occupancy separated by less than 300 m.

Index terms: Karner blue butterfly, *Lycaeides melissa samuelis*, butterfly dispersal, metapopulations, insect conservation

INTRODUCTION

Habitat heterogeneity can be a benefit and a disadvantage to the Karner blue butterfly *(Lycaeides melissa samuelis* Nabokov). This endangered subspecies benefits from a mixed landscape of sunny and shaded areas. This mixture helps to buffer the potentially negative effects, on larvae and adults, of hot or cold temperatures or drought during the spring and summer months (Lane 1994, Maxwell 1997, Grundel et al. 1998b). In the upper Midwest, oak savannas can provide this shade mixture.

Habitat heterogeneity can also be disadvantageous to the Karner blue butterfly. In many respects, Midwest oak savannas are ecotonal communities, containing elements of woodlands and grasslands and, often, wetlands (Packard 1993). Although ecotones can serve as movement corridors for butterflies (Wood and Samways 1991), some components of the contemporary savanna matrix, including heavily wooded, wet, or developed areas, probably serve as barriers to Karner blue movement or habitation. Such barriers can effectively subdivide a large population, or metapopulation, into many subpopulations (Thomas and Harrison 1992).

Balancing the advantages and disadvantages of habitat heterogeneity is a central management issue in Karner blue conservation. Karner blue subpopulations are often small and thus prone to local extinction. The butterfly prefers early to midsuccesional habitats whose suitability can deteriorate in a few years in the absence of disturbance (Andow et al. 1994). Because of these facts, adult dispersal from area to area is important for metapopulation viability. However, the Karner blue is often characterized as a low vagility species (Lawrence 1994, Bidwell 1995). The combination of the importance of dispersal with the likelihood of low vagility is problematic. Land managers face the challenge not only of maintaining quality habitat but also ensuring that habitat patches are situated over the landscape in a manner that allows movement and genetic ex-change among patches. An understanding of Karner blue butterfly adult movement patterns therefore is basic to effective conservation.

The importance of understanding movement patterns is heightened by the role of disturbance in Karner blue management. Both the Karner blue and its larval host plant, wild lupine *(Lupinus perennis L.)*, can benefit from disturbance that maintains open canopy conditions. Periodic fire commonly produces and maintains those open conditions. However, Karner blue populations often suffer high mortality during fires (pers. obs.). Fire, therefore, both improves habitat and, at least temporarily, suppresses resident butterfly populations. These opposing effects can be reconciled to the Karner blue's benefit if recolonization of burned areas is rapid. Understanding how far potential colonizers might move is therefore important in planning the geometry of prescribed burns. Thus there are several reasons why having detailed information on movement patterns of the Karner blue is critical for management. To quantify these patterns, we undertook a three-year-long mark-release-recapture study of the Karner blue butterfly at Indiana Dunes National Lakeshore. Here we examine movement patterns and some factors that affect the butterfly's population structure. We also provide some suggestions for standardizing census methods for the Karner blue.

METHODS

Karner Blue Butterfly Life History

The Karner blue butterfly overwinters as eggs that begin hatching in mid-April at Indiana Dunes National Lakeshore. The larvae that emerge pass through four in-stars. After the pupal stage, first brood adults emerge during late May and June. Following mating, females of this first, or spring, brood lay eggs that will lead to a second, or summer, brood of adults in July and August. Females of this second brood lay the eggs that overwinter, starting the cycle anew. In both broods, larvae feed on wild lupine, mainly on leaf mesophyll.

Study Site

We studied the Karner blue butterfly at Indiana Dunes National Lakeshore. This 6000-ha park is located at the southern tip of Lake Michigan and provides protection for over 1100 native plant species (Wilhelm 1990). The Karner blue butterfly in-habits several sections of historic oak savannas within the park. These areas have experienced significantly different fire histories during this century (Henderson and Long 1984). Although black oaks *(Quercus velutina* Lam.) dominate each area's canopy, the areas vary significantly in canopy, subcanopy, and ground vegetation density.

We marked butterflies at four sites (Figure 1, Table 1). The first, Inland Marsh, is a 200-ha oak savanna/marsh complex. A large wildfire in 1986, a moderately long interfire interval (Henderson and Long 1984), and a history of sand mining have produced a mixed landscape. Within Inland Marsh, Karner blues reside in sand-mined areas, in savannas with moderate woody vegetation density in the understory, and in some open areas surrounded by thick oak sprouting. Kamer blues are absent from most densely wooded areas and marshes.

