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Observations of Prairie Skippers *(Oarisma Poweshiek, Hesperia Dacotae, H. Ottoe, H. Leonardus Pawnee*, and *Atrytone Arogos Iowa*) [(Lepidoptera: Hesperiidae] in Iowa, Minnesota, and North Dakota During 1988-1997

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OBSERVATIONS OF PRAIRIE SKIPPERS (*OARISMA POWESHIEK, HESPERIA DACOTAE, H. OTTOE, H. LEONARDUS PAWNEE*, AND *ATRYTONE AROGOS IOWA*) (LEPIDOPTERA: HESPERIIDAE) IN IOWA, MINNESOTA, AND NORTH DAKOTA DURING 1988–1997

Ann B. Swengel[1] and Scott R. Swengel[1]

ABSTRACT

In transect butterfly surveys at 40 prairies in Iowa, Minnesota, and North Dakota in summer each year during 1988–1997, we recorded 2403 adults of Poweshiek skipperling (*Oarisma poweshiek*) at 20 sites, 547 Dakota skippers (*Hesperia dacotae*) at 12 sites, 27 Ottoe skippers (*H. ottoe*) at one site, 290 Pawnee skippers (*H. leonardus pawnee*) at eight sites, and 81 Arogos skippers (*Atrytone arogos*) at nine sites. In correlations of relative density (individuals/km) of the analyzable species (all but Ottoe skipper), geographical factors (latitude and longitude) produced the most significant correlations, followed by timing (with higher numbers nearer noontime), and lastly weather (positive correlation with temperature, negative correlation with wind speed). The relative densities of these analyzable species showed more significant differences in relation to habitat factors than to variables describing diurnal activity patterns or weather conditions. Relatively higher skipper densities occurred in drier, undegraded prairie vegetation in sites with diverse rather than uniform topography. Patterns of relative density also varied among species with respect to management by idling, grazing, haying, or burning. Nectar visits by species, and by sex if possible, are reported. More instances of courtship rejection than mating were observed. On later dates in the flight period, female Dakota skippers proportionately increased and the sex ratio became more variable. With increasing relative density, the sex ratio of Dakota and Pawnee skippers became less variable and tended toward values in the range of about an even ratio.

The tallgrass prairie of central North America contains vegetation dominated by herbaceous flora. Since European contact in North America, about 99% of tallgrass prairie has been destroyed in most central states and provinces, primarily for conversion to agriculture. Fragments of original (never tilled) prairie remain in preserves, parks, and unintensively utilized farmland (Curtis 1959, Samson and Knopf 1994). This vast habitat destruction has considerably reduced the abundance of many prairie-associated animals (Samson and Knopf 1994, 1995). Butterflies specialized to prairie are now relatively rare and primarily restricted to preserves (Opler 1981, Johnson 1986, Panzer et al. 1995, Panzer and Schwartz 1998).

Among these are five skippers (Lepidoptera: Hesperiidae): Poweshiek skipperling [*Oarisma poweshiek* (Parker 1870)], Dakota skipper [*Hesperia*

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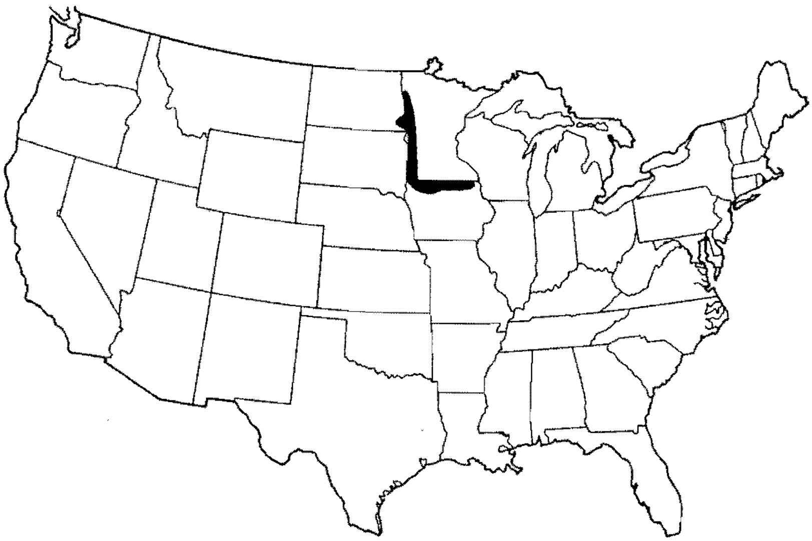

