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OBSERVATIONS OF *INCISALIA IRUS*  
(LEPIDOPTERA: LYCAENIDAE) IN CENTRAL WISCONSIN 1988-95Ann B. Swengel<sup>1</sup>

## ABSTRACT

In surveys conducted during 1988-95, 164 individuals of the frosted elfin (*Incisalia irus*) were found, 139 of them during formal transects that totaled 92.9 hr and 179.4 km of survey effort during the frosted elfin flight period. Individuals were observed between 10 May and 14 June, with maximum flight spans in a single year of 27-31 days. Peak flight occurred just before or at the beginning of peak flowering of the larval host, wild lupine (*Lupinus perennis*), and the first spring adults of Karner blue (*Lycaeides melissa samuelis*), also monophagous as larvae on wild lupine. Fourteen individuals exhibited oviposition behavior on young stalks of green lupine flower buds. 94% of individuals occurred in savannas, nearly evenly split between open (10-24% canopy) and closed (25-49% canopy) ones. Relative lupine abundance at both the microsite and landscape scales appeared more important as a habitat factor than actual size of the particular lupine patch occupied. Both long-term lack of site management and too frequent/intense management (forestry, rotational fire) appeared unfavorable. Recreational trailsides, areas burned by wildfire >4 years ago, and rights-of-way mowed annually or less often were favorable habitat. All frosted elfin sites also supported Karner blues, but within these sites, correlation of frosted elfin abundance with that of Karner blues was rather weak, indicating a fair degree of niche segregation between these two species.

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The frosted elfin (*Incisalia irus* Godart) is univoltine, with adults in spring (Opler and Krizek 1984, Scott 1986), and has three named subspecies (Ferris 1989). *Incisalia i. irus* (Godart) ranges from northern New England and New York through Ohio and Michigan to Wisconsin, with scattered populations also farther southeast, including eastern Maryland and northern Florida. This subspecies is generally documented or inferred to use wild lupine (*Lupinus perennis* L.) (Fabaceae) ("lupine") as larval host (Kuehn 1983, Gatrell 1991, Holmes et al. 1991, Iftner et al. 1992, Schweitzer 1992). This perennial herb prefers open-canopied, sunny habitats on xeric, sandy soil, often with soil disturbance (Dirig 1994).

*Incisalia i. arsace* (Boisduval and Le Conte) occurs in Atlantic coastal states generally farther south of the main range of *I. i. irus*: from southern New England to South Carolina, and possibly farther south. The *arsace* subspecies is often documented or inferred to use wild indigo (*Baptisia australis* R. Br. or *B. tinctoria* R. Br.) (Fabaceae) as larval hosts (Opler and Krizek 1984, Schweitzer 1992). Neither of these *Baptisia* species occurs naturally in Wis-

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consin, but two other species do, *B. leucantha* Torr. & Gray and *B. leucophaea* Nutt. (Curtis 1959). While phenotype is typically variable within frosted elfin populations, *I. i. irus* is generally smaller and darker ventrally while *I. i. arspace* has less contrasting, more obscure patterning on the ventral hind wing (Gatrelle 1991). *Incisalia i. hadra* Cook and Watson occurs in Arkansas, Louisiana, and Texas, also feeding on wild indigo as larvae (Scott 1986, Gatrelle 1991).

Since larval feeding habit and phenology vary by host, *I. i. irus* and *I. i. arspace* may actually be sibling species (Schweitzer 1992). The lupine-feeders consume flowers and pods while young leaves are consumed from wild indigo. Wild indigo appears 3–6 weeks later in spring than lupine, with a corresponding delay (relative to local phenology) in the adult flight period. Whether larval host assortment by subspecies is complicated by the fact that information on host association is not known for all specimens and populations.

The principal (northern) range of *I. i. irus* is sympatric with the Karner blue (*Lycaeides melissa samuelis* Nabokov) (Lepidoptera: Lycaenidae), also monophagous on lupine and federally listed as endangered. The frosted elfin also appears in decline (Iftner et al. 1992, Schweitzer 1992, Glassberg 1993). In this paper, I present field observations on the species in Wisconsin, where it is listed as threatened.