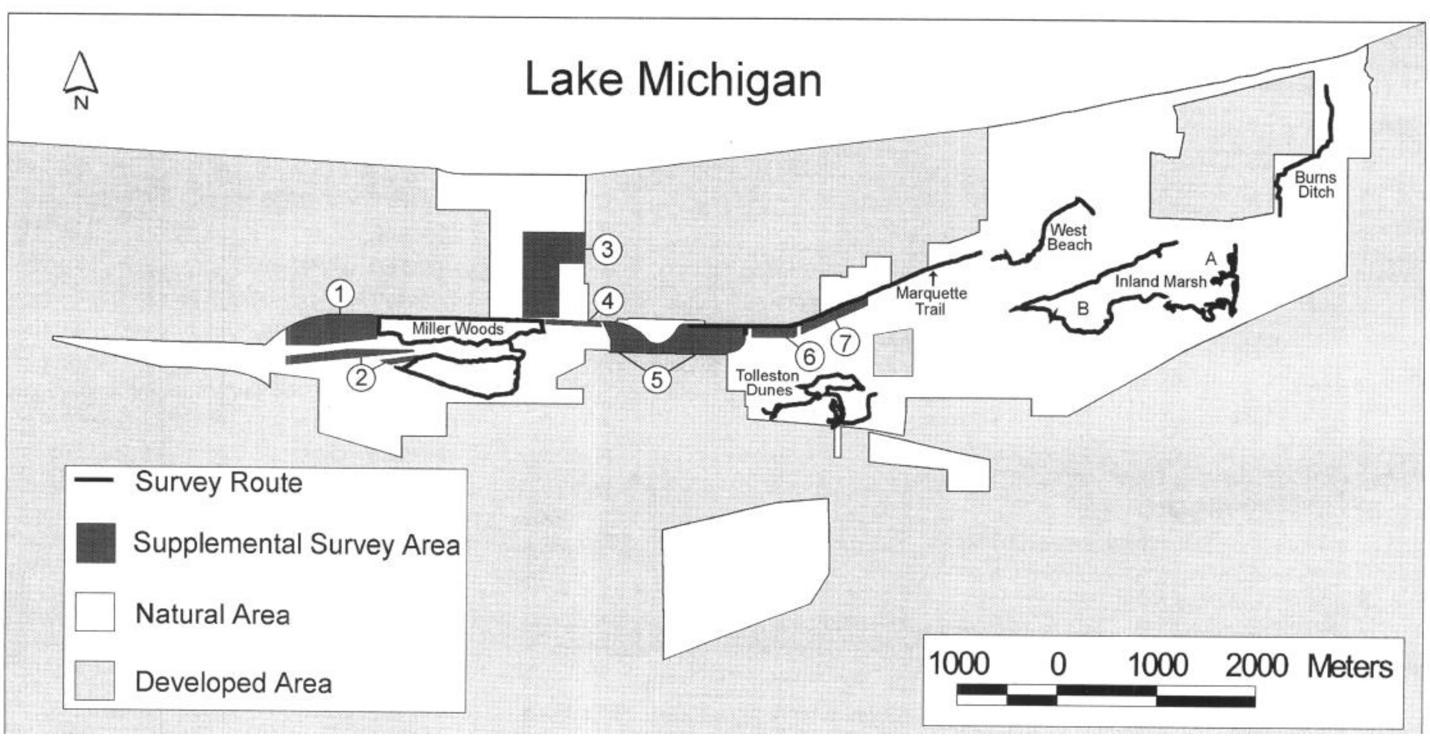

Figure 1. Map of Kamer blue butterfly study sites at Indiana Dunes National Lakeshore. Refer to Table 1 for survey type and frequency information. Numbered areas are the seven Supplemental Survey Areas. Developed areas are residential and industrial areas; natural areas include savannas, ponds, woodlands, open fields, and foredunes.

The second study area is Tolleston Dunes, a 110-ha black oak savanna/marsh complex. Karner blues reside both in open fields and in savanna areas that have minimal woody vegetation in the understory.

Table 1. Chronology of Karner blue butterfly surveys at Indiana Dunes National Lakeshore. Data are number of days the site was surveyed. Site names and Supplemental Survey Area (SSA) numbers are shown in Figure 1. For entries with two numbers separated by a slash, the first number is number of days on which mark-release-recapture surveys were performed and the second number is number of days on which walk-through surveys were performed. All single number entries are for walk-through surveys only.

	YEAR		
SITE	**1994**	**1995**	**1996**
Inland Marsh A	19/ 8	7	7
Inland Marsh B	2	7	7
Marquette Trail	4/2	3	8
Tolleston Dunes		25/ 7	9
West Beach		6	9
Burns Ditch		2	3
Miller Woods			31/ 9
SSA 1			10
SSA 2			11
SSA 3			12
SSA 4			8
SSA 5			7
SSA 6			2
SSA 7			3

The third study area, Miller Woods, is a 220-ha tract surrounded by development and bisected by a railroad and by a power-line right-of-way. Due to its high fire frequency, Miller Woods has a very open understory with few small oaks or shrub species. Canopy cover is high throughout most of this area.

The fourth study area, Marquette Trail, is linearly arrayed along a former railroad track. Sand mining along the north side of the track has left a nearly treeless area with little ground cover. A dune ridge on the south side has moderate canopy cover and little woody understory vegetation. We found most Karner blues along this dune ridge.

Sampling Methods

We conducted mark-release-recapture surveys during the first and second broods at each site, except at Marquette Trail, where we surveyed only during the second brood (Table 2). We surveyed as much of the known Karner blue butterfly habitat as possible in a day at a site and followed the same survey route, at about the same pace, each day. Surveying typically began several days before the population peak and continued for several days past that peak. We conducted most surveys on consecutive days (X = 1 in Table 2).

When surveying a route, four to six work-ers walked across each area, swinging in-sect nets above the vegetation to flush out butterflies. Upon sighting a Karner blue, the surveyor flagged the spot and then netted the butterfly. For butterflies captured for the first time, we numbered both outer hind wing surfaces using a permanent fine-tipped marker. We recorded sex, time, wing condition, and capture location and released the butterfly at the original sighting point. At Miller Woods and Tolleston Dunes we took a south-facing canopy density reading with a spherical densiometer (Lemmon 1957). If the butterfly was a recapture, we recorded the number, sex, wing condition, time, canopy density, and capture location and then re-leased the butterfly at the sighting location. We used five categories of wing wear: (1) teneral, (2) no obvious wing scale wear, (3) slight to moderate wear, (4) severe wear, (5) so worn that sexing was difficult, even though the sexes are colored differently.

We recorded location data with a global positioning system (GPS). Data were later differentially corrected by comparison with base station data to improve location accu-racy. Data collected in 1994 at Inland Marsh and Marquette Trail were mapped on a 1:2400-scale topographic map since a GPS was not available.

Table 2. Number of days on which mark-release-recapture (mrr) surveys were conducted. Number of surveys with 1, 2, and greater than 2 days between surveys.

Location	Brood	# mrr survey days	# of surveys with X days between successive mrr surveys			Maximum distance (m) between points on mrr survey route	Maximum distance (m) moved by an individual butterfly (range)
			X=1	X=2	X>2		
Inland Marsh	1	9	7	1	0	915	853
	2	10	4	5	0		540
Marquette Trail	2	4	0	1	2	2975	573
Tolleston Dunes	1	11	9	1	0	1225	469
	2	14	12	0	1		870
Miller Woods	1	12	11	0	0	1650	743
	2	19	16	1	1		989

Table 3. Number of butterflies marked, percent recaptured at least once, and percent of males among marked butterflies for each site and brood.

	Brood 1			Brood 2		
Site	# marked	% recaptured	% males	# marked	% recaptured	% males
Inland Marsh	793	33.3	60.5	1118	28.9	58.8
Marquette Trail				319	11.9	56.1
Tolleston Dunes	764	33.1	75.9	908	31.2	63.4
Miller Woods	402	30.3	55.0	1309	17.3	70.6

Along with each year's mark-release-recapture study, we concurrently conducted separate walk-through surveys, both at the mark-release-recapture site and at other sites (Table 1). During walk-through surveys butterflies were counted but not marked or handled. To expand the distance over which the study could detect marked individuals, however, walk-through surveyors also noted whether counted butterflies were marked. In addition, during the first and second broods of 1996, we searched seven supplemental survey areas near the mark-release-recapture site at Miller Woods for marked individuals (Figure 1). Those supplemental surveys ex-tended from the mark-release-recapture area boundary, through areas containing nectar plants and, occasionally, lupine, to other areas where we knew Karner blues to reside outside the marking area. We surveyed each of the seven areas at least once during each brood (Table 1).

We calculated data means ± standard error. Significant differences between means of more than two groups were determined by Tukey's honestly significant difference test if homogeneity of variance existed or, otherwise, with Tamhane's T2 test (SPSS 1996). Significant differences between means of two groups were determined by t-test. We used a pooled-variance t value if homogeneity of variance existed and a separate-variance t value otherwise.