Figure 1. Map of study area (in black), where the 40 study sites (listed in App. 1) are located.

dacotae (Skinner 1911)], Ottoe skipper (*H. ottoe* W. H. Edwards 1866), Pawnee skipper (*H. leonardus pawnee* Dodge 1874), and Arogos skipper [*Atrytone arogos iowa* (Scudder 1869)]. These species have been the subjects of surveys and studies concerned with their conservation, such as McCabe (1981), Dana (1991), Royer and Marrone (1992a-c), Schlicht and Orwig (1998), and Bureau of Endangered Resources (1999).

This paper presents analyses of observations of these prairie skippers during ten years of transect surveys at 40 tallgrass prairies in Iowa, Minnesota, and North Dakota (Fig. 1). The first set of analyses contributes to understanding how to design and interpret field surveys of these skippers. We (1) compiled observation dates for these skippers, with notes on phenological variation among years; (2) correlated these species' relative density (individuals/km) with factors related to geography (latitude, longitude), diurnal timing, and weather; and (3) examined variation in sex ratio of species readily sexed in the field and seen in sufficient numbers for patterns related to protandry (appearance of males before females) and density. These results are useful for understanding when, where, and under what conditions to conduct surveys for these species, and for interpreting observations given the timing, location, and circumstances under which surveys occurred. Such information is useful for effectively monitoring these species of conservation interest. Our second set of analyses addresses the ecology of these prairie skippers. We tested for differences in their relative density (individuals/km) by habitat factors (prairie type, vegetative quality, topographic diversity, management). We also compiled the species' nectar visits and reproductive behavior observed on the surveys. These analyses contribute to a greater understanding of the habitat associations, behavior, and adult food preferences of these skippers. Such information is useful for implementing appropriate conservation programs on their behalf.

METHODS

Sites and surveys. The study sites (listed with location information in App. 1) were deliberately selected for their conservation interest—i.e., they were known or predicted to support prairie-specialized butterflies. Most sites were reserves in private or government ownership because of their accessibility (without concern for trespassing) and importance for conserving rare species. They ranged from 2 to 2024 ha in prairie patch size (mean 250 ha, median 97 ha). Management by cool-season burning, typically in a rotation of 2–5 years, occurred at 28 sites. Three sites and the unburned part of a fourth site were hayed (mowed, with subsequent removal of clippings) in late summer or early fall no more often than once per year, sometimes in a rotation over two years (either part hayed per year, or all hayed one year and none hayed the next). Haying and burning both occurred throughout one site. The unburned parts of four sites were idle (i.e., no active management occurred or was evident during the study) but had been in some form of non-tilled farm usage at some time prior to preservation. Eight areas in Sheyenne National Grassland (North Dakota) were considered separate sites because they were non-contiguous (because of intervening non-public land that was not prairie vegetation) and scattered over an area 53 km north-south by 42 km east-west. These eight areas had rotational range grazing for both ecological and economic purposes, at a stocking rate of 0.3–0.6 animal use months/ha/yr (AUM=500 kg of cattle for 1 month) with grazing from mid-May to early November (Kobriger et al. 1988, Manske et al. 1988, Sheyenne Ranger District—Custer National Forest unpubl. report). One of these sampled areas was also burned.

We conducted transect butterfly surveys along similar routes each year (Table 1), as reported in Swengel (1996, 1998) and Swengel and Swengel (1997). Walking at a slow pace (1.5–2 km/hr) on parallel routes 5–10 m apart, we counted all adult butterflies observed ahead and to the sides, to the limit of species identification (possibly with binoculars after detection) and our ability to track individuals. Within a site, a new sampling unit (i.e., subsite) was designated whenever the habitat along the route changed markedly by vegetation type (wetland, wet, mesic, dry, "extra dry" sand), management (type and/or years since last treatment), and/or vegetative quality (degraded, semi-degraded, undegraded) based on amount of brush and diversity and

Table 1. Summary statistics on formal surveys at study sites (see App. 1).