## METHODS

**Study sites.** Surveys occurred at 141 pine-oak barrens in central and northwestern Wisconsin (43.5–46.8°N, 89.8–92.7°W) sampled because of their apparent potential to support barrens-specialized butterflies. These sites represented a diversity of ownerships and land uses, including government or private conservation reserves; government-owned forest reserves for timber harvest, some of which had been burned by wildfire and some used as recreation lands for off-road vehicles; military reservation; and rights-of-way for highways and utility lines. Since the 44 lupine sites in Burnett, Clark, Eau Claire, and Sauk Counties were surveyed during frosted elfin flight period but never produced any individuals, this study is restricted to the 97 sites (43.7–44.7°N, 89.9–91.0°W) within known range for the frosted elfin in Adams, Jackson, Juneau, Monroe, and Wood Counties, all in central Wisconsin (Kuehn 1983; Ferge 1988, 1989, 1992).

**Field observations.** All frosted elfin observations were recorded in field notes treating such subjects as behavior, appearance, and microhabitat. A few individuals (N=25) were found during informal site visits or Karner blue larval searches (Swengel 1995). Most sightings (N=139) occurred during butterfly transect surveys that my research assistant and I conducted. Similar to the butterfly walk (Pollard 1977), these surveys followed similar routes within each site each year (Swengel 1995, 1996). Nomenclature for butterflies follows Ferris (1989), with English names after NABA (1995). All observed butterflies were counted and identified to species, if possible. The Persius duskywing (*Erynnis persius* Scudder) (Lepidoptera: Hesperidae) was identified at the species complex level because field identification cannot always distinguish this species from the columbine duskywing (*E. lucilius* Scudder and Burgess), whose larval host is wild columbine (*Aquilegia canadensis* L.) (Ranunculaceae), and the wild indigo duskywing (*E. baptisiae* Forbes), whose larval hosts include lupine and wild indigo (Opler and Krizek 1984, Iftner et al. 1992). Very little wild columbine or wild indigo occurred in this study's barrens sites.

A new survey unit was designated whenever the habitat along the route

varied by *management* (type and/or years since last treatment), *vegetation type* (wet, mesic, dry, "extra dry" sand; all barrens were "extra dry"), *vegetative quality* based on diversity and abundance of native and exotic flora (undegraded, semi-degraded, highly degraded), and/or estimated macrostrate *canopy* of under- and overstory (grassland <10%, open savanna 10–24%, closed savanna 25–49%, forest opening 50–75%; most but not all barrens had >9% canopy). A unit's management was coded based on the entire management history observed or evident during the study, including management combinations (e.g., burn & mow) as necessary. A unit occurred in a "diverse" site if it contained contiguous non-forested and non-cultivated habitats both wetter and drier than mesic; otherwise the site was rated "uniform." For each unit, we recorded temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying. Data from each unit were kept separate.

**Statistical analysis.** Analysis was done with ABstat 7.20 software (1994 Anderson-Bell Corp., Parker, Colorado), with statistical significance set at  $p < 0.05$ . Before analysis, I adjusted the survey dates based on plant development to approximately similar phenology as follows: 1988 & 1991 +14, 1990 -4, 1992 -14, 1993 -14, 1994 +4, 1995 -16. In comparisons *within* a unit either (1) among years (long-term monitoring) or (2) among species (interspecific correlations), the peak raw number observed per flight period (if during main flight) was used since survey route within a unit was held constant. To allow valid comparisons *among* units, I standardized the data by converting the raw number observed into an observation rate of individuals per hour per unit (i.e., an index of relative density). For parametric tests (Pearson product-moment correlation matrix and stepwise linear regression), the tested values (dependent variable) were log-transformed first in order better to meet parametric assumptions.

Stepwise linear regression allowed extensive multivariate analysis but assumed a progressive (correlative) effect for each independent variable. With most variables, this assumption was plausible (e.g., temperature, wind), while others could be manipulated to become a logical continuum (described below). But these continua are not necessarily the only valid ordination, and regression would not necessarily detect a significant effect for bimodal or intermediate peaks. The first regression included the following variables: *geography* (latitude, longitude), *survey* (N surveyors — usually two but occasionally the author alone; beginning time; time difference between beginning time and 1200 hr CST; calendar and phenological date); *unit* (quality, canopy, site diversity); *weather* (percent sunshine, average temperature, average wind speed); *flight period* (difference between survey date and midpoint of flight period observed in entire study as calendar and phenological dates); *year* (calendar, ranking of annual fluctuation — explained below); and *management* (unintrusiveness — explained below). The annual fluctuation variable ranked the years of survey data based on mean unweighted observation rate in all units that year. For testing effect of management type, consecutive codes were ordered along this continuum: nothing long-term, recreation (vehicle trailsides), mowing, timber cutting, wildfire, rotational fire. Mixed managements (e.g. rotational burn & mow, wildfire & recreation) were placed between both types.