We estimated population sizes using the computer program JOLLY (Pollock et al. 1990) for the standard Jolly-Seber capture-recapture model for open populations. This program also estimates probability of survival for the adults (Jolly's 4)) between marking periods. Since emigration from an area cannot be distinguished from death in this study, it is preferable to refer to this probability as representing the likelihood of maintaining residence within an area (Ehrlich 1961, Gall 1984). However, as the results will show, long-distance movements out of areas seem infrequent. Thus, while we use the term "residence" for Jolly's 4), this probability is likely to be similar to survival probability.

RESULTS

Capture Statistics During Mark-Release-Recapture

We recaptured 26.9% of butterflies at least once after the initial marking (n = 5613 marked, Table 3). Males (29.9%, n = 3617) were significantly more likely to be recaptured than females (21.6%, n = 1971) (χ = 45.2, p < 0.001; 25 butterflies not sexed). This intersexual difference held at each site although the difference was not significant at Marquette Trail. We captured individual males an average of 1.44 ± 0.01 times (n = 5203 captures) and females 1.28±0.01 (n=2530)(t=8.1,p<0.001). After we excluded data from Marquette Trail, where we only surveyed during the second brood, butterflies in the first brood were more likely to be recaptured (32.3%) than in the second brood (21.4%) (= 5.31, p < 0.001). This held true at each of the three sites, although the difference was not significant at Tolleston Dunes. We captured first brood individuals an average of

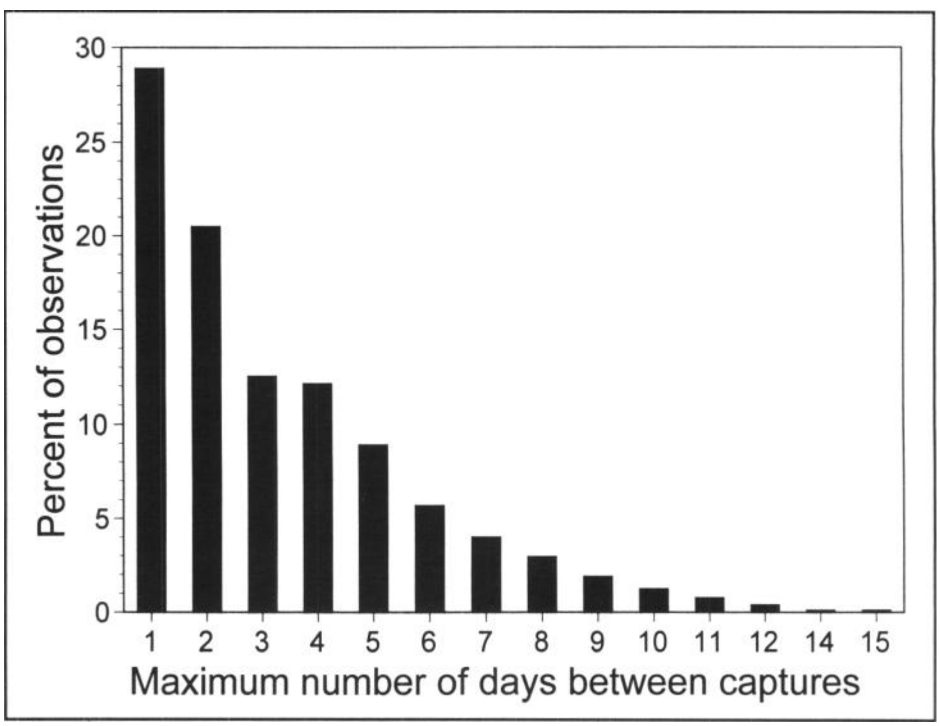

Figure 2. Number of days between first and last captures of all butterflies showing minimal wing wear (wing condition < 2) at the time of first capture (n = 1055).

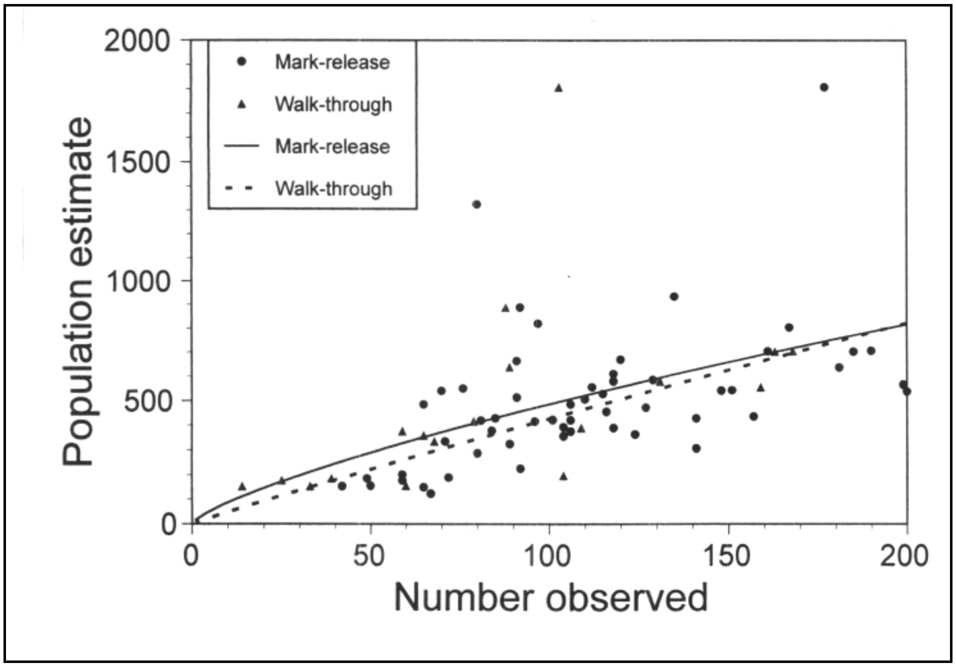

Figure 3. Relationship between number of butterflies captured daily in mark-release-recapture surveys (circles), or number of butterflies counted during walk-through surveys (triangles), and Karner blue population size estimated by Jolly-Seber model. Continuous line is best-fit line for mark-release-recapture data, and dotted line is best-fit line for walk-through data. Equations for lines are given in text.