	All surveys	Surveys in study species' flight periods
N sites	40	40
Range of latitudes of survey sites	42.58–47.20	42.58–47.20
Range of longitudes of survey sites	92.36–97.40	92.36–97.40
N unit surveys	926	811
Span of survey dates	18 June–21 August	20 June–20 August
Span of consecutive years of surveys	1988–1997	1988–1997
Total kilometers of survey effort	458.8	393.4
Total hours of survey effort	258.7	219.4

abundance of native and exotic flora. Routes crossed rather than followed ecotones and management boundaries to reduce edge effects, and were designed to maximize sampling per unit but minimize number of unit changes while sampling representative areas of the site.

We used several means to avoid double-counting individuals either within or among units at a site. We placed our parallel routes further apart than the effective distance for detecting and identifying most species, especially skippers. We advised each other of individuals moving toward the other's route, and we strove to maintain continuous forward movement except for stops to identify individuals. We limited our censuses only to individuals within the area where we could continue to track their movements. We also tried to apply a consistent procedure for whether an individual should be counted or considered already counted. For example, if a Poweshiek skipperling flew behind the senior author, and shortly afterward, another flew past her from behind her, that second observation would be considered a repeat of the first individual. But if a second Poweshiek skipperling flew toward her from in front of her, that individual would be counted. It is impossible to expect double-counting to be eliminated, but this should add little bias to our analyses so long as all the surveys were consistent in the determination of whether an individual should be counted or not. Since the same two people staffed all the surveys in this study, it is likely our surveys had this consistency. Even if our rate of double-counting might vary by density of individuals being counted, this does not confound our statistics, especially since they are all non-parametric, so long as our rate of double-counting relates progressively to the number of individuals actually present, whether in a linear, exponential, threshold, or other manner.

For each unit, we recorded temperature and time spent surveying, and estimated wind speed, percent cloud cover, and percent time the sun was shining. These measurements could mostly be made (except during highly changeable weather) before and after each unit survey, and not during the timed survey of the unit. When more than negligible time was required during a unit survey to record weather descriptors or identify an individual, that time was deducted from the formal survey total. Route distance was estimated based on site maps and land features such as road junctions along borders of "sections" (square mile plots systematically placed by land surveyors). Data from each unit were kept separate. Site selection, vegetative type and quality, prairie size, and management treatments during the study period were based on Iowa State Preserves Board (1981), Wendt (1984), The Nature Conservancy (1988, 1994), Minnesota Department of Natural Resources (1995), as well as brochures, maps, and personal communications from the agencies that own and manage the sites. A unit occurred in a topographically "diverse" site if it contained contiguous unforested and uncultivated habitats both wetter and drier than mesic; otherwise the site was "uniform". Most surveys occurred during 1990–1997, with a few also from 1988–1989.

The five study species varied in ease of field identification. Poweshiek skipperling was easiest because of the distinctiveness of its dark dorsal surfaces and silvery ventral hindwing venation. This contrast, combined with its often slow and whirring flight, enabled identification even when it was flying. The Arogos skipper, although superficially similar to other yellow-orange skippers, especially the Delaware skipper [*Anatrytone logan* (W. H. Edwards 1863)], was readily identified based on dorsal front wing pattern, which was also observable when the wings were closed if backlit. Females of the *Hesperia* study species were also readily separable, although it was usually beneficial to observe both the dorsal surface (to verify gender) and the ventral surface (to determine species). Males of the *Hesperia* study species required the most careful inspection. We were especially mindful to distinguish them from *Polites* Scudder 1871 and Sachem [*Atalopedes campestris* (Boisduval 1852)]. If we did not obtain an adequate view of all necessary features for identification to species (because of wing wear, obscure view, or flight away), we recorded the individual at the lowest taxonomic level possible (genus, subfamily, or family).

Dakota, Ottoe, Pawnee, and Arogos skippers can be sexed in the field based on wing pattern. Starting in 1990, we recorded the sex of these individuals, if possible. Poweshiek skipperling is not readily sexed in the field. Also starting in 1990, we recorded the behavior of all individuals of the study species when first observed, and all instances of feeding and mating noticed (whether the first behavior or not).