Successive regressions added variables, which reduced sample size since values were unavailable for some units. The second regression added one unit variable, estimated relative abundance of lupine plants based on the following categories with the indicated arithmetic ratios: superabundant (100,000), abundant (10,000), common (1000), uncommon (100), rare (10), absent (0). The third regression added two management variables, age class (years since

last treatment) and an intensity index calculated as the unintrusiveness code  $x$  (age class + 1). Age classes were coded as 0 (treatment since last growing season), 1, 2, etc. For rotational fire, age classes  $>4$  were lumped as 5+. Wild-fire age classes ranged from 4 to 18, with  $>14$  lumped as 15+. "Nothing" was coded as 20+, with no age class exceeding that. The fourth regression added four unit variables: lupine patch size, uniformity of lupine distribution (from 1=very patchy to 4=very uniform), lupine volume (relative abundance  $\times$  patch size), and lupine "core" (3=unit in large landscape context of abundant lupines with numerous other lupine patches within 2 km; 2=on edge of such a core or few lupine patches within 2 km; 1=isolated lupine patch).

## RESULTS AND DISCUSSION

During 1988–95, 164 frosted elfins were found, 139 of them during formal transects that totaled 92.9 hr and 179.4 km of survey effort in frosted elfin range and flight period.

**Larval host.** Although *Baptisia leucophaea* was present ("rare" in abundance) at a few frosted elfin sites, no frosted elfins were observed associating with this wild indigo. They frequently associated closely with lupine (as reported also by Iftner et al. 1992): 69 (54%) of 127 individuals for which notes were conclusive were directly associated with a lupine plant (i.e., first found perched on, flushed off, or landing on lupine). Of the remaining individuals, many perched on vegetation within 3 cm of lupine or subsequently perched on lupine. Nearly all individuals were near (within 0.5 m of) lupine, and all were in locations with a lupine patch in the vicinity.

**Identification.** Except for the most worn and torn individuals, frosted elfin identification was not difficult based on ventral hind wing features: "tail," dark "thecla" spot next to tail, and disjointed white and dark dashes in the postmedial line (Figs. 1–2). The most similar elfin is Henry's (*Incisalia henrici* Grote and Robinson), but this species has a more prominent and straight postmedial line, lacks the thecla spot, is more distinctly and sharply two-toned (dark near body, light brown toward margins), and is more active and prone to flush. The Henry's elfin is apparently even rarer in Wisconsin, at least in frosted elfin habitat and range (7 observed on formal transect surveys there, with 5 more in barrens outside frosted elfin range).

Nonetheless, all elfins must be seen well for species identification and four other elfin species occurred in units with frosted elfins. Their flight periods all overlap greatly but the other species except Henry's start and end a bit earlier (Tables 1,2). The percentage of unidentified elfin individuals significantly increased with density (rate per hour) of all elfin individuals, identified to species or not ( $r=0.252$ ,  $p=0.0010$ ,  $N=169$  units with any elfins found). This rather logical outcome indicates that the more elfin individuals observed, the lower the proportion of elfins identified to species. Regression also indicated a significant effect from number of surveyors (Table 3), also logical in that the two surveyors worked together and the second surveyor was not distracted by writing observations.

However, observation rates of each elfin species correlated even more strongly with the rate of all elfin individuals: eastern pine elfin (*Incisalia nippon* Huebner)  $r=0.675$ ,  $N=452$ ; hoary elfin (*I. polia* Cook and Watson)  $r=0.639$ ,  $N=363$ ; frosted elfin  $r=0.547$ ,  $N=328$ ; brown elfin (*I. augustinus* W. Kirby)  $r=0.430$ ,  $N=354$ ;  $p=0.0000$  for all (Henry's elfin was not analyzed because of small sample size). This suggests that our ability to identify species kept reasonable pace as elfin density increased. The most distinctive species correlated the strongest; the least distinctive species, identified by lack of



Figure 1. Frosted elfin probing young green flower bud of wild lupine with proboscis for extended period of time; 30 May 1995, Jackson County, WI.

characteristics but very active, correlated the least strongly. This suggests that relatively the most brown elfin individuals eluded identification, possibly because of the need for a closer, longer look to confirm absence of identifying characteristics for other species. Brown, hoary, and eastern pine elfins all achieved a higher maximum density in a single unit than the frosted elfin. Hoary and eastern pine elfins also had higher average rates in all units surveyed during their flight period. The frosted elfin's correlation coefficient may have been somewhat lower than the latter two because the upper limit on frosted elfin rate is reached sooner than for the other species. The even lower brown elfin coefficient suggests that it may become relatively more active and unidentifiable at lower thresholds of weather and elfin density than for the other species.