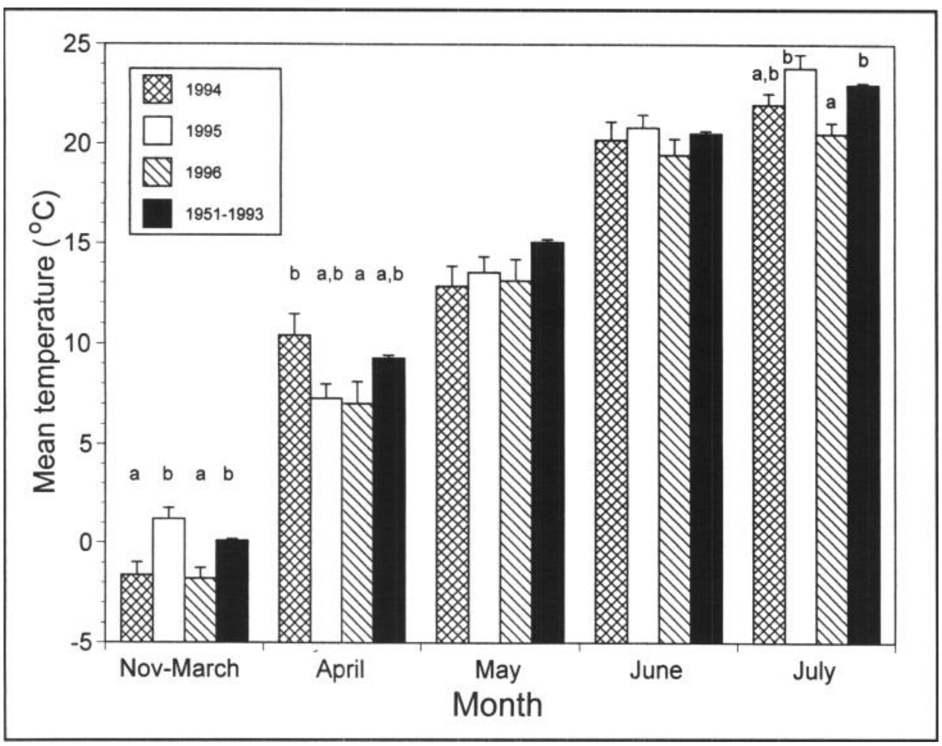

Figure 4. Temperatures (°C) **recorded at** the **Indiana Dunes** from **1951 to 1993 and for** the three years of this **study-1994, 1995, and 1996.** The **averages of** the **high and low** temperatures were **used** as **daily** data. Within each set of **four** bars, years with different letters **above** the **bars** differed significantly (one-way ANOVA,p < **0.05, Tukey's** HSD multiple **comparisons** test); years with the same letter, or with no letters, **did not** differ significantly. No **significant** differences were **found among** years for May **or**

1.48 ± 0.02 times and second brood individuals 1.33 ± 0.01 (t = 6.7, p < 0.001).

The interval between first and last captures has been used to estimate adult life span (Bidwell 1995). For individuals with little wing wear (wing condition < 2) at first capture, the mean interval between first and last captures was 2.77 days ± 0.07 (*n* = 1061), with a maximum of 14.95 days (Figure 2). Means for males (2.64 ± 0.07, *n* = 719) and females (3.04 ± 0.14, *n* = 342) differed significantly (t = 2.49, p = 0.013). Mean values for Inland Marsh (2.98 ± 0.13, *n* = 340), Tolleston Dunes (2.67 ± 0.09, *n* = 471), and Miller Woods (2.59 ± 0.15, *n* = 227) did not differ significantly (F = 2.8, *p* = 0.06).

The relationship between the estimated population size (Y) and the number of butterflies captured on a day (X), whether new captures or recaptures, was: $Y = 5.57 * X^{0.943}$ ($F_{1,53}$ = 39.4, p < 0.0001, R^2 = 0.43). The relationship between the estimated population size and the number of butterflies counted during walk-through surveys was: $Y = 15.52 * X^{0.748}$ ($F_{1,16}$ = 16.9, p = 0.0008, R^2 = 0.51) (Figure 3). These equations are based on days on which estimated population size was greater than 50.

The estimated probability of adult residence from one day to the next was 0.721 ± 0.026 (*n* = 51) for days with an estimated population size greater than 50. Residence probability did not differ significantly as a function of either site or brood in a two-way analysis of variance ($F_{3,45}$ = 0.50, p = 0.68 for main effects; $F_{2,45}$ = 1.29, p = 0.29 for brood x site interaction). Using a maximum life span of 15 days and the estimated residence probability of 0.721, the average age at death of an individual would be 3.45 days, if we equate residence probability with survival. This corresponds well with the mean span between first and last captures for fresh individuals.

Seasonal Patterns of Population Characteristics

The three years of this study often had cooler April–July temperatures than over

Table 4. Date on which the **peak number** of captures occurred. Percent of all butterflies captured that were females on **peak day.** Average of three **highest daily population** estimates.

Location	**Brood**	**Peak**	% **Females at Peak**	**Average** of **Highest Daily Population Estimates**
Inland Marsh	1	10 June 1994	35.4	615
	2	18 July 1994	35.2	706
Tolleston Dunes	1	13 June 1995	24.2	594
	2	23 July 1995	35.7	494
Miller Woods	1	23 June 1996	43.1	251
	2	12 August 1996	33.3	1356