All sites could not be visited each year but most were visited more than once both within a year (3–5 weeks or more apart) and among years (App. 1). The site (Hole-in-the-Mountain) contributing the most unit surveys to this study comprised only 15% of the unit surveys. Survey timings were selected especially to sample prairie-specialist butterflies, as classified in Swengel (1996, 1998), including the study species in this paper. Surveys occurred during a wide range of weather conditions and times of day. Occasionally surveys occurred in intermittent light drizzle, so long as butterfly activity was apparent, but not in continuous rain. Butterfly nomenclature follows Ferris (1989).

Analyses. We computed all statistics with ABstat 7.20 software (Parker, Colorado), with significance set at two-tailed $P<0.05$. Observation rates (relative densities or abundances) were calculated for each species as individuals observed per km in each unit survey. It was necessary to standardize the data as observation rates because the routes varied in length among units. Unit surveys were included in an analysis only if held on dates during the species' flight period (i.e., within the span of dates adults of the species were observed in the study region that year) at sites where the species was ever recorded during these surveys. Analysis was performed at the scale of the unit rather than by site, because unit surveys within the same site varied, sometimes considerably, in vegetative characteristics and weather.

The Spearman rank correlation was used to test for significant patterns in the observation rates of each study species relative to geography (latitude, longitude), timing (beginning time of survey, crepuscularity—difference between 1200 h CST and time when unit survey started), and weather (percent time sun was shining, percent cloud cover—mean of beginning, ending, lowest, and highest percent cloud cover, temperature—mean of beginning, ending, lowest, and highest temperature, and wind speed—mean of lowest and highest wind speed).

The Mann-Whitney U test was used to test for differences in observation rates of each skipper species relative to habitat factors. These included both ones at the unit level (prairie vegetation type, quality, management) and at the site level (topographic diversity, prairie patch size) that are relevant as a context for the unit. Although management was classified by unit, only in a few cases did different units in the same site have different management types. Prairie patch sizes were grouped into three classes—small (13–20 ha), intermediate (>30 and <130 ha), and large (>140 ha)—with 6, 17, and 17 sites, respectively. These size categories were defined such that a considerable break (>10 ha) would occur between each category.

We also tested whether these habitat factors might have significant intercorrelations, such as larger prairies more likely having topographic diversity or less degraded vegetation. We used the Spearman rank correlation to test for significant relationships among vegetation type, quality, topographic diversity, and prairie size (N=40 study sites, as in App. 1). All these factors can be ordered along a numerical continuum (e.g., 1 for wet prairie, 2 for wet-mesic, 3 for mesic, etc.; and 1 for degraded, 2 for semi-degraded, 3 for undegraded), or have only two states (uniform vs. diverse). For unit characteristics (type and quality), we used the mean for that factor on all unit surveys at that site. Since management type is a qualitative rather than quantitative factor, we used the Mann-Whitney U test to determine whether the sites in each management category differed in type, quality, diversity, or size. Sites with more than one management type were tested separately by each management type.

RESULTS

We recorded 4305 individuals of grass skippers (Hesperiinae) on formal surveys in this study (App. 2). We found 17 species but did not identify 410 individuals (10%) to species. The proportion of unidentified grass skippers (out of total grass skippers, per unit survey) correlated significantly with relative density of grass skippers (individuals, identified or not, per km) (r=+0.103, N=438 unit surveys, P<0.05, Spearman rank correlation), but not with the relative density of *Hesperia*, *Polites*, or total butterflies, nor with relative species richness (species per km per unit survey) of grass skippers or total butterflies, nor with year.

We observed one or more of the five study species on 46 of the 67 dates we conducted surveys at the study sites (Fig. 2). For Poweshiek skipperling and Dakota and Arogos skippers, we recorded a sufficient number of individuals (2403, 547, and 81, respectively) over a broad enough span of dates to