**Flight period.** Our frosted elfin observations occurred between 10 May and 14 June (Table 1). In most years, surveys occurred in appropriate sites before and/or after the observed flight period for frosted elfins that year (Table 2). During 1993–95, the time period with the most survey dates during the potential flight period covering a variety of both known and potential sites, the

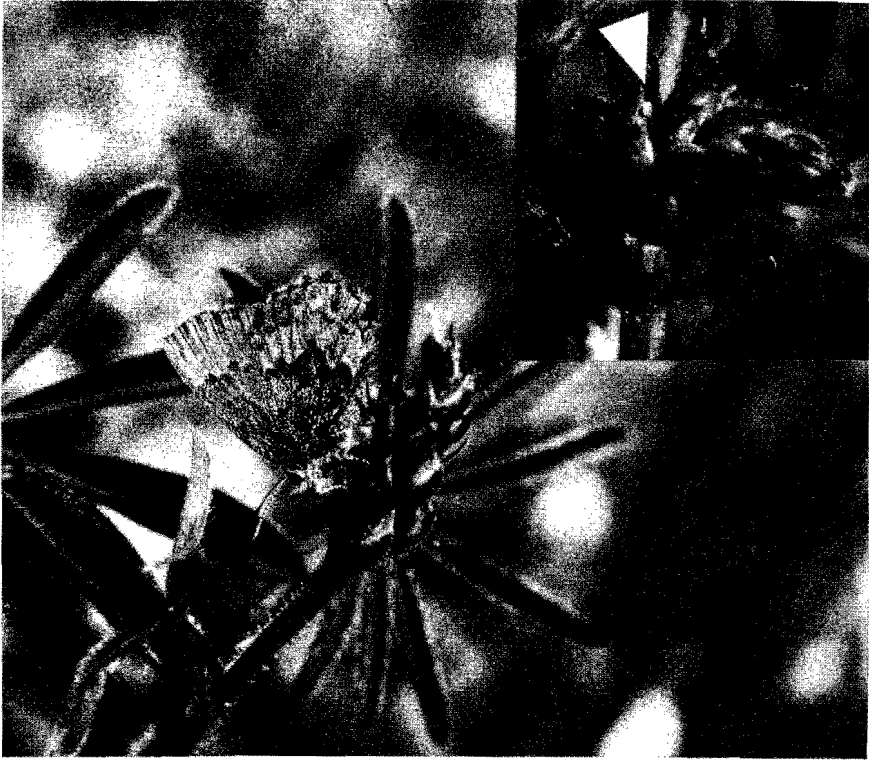


Figure 2. Frosted elfin ovipositing in typical location, young whitish-green flower bud of wild lupine; 27 May 1992, Wood County, WI. Inset: Frosted elfin egg (indicated by white arrow) hidden among young lupine flower buds (flower stalk gently curled back to reveal egg); 20 May 1991, Wood County.

Table 1. Summary information on elfin flights within known frosted elfin range in Wisconsin during 1988–95 (Henry's elfin sample very small). \* 22.V had the second highest total of frosted elfin individuals.

	first date	peak date	last date	span (days)
Brown elfin	26.IV	16.V	1.VI	37
Hoary elfin	28.IV	10.V	1.VI	35
Frosted elfin	10.V	30.V*	14.VI	36
Henry's elfin	16.V	30.V	30.V	15
E. pine elfin	28.IV	16.V	6.VI	40

Table 2. Flight period details for the frosted elfin during 1987–95: the closest survey dates (up to three) in lupine sites within known frosted elfin range immediately before and after the observed frosted elfin flight (if within three weeks), first and last dates of observed oviposition behavior (ovip. beh.), first date of adult Karner blues, and years of markedly advanced (fast) and retarded (slow) spring phenology. Peak date(s) are those when the most individuals were seen if >1 were observed that day.