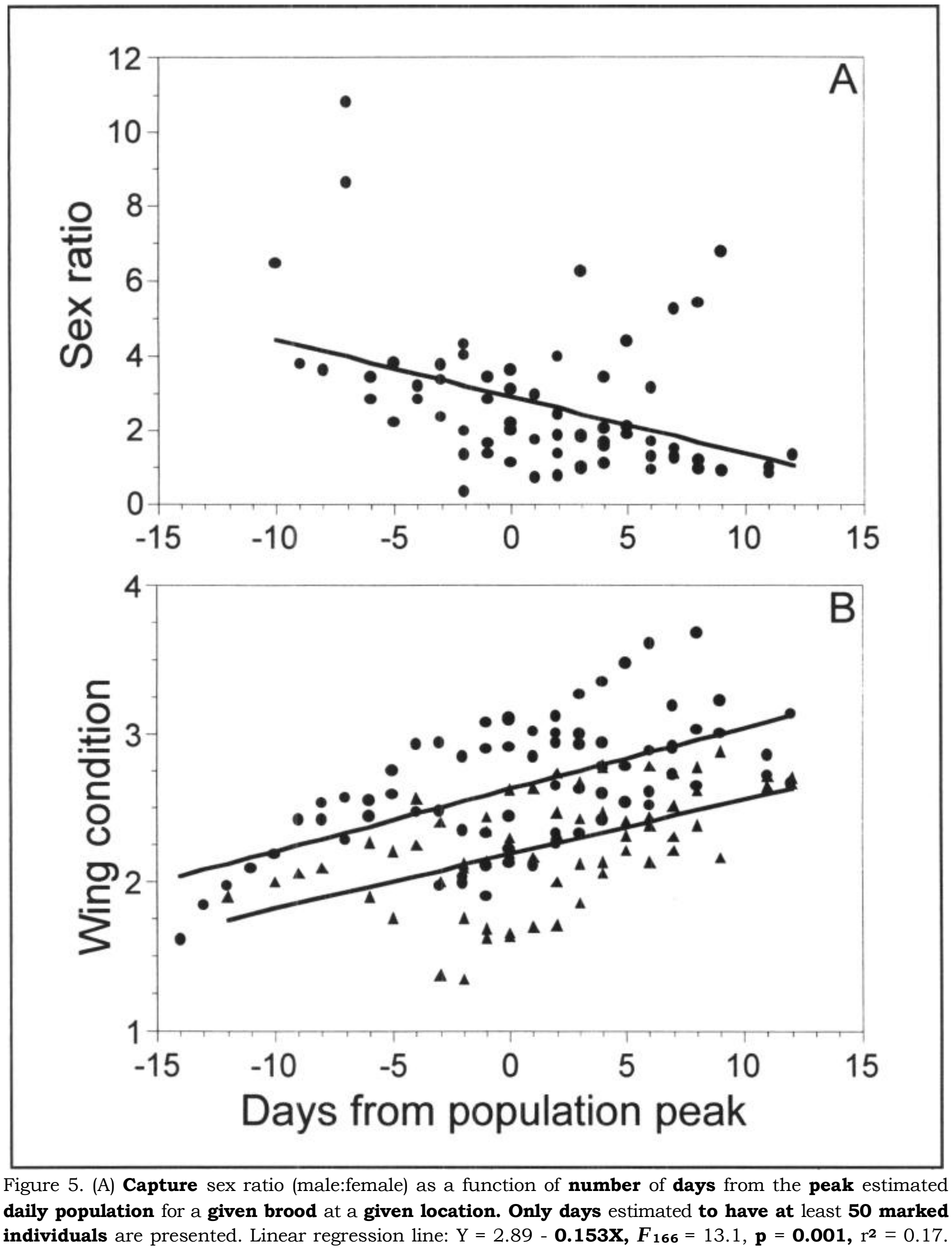

Figure 5. (A) **Capture** sex ratio (male:female) as a function of **number** of **days** from the **peak** estimated **daily population** for a **given brood** at a **given location. Only days** estimated **to have at** least **50 marked individuals** are presented. Linear regression line: Y = 2.89 - **0.153X,** F_{166} = 13.1, **p** = **0.001,** r^2 = 0.17. (B) Mean daily wing **condition** as a **function of days** from **daily population** peak. **Only days** with **at** least **10 captured individuals** are **presented.** Males are **designated by circles,** females **by triangles. Upper** line (Y = 2.63 + **0.042X,** F_{171} = **38.'7,p** < **0.001,** r^2 = **0.35)** is linear **regression** for males, lower line (Y = 2.19 + **0.037X,** F_{165} = **26.6, p** < **0.001,** r^2 = **0.29)** is **for** females.

the previous 42 years (Figure 4). April temperatures in 1994 were above average as were July temperatures during 1995. July temperatures were lower than aver-age in 1996. The November through March months were significantly cooler preceding the 1994 and 1996 breeding seasons than in the 1951—1993 period.

Peak population numbers in the second brood of 1994 were somewhat higher than in the first brood (Table 4). The opposite was true in 1995. In 1996, however, second-brood peak numbers were more than five times greater than in the first brood. The peak number of butterflies captured in the first and second broods occurred later in 1996 than in 1994 or 1995.

At the day of the estimated population peak, males outnumbered females at an average ratio of 2.32 : 1 (Figure 5a). On the day of peak number of captures, females made up 34.8% of captures for a 1.90:1 ratio of males to females (Table 4). The mean date on which butterflies with wing condition 1 or 2 were first captured differed by 1.8 days ± 0.5 (*n* = 7) between sexes with males appearing earlier in each brood at each location. Average wing condition systematically deteriorated with population age, as expected (Figure 5b). At the day of the population peak, males exhibited, on average, slight wing wear and females no apparent wear.

Movement Statistics

We calculated both the mean distance an individual butterfly moved between consecutive calendar days and the range, or maximum distance, between capture points, regardless of the time interval between captures. For both measures more than 75% of movement distances were less than 100 m (Figure 6). Mean consecutive-day distance moved was 50.3 m ± 2.3 (*n* = 794); maximum distance moved was 870 m. Mean range was 73.4 m ± 2.3 (*n* = 1499) with a maximum of 989 m (Table 2). Mean ranges were highest for individual butterflies with 3 days or more between captures (Figure 7). Similarly, mean ranges increased significantly if an individual was captured three or more times.

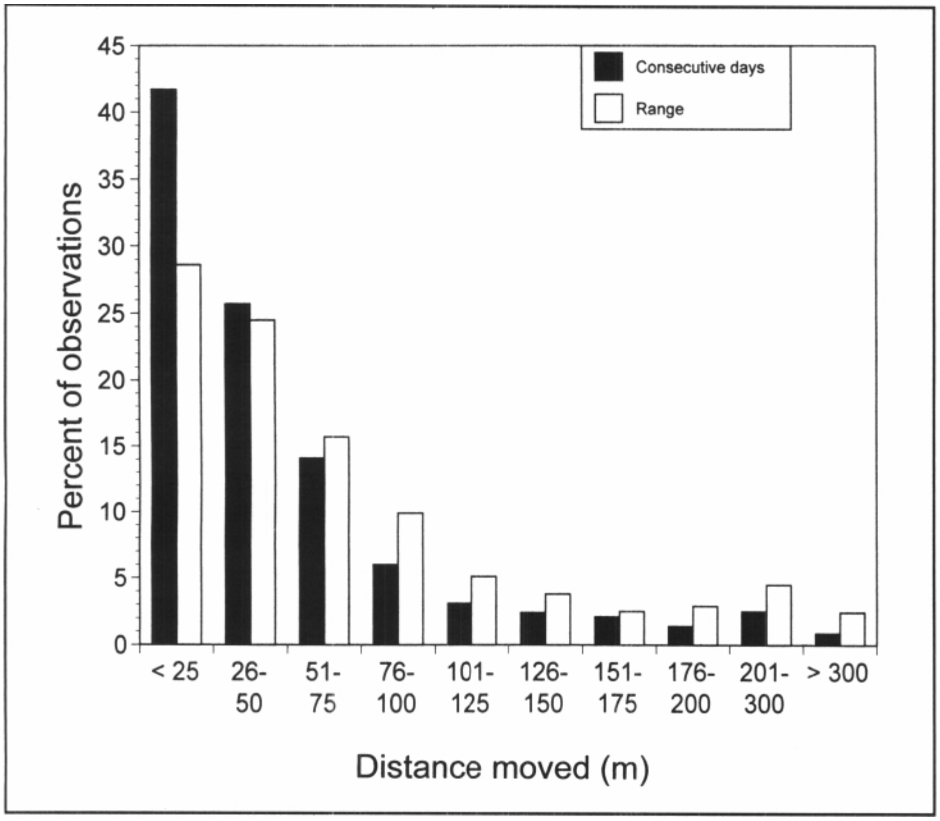

Figure 6. Distribution of distances moved by individual butterflies on consecutive days (dark bars) (*n* = 794) and maximum distance between any two capture points, or range (open bars), regardless of number of intervening days (*n* = 1499). Distances on consecutive days are based on mean values for each individual.