	surveys before flight period	first date	first ovip. beh.	peak date	last ovip. beh.	last date	flight span (days)	surveys after flight period	first Karner date	phen- ology
1987	30.IV									fast
1988		17.V				18.V	2	27.V		fast
1989	11.V 17.V 26.V									
1990								6.VI	6.VI	
1991	10.V 14.V 15.V	20.V	20.V		20.V	20.V	1	28.V 29.V	23.V	fast
1992	5.V 6.V	20.V	20.V	20.V 1.VI	1.VI	1.VI	13	2.VI 10.VI	26.V	slow
1993	5.V 11.V 19.V	11.V		1.VI		5.VI	27	6.VI	1.VI	slow
1994		10.V	16.V	17.V	22.V	1.VI	28	4.VI 6.VI 13.VI	22.V	fast
1995	2.V 5.V 9.V	15.V	22.V	30.V	3.VI	14.VI	31		31.V	slow



Table 3. Results of stepwise linear regressions (set for  $p < 0.1$ ), with significant  $p$  values ( $< 0.05$ ) boldfaced, that tested 17 variables and (1) one management variable, (2) one management and one lupine variable, (3) three management variables, and (4) three management and five lupine variables. Phenological (phen.) date is defined in "Methods."

Regression	Regression 1			Regression 2			Regression 3			Regression 4		
	N	r	<i>p</i>	N	r	<i>p</i>	N	r	<i>p</i>	N	r	<i>p</i>
	319	0.345	<b>0.0000</b>	296	0.348	<b>0.0000</b>	140	0.368	<b>0.0000</b>	103	0.523	<b>0.0000</b>
	Step	r	<i>p</i>	Step	r	<i>p</i>	Step	r	<i>p</i>	Step	r	<i>p</i>
Temperature	1	+0.162	<b>0.0036</b>	1	+0.129	<b>0.0342</b>	1	+0.296	<b>0.0004</b>	1	+0.364	<b>0.0002</b>
Fluctuation	2	+0.174	<b>0.0035</b>	2	+0.363	<b>0.0000</b>						
Peak-phen.	3	+0.165	<b>0.0051</b>									
N surveyors	4	+0.200	<b>0.0007</b>	3	+0.242	<b>0.0000</b>						
Peak-date	5	+0.145	<b>0.0170</b>									
Quality	6	+0.104	0.0532							4	+0.464	<b>0.0035</b>
Phen. date				4	+0.263	<b>0.0039</b>						
Lupine abundance		—		5	+0.107	0.0556						
Management unintrusiveness							2	+0.164	<b>0.0457</b>			
Lupine core		—								2	+0.294	<b>0.0106</b>
Diversity										3	-0.417	<b>0.0003</b>
Management non-intensity		—								5	-0.267	0.0661

flight period spanned 27–31 days. These three years represented both markedly advanced and retarded spring phenologies, with peak dates shifting in correspondence to phenological development. Peak flight occurred just before or coinciding with the beginning of peak lupine flowering and also usually around the time of the emergence of the first Karner blue adults for the year, with this latter species' prime spring flight usually ensuing about one week later. Shapiro (1974) reported a similar relationship between frosted elfin and Karner blue flight periods, but with the beginning and peak of the former's flight slightly earlier in the year. In regression (Table 3), three date variables produced significant effects, suggesting that both calendar date and phenological development affect flight timing.

**Weather effects.** In multivariate analysis, frosted elfin density (detection) covaried strongly with increasing temperature, an expected result given its early flight period, but not with other weather variables (percent sunshine, wind) (Table 3). Likewise, in univariate analysis frosted elfin density correlated significantly with temperature ( $r=0.176$ ,  $p=0.0014$ ,  $N=328$ ) but not the other weather variables. Nonetheless, frosted elfins occurred on surveys from 14 to 31.5°C. Individuals sometimes perched and flew in the shade, but if the sun was shining, they usually occurred in sunny patches even in areas of high-density canopy. Individuals sometimes exhibited heat minimizing perch behaviors (angling to reduce its shadow, perching within shaded vegetation) at temperatures  $>27^{\circ}\text{C}$ .

**Approachability.** Frosted elfins seem rather approachable and sedentary, evident in that I photographed 79 (48%) of 164 individuals observed. I did not try to photograph 20 (12%), I was unable to photograph 49 (30%), and for 16 (10%) my notes are indeterminate. Thus, 79 (62%) of 128 concerted attempts to photograph individuals were successful. Like Iftner et al. (1992), we found this species relatively easy to track, with a flight that is typically slow and low. Even when an individual was flighty or rather active at first, it often stayed in the vicinity, calmed down, and then landed on or near lupine.

**Adult feeding.** Thirteen individuals were noted in apparent feeding behavior: 10 probing with the proboscis on and among lupine buds (Fig. 1), including three ovipositing females (see below), 1 on a lupine flower, 1 on bird-foot violet (*Viola pedata* L.) (Violaceae), and 1 on moist sand in a vehicle trail. Feeding occurred between 0730 and 1530 hr CST, with temperatures of 18–32°C and mostly sunny conditions.

**Oviposition.** Fourteen individuals exhibited oviposition behavior, with 10 eggs confirmed for 8 of 11 individuals checked (Fig. 2). These behaviors occurred throughout much of the flight period (Table 2). Consistent with Scott's (1986) statement that females oviposit on host inflorescences, nearly all oviposition behaviors occurred on young stalks of green or greenish-white lupine flower buds; only one had purple color lower on the flower stem. One individual showed oviposition behavior on both a flower bud and an axillary leaf bud, with an egg confirmed only in the latter location.

The oviposition sequence is slow and deliberate, similar to that described for two European lycaenid species (Fiedler and Schurian 1994, Fieldler et al. 1994). Often the female slowly paced up and down the flower buds with much bending down of her antennae and probing in and out by her rear abdomen among the small tightly packed buds. Sometimes this suggested difficulty getting the abdomen positioned as deeply as desired (which hinders locating the egg later without damage to the flower stalk) and sometimes extreme selectiveness about egg placement. Only one female was confirmed to lay  $>1$  egg, each of three on a different plant. After laying one egg, three females probed other very young lupine flower stalks (on and among buds) with their proboscis. It is unclear whether this was feeding behavior or a sensory evaluation

of future oviposition sites. After laying one egg, some flew from lupine to lupine, not necessarily landing on each, but seeming to search for more oviposition sites. Ovipositing females appeared to use two flight types: fluttery (slow erratic movement low over the vegetation for apparent search and inspection) and direct (rapid linear movement from lupine to lupine). Oviposition behaviors occurred between 1100 and 1630 hr CST, with temperatures of 18–30°C and mostly sunny conditions, except for two individuals at 25°C with 20–25% sunshine. Oviposition behavior and associated flights usually but not always occurred in unshaded places.

**Habitat associations.** Frosted elfin units typically contained a large patch or series of smaller patches of high-density lupine. Only 1 (0.7%) of 149 individuals for which data are available occurred in a unit with rare to uncommon lupine (adjacent to a unit with common lupine) and 13 (8.7%) in units with uncommon lupine, while the remainder (91%) occurred in sites with lupine ranging from uncommon/common to abundant/superabundant. Only 5 (3%) of 149 individuals occurred in lupine patches of  $\leq 0.4$  ha, with 97% in patches of 0.8–32 ha, and 50% in patches  $\geq 2.4$  ha. One hundred fifty-one (92%) of 164 individuals were in lupine core areas, 13 (8%) in intermediate areas, and 0 in isolated areas. In regression, lupine patch size was not significant while lupine abundance produced a near-significant ( $p < 0.06$ ) effect in the second regression but no effect in the fourth (Table 3). Lupine core produced a significant effect in the only regression in which it was included. These results together suggest that lupine abundance at both the microsite and landscape scales is more important than size of the particular lupine patch occupied. Vegetative quality was near-significant in the first regression and significant in the fourth, but with no significance in the other two regressions (Table 3). Site diversity (i.e. wet habitats) had a significant negative effect in the fourth regression (Table 3, but with no effects in the first three regressions) possibly because it reduces volume of lupine (dry) habitat on a landscape level.