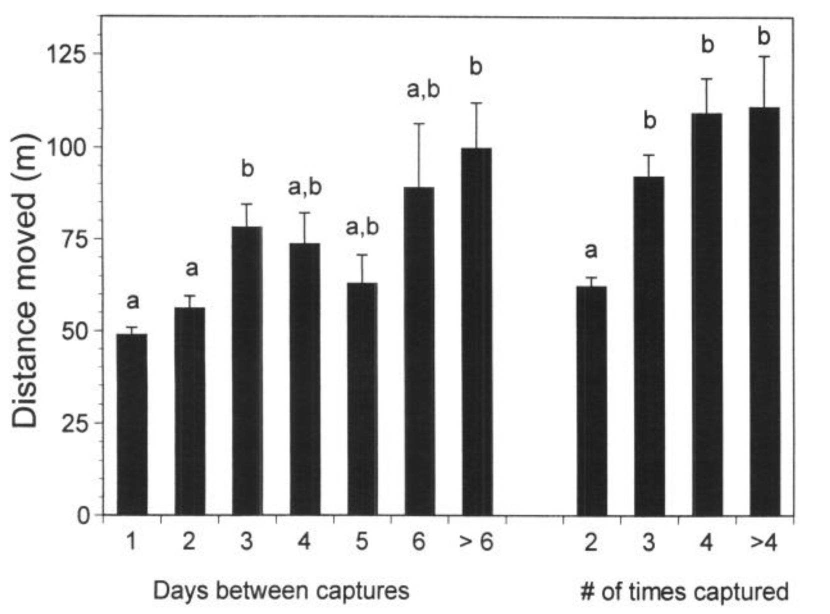

Figure 7. Distance moved by individual butterflies as a function of number of days between captures (*n* = 2119) and maximum distance moved as a function of number of times butterfly was captured (*n* = 1461). Within each set of data, bars with different letters above bars differ significantly (one-way ANOVA, p < 0.05, Tamhane's T2 test).

Mean distance moved on consecutive days did not differ significantly as a function of sex, brood, location, or wing wear (Table 5). Range, however, did differ significantly as a function of sex, brood, and location. Miller Woods had a significantly greater percentage of maximum movements greater than 300 m (4.3%, n = 351) than Tolleston Dunes (1.9%, n = 537) or Inland Marsh (1.7%, n = 573) (%2 = 7.0, p = 0.030). Finally, canopy cover above capture sites of males (19.7% ± 0.45, n = 3278) was significantly lower (t = 6.9, p < 0.001) than above females (26.0% ± 0.78, n = 1338).

Marked Butterflies Outside the Marking Area

In 1996 we established seven study areas in Miller Woods next to, but outside of, the area where Karner blue adults were marked (Figure 1). In total, we surveyed 48 km of routes in the first brood and 110 km in the second brood in these seven areas. We observed 294 Karner blues of which two were marked individuals. These two individuals were found 114 m and 335 m from their original point of marking. Karner blues were found in each of the seven supplemental survey areas, although the totals varied from a low of 2 to a high of 132.

Walk-through surveys were also conducted yearly both within and outside the marking area (Figure 1, Table 1). We counted 4072 butterflies during walk-through surveys outside of the marking areas but did not observe a single marked butterfly more than a few meters outside the marking area.

DISCUSSION

Our observations of Karner blue butterfly movement patterns at Indiana Dunes National Lakeshore support the claim that this endangered species does not frequently move long distances (Lawrence 1994, Bidwell 1995). More than 75% of movements, whether measured over a single day or over a span of several days, were less than 100 m (Figure 6). Thus the Karner blue butterfly at the Indiana Dunes probably exists as populations in *which* most

Table 5. Mean distance moved by Karner blue butterfly adults on consecutive days, and mean range, as a function of sex, brood, and location. Data from Marquette Trail are not used since surveys were not carried out on consecutive days there. Mean ranges with different superscript letters differed significantly among the three sites (p < 0.05, Tamhane's T2 multiple comparisons test). Because wing wear can change significantly over several days the effect of wing condition on mean range is not assessed.

Variable	State	Mean Consecutive Day Distance (m)	n	*F*	*p*	Mean Range (m)	n	*F*	*p*
Sex	Male	51.2 ± 2.7	593	0.6	0.542	76.9 ± 2.8	1052	2.3	0.019
	Female	48.0 ± 4.5	200			64.9 ± 4.3	406		
Brood	First	55.0 ± 3.5	362	1.8	0.067	84.5 ± 4.1	634	4.0	< 0.001
	Second	46.4 ± 3.0	432			65.0 ± 2.7	827		
Location	Inland Marsh	58.0 ± 3.7	274	3.0	0.051	78.8 ± 3.2[1']	573	5.4	0.005
	Tolleston Dunes	45.4 ± 4.3	292			63.8 ± 3.9	537		
	Miller Woods	47.5 + 3.8	228			82.7 ± 6.3[1']	351		
Wing wear	Little (Condition < 2)	45.2 ± 4.1	217	1.1	0.343				
	Moderate (3)	48.7 ± 2.7	577						
	Severe (>:. 4)	54.3 ± 4.8	186						

individuals spend their life within a few hundred meters of their hatching location.

Methodological problems can readily pre-vent documentation of longer movements. In a mark-release-recapture survey, the maximum movement distance detectable is the maximum linear dimension of the survey area (Table 2). As the dispersal distance we try to detect increases, the area that must be searched increases exponentially. These facts suggest that it may be difficult to detect butterflies that move long distances. Also, there may be a tendency for handled individuals to leave an area and, thereafter, to be less often recaptured or to be recaptured at longer distances (Singer and Wedlake 1981, Mallet et al. 1987, Morton 1989).

Distance measurements may also contain a sexual bias. Karner blue populations exhibited protandry, or earlier appearance of adult males than females within a brood. Protandry probably results from sexual selection, on one or both sexes, to increase mating opportunities (Darwin 1871, Kleckner et al. 1995). The mean date of capture of fresh males was about 1.8 days earlier than that of fresh females. This span is similar to the mean intersexual difference in larval development time, 2.8 days shorter for males, that we previously documented (Grundel et al. 1998a). Male-biased capture sex ratios persisted until late in the brood (Figure 5a). Because of this, we captured nearly twice as many males as females, increasing the likelihood that we might detect longer male movements.

Several pieces of evidence, however, suggest that the results presented here do reasonably represent actual movement pat-terns of the Karner blue butterfly at Indiana Dunes. First, although movement distances increased with time between captures and with number of captures, as would be expected, the absolute size of these in-creases was not great and the differences were not statistically significant after the third capture (Figure 7). Even with long intervals between captures and with multiple captures, the mean movement distance only increased to about 100 m, compared to about 50 m for day-to-day movements. Second, many searches through suitable habitat at various distances outside marking areas failed to find any butterflies that had dispersed a greater distance than found during the mark-releaserecapture surveys (Figure 1, Table 1). Third, maximum ranges were often much shorter than the maximum possible distance between points within mark-release-recapture routes despite 79 days of surveying with four to six surveyors per day (Table 2). Finally, we found males in habitats with significantly more open canopy than was true for females, corroborating results of a previous study on intersexual behavioral differences for the Karner blue (Grundel et al. 1998b). This suggests that survey techniques sampled butterflies in typical behavioral situations.

We can compare the dispersal statistics documented in the present study with those from three other Karner blue dispersal studies (Lawrence 1994, Bidwell 1995, King 1997). In the present study, the mean consecutive-day movement distance of 50.3 m did not differ significantly between males, at 51.2 m, and females at 48.0 m (Table 5). However, males had significantly longer ranges, at 76.9 m, than females at 64.9 m. We also previously found that individual males moved greater distances over short time intervals (ca. one minute) than did females (Grundel et al. 1998b). Thus, males may be more active fliers but they tend to move only slightly longer distances than females over their life span. Lawrence (1994) found an average movement of 191 m between captures for males and 162 m for females; Bidwell (1995) documented mean consecutive-day movements of 99 m for males and 32 m for females. King (1997) documented a mean distance per move of 456.9 m and 214.7 m for first and second brood males and 69.8 m and 359.2 m for first and second brood females. Therefore, except for the second brood butterflies at King's site, male movements were slightly longer than female movements in these four studies.

We did not observe long-distance movements from one mark-release-recapture point to another or to walk-through sites. Neither did we observe long-distance movements out of our Miller Woods marking area into adjacent supplemental survey areas (Figure 1). In comparison, Lawrence (1994), in southwest Michigan, observed no movements among five sites separated by 0.5 to 2.5 km. Bidwell (1995), working in central Wisconsin, recorded 14 of 550 marked butterflies (2.5%) moving between two sites separated by a 50-m barrier of dense vegetation and 7 of 627 (1.1%) moving greater than 1 km between two other sites. King (1997), also working in central Wisconsin, reported 7.4% and 12.3% of first and second brood individuals moving greater than 1 km between sites. He ascribed this frequent longer distance movement to the butterflies seeking out higher quality habitat patches. That would be similar to the lycaenid butterfly *Euphilotes enoptes* Behr, which has been documented migrating up and down mountain sides in search of suitable host plants as these plants change in quality during the growing season (Peterson 1997). Variation in dispersal across a butterfly's range has rarely been documented. These comparative data for the Karner blue show that geographically separate populations of Karner blue butterflies exhibit moderate variation in dispersal tendency.

Overall recapture rates in the current study (26.9%), in Lawrence's study (Lawrence 1994) (27.1%), and in King's study (King 1995) (31.6%) were similar, suggesting that Karner blue life spans and survey efforts were comparable across these studies. Only Bidwell (1995) had a much higher recapture percentage (49.8%). His study sites were generally less than 100 m wide and 1 km long and were surrounded by dense woods and roads. Thus, site size and layout may have contributed to a higher recapture rate. In a southwestern Michigan study (Lawrence 1994), the mean Jolly's o, the daily probability that an individual survived, or remained resident in an area over consecutive days, was 0.61 (n = 28). In our study Jolly's 4) was 0.72. If we equate Jolly's 4) with survival, a given adult Karner blue at Indiana Dunes has a 50% probability of surviving about two days. The mean estimated life span, 3.45 days, was lower than the 5.6 days for females and 4.0 days for males reported by Bidwell (1995). These results hint that adult survivorship in our study was intermediate between survivorship during Lawrence's Michigan study and Bidwell's Wisconsin study. That intermediate life span did not obviously translate into intermediate dispersal tendency, however.

The Karner blue butterfly on wild lupine leaves.

The fact that movement distances at Indiana Dunes for the Karner blue are lower than at the other three sites may be related to topographic differences, especially the dune landscape that differentiates Indiana Dunes from the other three study sites. The undulating, dune ridge systems that characterize Indiana Dunes National Lake-shore produce considerable habitat heterogeneity relevant to dispersal by the Karner blue. North-facing aspects, for example, tend to be shadier and more heavily wood-ed. Lupine does poorly in the interior of such heavily shaded habitat and we have not usually observed Karner blues there. The dunes become shorter and more widely separated as one proceeds westward across the park, affecting both the frequency of north aspect shading and the spread of fire. This longitudinal gradient, along with greater fire suppression in the eastern part of the park, may have contributed to the recent loss of the Karner blue butterfly from the eastern part of the park.

Our flattest, most homogeneous, and most westerly site, Miller Woods, has a very open understory and many ponds. Movements greater than 300 m were more than twice as frequent there than at two other sites. At Necedah National Wildlife Refuge, Wisconsin, where King (1997) re-corded considerably longer movements than at Indiana Dunes, the landscape is also flat and open with dispersal over large ponds necessary to move among several of the sites (R. Grundel, pers. ohs.).

Mean movement distances have been published for populations of several dozen butterfly species. Scott (1975) summarized studies of 42 butterfly species and found that nearly equal percentages of these species moved less than 100 m, moved sever-al hundred meters, sometimes moved a kilometer, or often moved several kilometers. Two species migrated thousands of kilometers. Of eleven species that he subsequently studied, two lycaenids, *Lycaena arota* Boisduval and *Hypaurotis crysalus* Edwards, had the shortest mean ranges, from 15 to 35 m. In a study of six endangered lycaenid species in California, Arnold (1983) recorded mean distances between captures ranging from 17.8 to 78.5 m. About 70% of maximum distances between captures of the lycaenid, *E. enoptes*, were less than 100 m and about 5% were greater than 500 m (Peterson 1997). No recorded movements of the lycaenid *Plebejus argus* L. were greater than 50 m (Thomas 1985). New (1993) concluded that lycaenids as a group exhibit low vagility. The studies just cited support that conclusion, and the Karner blue's vagility seems representative of this family.