Of 164 individuals, 157 (94%) occurred in savannas, nearly evenly split between open and closed ones, with only 4% in more open sites and 2% in forest openings. Consistent with this, the microsite occupied by frosted elfin individuals had a mean estimated canopy of 32% (range 3–80%,  $N=54$ ). Sometimes this microsite occurred in a linear herbaceous corridor (right-of-way) bounded on one or both sides by forest. Otherwise, this microsite often appeared to be an "arena" (opening or glade) surrounded by greater canopy, with a mean estimated diameter of 7.7 m (range 2–25,  $N=34$ ) (Figs. 3–4). Apparent territorial males often flew in deliberative oval or circular routes within these arenas. They did not necessarily perch on lupine; sometimes they consistently alit on something else, such as a twig. Paired spiral intraspecific (courtship or combative) flights emanated vertically, sometimes well out of the arena. One such flight was followed by courtship rejection 2 m off the ground on the sprouting leaves of an oak. With frequent pauses, the male and female walked over the sprouting leaves, the male in close pursuit, until he finally returned to the herb layer.

The limited distribution and possibly abundance of frosted elfins in Wisconsin may be due to the restriction of their larvae to feeding on lupine flowers and pods (Opler and Krizek 1984, Scott 1986, Schweitzer 1992). Dense lupine patches would be beneficial, because the more lupines per area, the less effort required for females to find them and the more forage accessible to the larva. Greater local canopy diversity and higher canopy density (until lupine flowering drops markedly) would be favorable because phenological advance would be moderated and the lupine flowering season lengthened.

**Site management.** Intrusiveness of management type had a significant



Figure 3. Habitat microsite of ovipositing female in Fig. 2, showing herbaceous "arena" surrounded by brushy under- and overstory; 27 May 1992, Wood County, WI.

negative effect in the third regression (but not the other three) while management intensity (a combination of intrusiveness and recency) had a positive near-significant ( $p < 0.07$ ) effect in the fourth (but not third) (Table 3). This suggests that some management is needed but it should not be too intensive. The distribution of individuals by management category generally supports this (Table 4). Underrepresented managements relative to survey effort included no management, but also forestry and rotational fire (the standard conservation management), which may be too intense. Overrepresented managements included recreation (vehicle trailsides) and mowing, which occur more frequently but less intensively, and wildfire types, which are intensive but less frequent. The only inconsistent result was mixed cutting, which was also underrepresented but would seem to be a moderate management (Table 4). Only 6 (3.7%) individuals occurred in "reserves" (wildlife areas and refuges), with the remainder in timber reserves, recreational vehicle trails and trailsides, rights-of-way, and military reservation. Our best and most consistent frosted elfin site was managed with late-season mowing no more frequent than one cut/year, with only a partial cutting of the habitat in many years. Dense larvae (Swengel 1995:165) and consistently numerous adults (Swengel 1994:84–85) of the Karner blue have also been observed at this site.

Rotationally burned sites were seemingly excellent habitat with abundant lupine and canopy diversity usually on the opener end of the spectrum. One of four individuals in such sites occurred on the unburned far edge of a fire-break (and the adjacent unmanaged and more forested unit with sparse lupine also produced an individual). The three actually found within this



Figure 4. Habitat microsite with research assistant at left where three frosted elfins occurred, showing "arena" surrounded by woody overstory; 30 May 1995, Jackson County, WI.

Table 4. Distribution by management category of frosted elfin individuals (on formal surveys only), transect survey hours, units, and sites. Observed (obs) individuals compared to expected (exp) individuals (based on proportion of survey time spent in that management category) were significantly non-random in distribution (Chi-square=48.4197,  $df=7$ ,  $p=0.0000$ ).

	N frosted elfins		hours	units	sites
	(obs)	(exp)			
<b>Relative underrepresentation</b>					
forestry	2	4.3	2.8	8	2
mixed cutting	1	17.6	11.5	30	12
rotational fire	4	20.2	13.2	40	7
nothing	3	6.1	4.0	23	10
<b>Relative overrepresentation</b>					
recreation	9	5.4	3.5	9	2
wildfire & other	23	15.6	10.2	34	19
wildfire	47	31.8	20.8	75	8
mowing	50	38.0	24.8	98	31
total	139	139.0	90.8	324	91

same burn unit occurred just over four years since the last fire. By contrast, areas of wildfire (single unplanned non-management fires caused by accident, arson, or lightning) produced numerous frosted elfin observations, but even there, none were found in the third and fourth years postfire (the soonest surveys occurred after a wildfire). Most individuals were found over a decade since wildfire. Thus, suitable habitat can result following fire and it can persist a long time after a single fire. Since frosted elfins appear to occupy burned sites very slowly, this suggests that mortality during and/or immediately after fire is rather high and dispersal back into burned areas rather slow.

**Annual fluctuations.** By far the most individuals, 99 (60%), were found in 1995, followed by 38 (23%) in 1994. But in comparisons within unit among sites surveyed during main frosted elfin flight period each year 1992–95, the major increase (+200%) in numbers occurred in 1994, with 1995 levels only slightly above (+13%) 1994 levels and 1993 levels above (+25%) 1992 levels. Thus, most of the increase in 1995 was attributable to surveying new sites with large patches of suitable habitat, while the increase in 1994 likely resulted at least in part from a fluctuation in abundance. Elsewhere this species has a reputation for marked annual fluctuation (Glassberg 1993), and our dataset showed a strong significant effect from annual fluctuation in two regressions (Table 3).

**Species correlations.** These should be interpreted with caution since they paired data from the same year. If the two species were fluctuating in different directions in the same year, this would confound the correlation. Averaging species indices per site over multiple years could overcome this, but this procedure greatly reduced sample size and statistical power.

Of the three butterflies largely restricted to lupine as larval host, the Karner blue was the most numerous and widespread; the frosted elfin, the least. The *Persius duskywing* species complex was intermediate between these two species. Shapiro (1974) reported a similar number of sites for these two species in his study region, but the frosted elfin was also much less numerous within a site there than the Karner blue. The relative abundance of the two univoltine species (frosted elfin and *Persius duskywing* complex, which both fly in spring) typically correlated more strongly with the abundance of spring rather than summer Karner blues (Table 5). This suggests that conditions favoring high Karner blue numbers may differ somewhat between spring and summer. Conditions favoring high spring Karner numbers also seem to favor the other two species, but conditions that favor the highest summer Karner numbers seem less favorable for the other species. Abundance of the *Persius duskywing* complex always correlated more strongly with Karner blue abundance than did frosted elfin abundance. However, *Persius duskywing* abundance correlated as strongly with that of the frosted elfin as with that of spring Karner blues.

The larger the geographic scope of the abundance correlations (i.e., both within and outside of lupine barrens), the stronger the correlations (Table 5c). This reflects their range overlap and common restriction to lupine sites. But within lupine habitat, within known range of both species, the correlation weakens considerably between frosted elfin and Karner blue (Table 5a). While all our frosted elfin sites also supported Karner blues, these results also suggest a fair degree of niche segregation, as discussed in Shapiro (1974).

## CONCLUSION

Given the relatively low numbers of frosted elfins found anywhere in this study, our surveys outside current known range do not rule out the species'

Table 5. Pearson product-moment correlations of peak number observed within main flight period in the same unit of the three lupine-associated species, with significant *p* values (<0.05) boldfaced. 1st=spring flight; 2nd=summer flight.

	Frosted Elfin			Karner Blue 1st			Karner Blue 2nd		
	N	r	p	N	r	p	N	r	p
<b>a. Frosted Elfin Range</b>									
Frosted Elfin				116	0.195	<b>0.0361</b>	84	0.065	0.5547
Persius Complex	217	0.407	<b>0.0000</b>	212	0.389	<b>0.0000</b>	159	0.347	<b>0.0000</b>
<b>b. All Lupine Sites</b>									
Frosted Elfin				147	0.283	<b>0.0005</b>	139	0.276	<b>0.0010</b>
Persius Complex	270	0.385	<b>0.0000</b>	212	0.389	<b>0.0000</b>	159	0.347	<b>0.0000</b>
<b>c. All Barrens Sites</b>									
Frosted Elfin				161	0.317	<b>0.0000</b>	162	0.330	<b>0.0000</b>
Persius Complex	318	0.408	<b>0.0000</b>	226	0.410	<b>0.0000</b>	182	0.407	<b>0.0000</b>

presence there. Because of the spotty but widespread range of the frosted elfin throughout eastern North America (Opler and Krizek 1984), this species should be looked for elsewhere in the state, even in sites with wild indigo. While frosted elfins co-occur with Karner blues, the latter is more widespread and abundant in Wisconsin. Thus, habitat preservation and management suitable for maintaining the Karner blue may not adequately address the more restrictive habitat and management needs of the frosted elfin. Where these two species co-occur, however, management can be favorable for both by applying moderate treatments (and avoiding too intense, too frequent treatments) to maintain locally dense lupine in heterogeneous and intermediate canopy.

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