Scott's study (Scott 1975) of movement pat-terns of eleven butterfly species in six families related life history characteristics to vagility differences among these species. Karner blue movement data are generally not consistent with the relationships he observed. Unlike the Karner blue, the females of all of his study species moved farther than males. Although Scott found that female life spans were longer than male life spans, as seems true for the Karner blue, he suggested that longer female life span would result in female ranges being longer than male ranges, which we did not find to be true. He also suggested that Lepidoptera whose larvae feed on early successional plant species, and Lepidoptera with more than one annual brood, should have greater rang-es. Although the Karner blue is an early successional feeder with two annual broods, it fits into Scott's shortest movement category—Lepidoptera that usually move less than 100 m. One of Scott's proposed relation-ships might hold true for the Karner blue, however. He found a positive correlation between an individual butterfly's movement range and the areal extent of its population. Since Karner blue subpopulations at the Indiana Dunes probably persist in areas perhaps a few hundred meters across, we might expect them not to disperse over greater distances.

Typically, the number of second brood Karner blue adults is much higher than the number of first brood adults (Lawrence 1994). However, the ratio of peak population numbers in the first and second broods differed among the three years of this study. The second brood was larger than the first brood in 1994, smaller in 1995, and much larger in 1996 (Table 4). Maxwell (1997) documented a similar switching of the relative size of first and second broods in Wisconsin in 1994 and 1995. In our study both years with larger second than first broods were preceded by cool winters relative to 1951–1993 (Figure 4). In 1995 July was unusually hot, including the highest daily temperature recorded at the Indiana Dunes. In 1996 the cool winter was coupled with a cool July. The early first brood peak in 1994 occurred after the warmer April in that year. Although the small sample size precludes definitive conclusions, the congruent first and second brood differences in Wisconsin and Indiana in 1994 and 1995 suggest that climate is playing a major role in determining the relative success of the first and second broods. The trends at Indiana Dunes could indicate that cool winters, or small second broods during the previous summer, de-press first brood populations while cool summers elevate, and hot summers de-press, second brood populations. This is consistent with high overwinter mortality of eggs (Dirig 1994) and with our previous finding that water-stressed and senescent lupines do poorly in supporting Karner blue larval growth (Grundel et al. 1998a). Hot summer temperatures will accelerate both water-stress and senescence, especially during the second brood; cool summers should have the opposite effect.

As plans are formulated for the recovery of the Kamer blue butterfly, one of the major methodological challenges we face is properly and consistently assessing population trends across the butterfly's range. If we are to compare population statistics across the range, it is important to understand when to count the butterflies within the cycle of population increase and decrease that occurs during a given brood. It is also important to understand how well different ways of counting butterflies relate to each other. While we undertook a labor-intensive mark-release-recapture study, over the course of several years, many locales will not be able to muster the resources to do the same. In addition, mark-release-recapture studies can negatively affect endangered butterfly populations (Murphy 1988, Harrison et al. 1991). Our results allow us to discuss the effectiveness of alternative ways of counting butterflies. These results also provide characteristics of the Kamer blue populations at their peaks, which should allow workers at different sites to do their counts near that peak. Specifically, at peak numbers, an approximately 2:1 male:female sex ratio occurred, the males exhibited slight wing wear and the females little, if any, wing wear, on average (Figure 5). The relationships between butterfly captures and estimated population numbers, and between walk-through butterfly counts and estimated population numbers, were very similar (see regression lines in Figure 3). The fit of the lines between estimated population numbers and capture or walk-through counts were fairly good, supporting the potential use of any of these three census methods for population trend description. Of course, the sex ratio and wing wear data, and the specific relationships among the three census methodologies, may be location sensitive. Because of this it would be very useful if analyses of mark-release-recapture data sets elsewhere in the Karner blue butterfly's range could be undertaken as a comparison to our results.

As noted at the beginning of this paper, habitat heterogeneity can benefit the Karner blue butterfly. In woodlands, this heterogeneity provides beneficial mixtures of shade and sun but can present barriers to movement. Rangewide, existing sites occupied by Karner blue butterflies exhibit significant variability in size and in degree and type of heterogeneity (Schweitzer 1994). Sites vary from a few hectares to more than 1000 ha and from treeless areas, where grasses might provide shade heterogeneity, to closed canopy locations. With-in this spectrum, Indiana Dunes probably is intermediate in the size of its occupied sites, and these sites are composed of many occupied and unoccupied sections or patch-es. At the sites with the highest shrub density in the understory, Inland Marsh and Tolleston Dunes, 1–2% of Karner blues moved distances greater than 300 m. Since most subpopulations will only contain dozens to a few hundred butterflies during a brood, we expect that only a few adults per generation from a given patch will move more than 300 m at these sites.

We previously documented that male Karner blues prefer large canopy openings, perhaps 25 m or more in diameter (Grundel et al. 1998b). Such areas, when surrounded by woody vegetation, not only provide sunny areas for the males but also a variety of shading conditions for oviposition by the females. Several such openings typically comprise a patch that sup-ports a subpopulation at Indiana Dunes National Lakeshore. The ultimate goal of management is to provide this endangered species with a landscape that contains quality habitat patches situated to allow gene flow among patches and to allow recolonization following local extinctions. The data collected on movement patterns of the Karner blue suggest that a patch of several 25-m openings, providing a gradient of shading, and positioned less than 300 m from a neighboring patch, will al-low the butterfly to persist in the patch and to disperse, in at least a minimal fashion, among patches in most generations.

The above recommended arrangement of patches comes with caveats. Recolonization of extinct patches requires dispersal of mated females that typically make up less than half the population of a patch, given the observed sex ratios. Any factor, such as this, that decreases the size of the population of potential dispersers decreases the likelihood that at least one disperser will move further than 300 m in a brood. In addition, areas between subpopulations are often likely to contain unsuitable habitat that serves as a barrier to movement. More closely spaced patches are, there-fore, obviously preferable when dispersal is critical. Low gene flow and founder effects are also potential problems that can be mitigated by more closely spacing patches (Brookes et al. 1997). Questions remain concerning what constitutes an absolute, or very difficult, barrier to dispersal, and how population size relates to patch area. These factors can negatively affect the likelihood of dispersal over a given distance. Nonetheless, the suggested prescription may represent a minimally acceptable formula for the persistence of the Karner blue butterfly in the heterogeneous oak woodlands where it best thrives today in the upper Midwest.

CONCLUSIONS

Two conclusions important for Karner blue butterfly landscape management and monitoring are suggested by our data: (1) Efforts should be made to maintain subpopulations of Karner blues within 300 m of each other to allow dispersal among those subpopulations. (2) A 2:1 male:female sex ratio occurred at the population peak with-in a brood. We can use this observation to better synchronize population counts across the butterfly's range if other studies corroborate this finding. Walk-through survey population counts were significantly correlated (R^2 = 0.51) with population estimates derived from mark-release-recapture surveys.

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