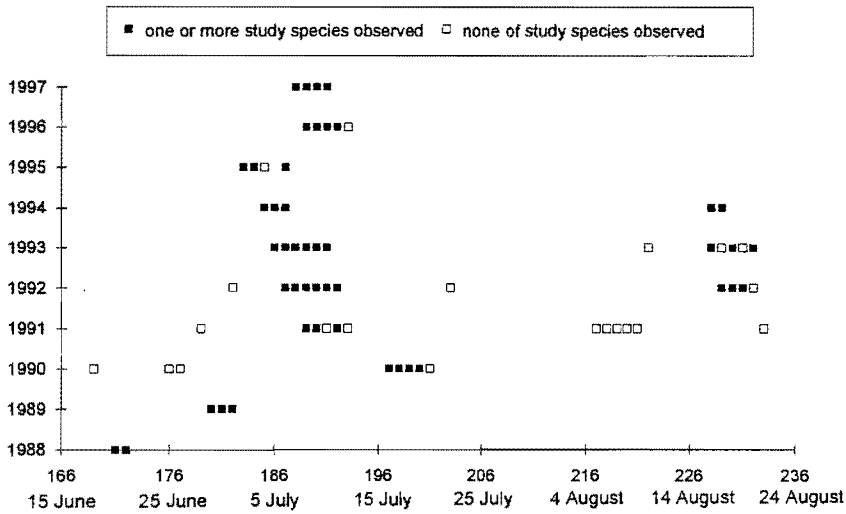

Figure 2. Survey dates of this study, with indication whether or not any of the study species were observed on each date. Only informal observations occurred on 21 June 1988, 29 June 1989, and 1 July 1989.

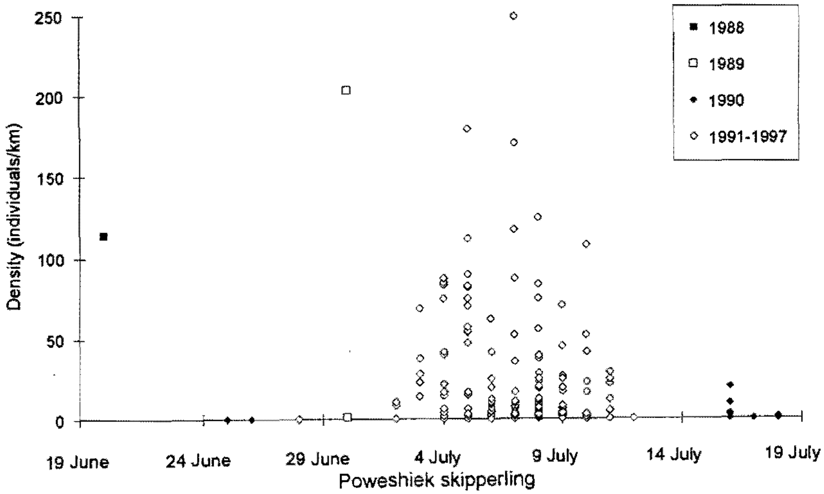

Figure 3. Relative Poweshiek skipperling density (individuals/km per unit survey) by date, at sites where the species was ever recorded during these surveys.

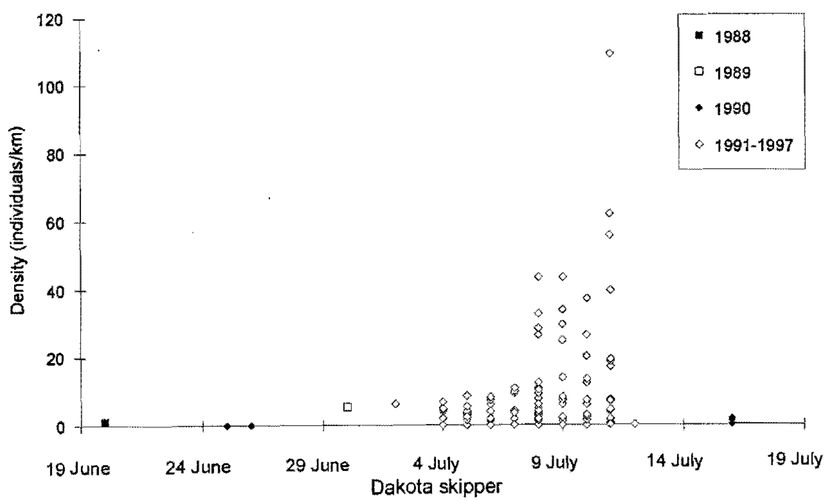

Figure 4. Relative Dakota skipper density (individuals/km per unit survey) by date, at sites where the species was ever recorded during these surveys.

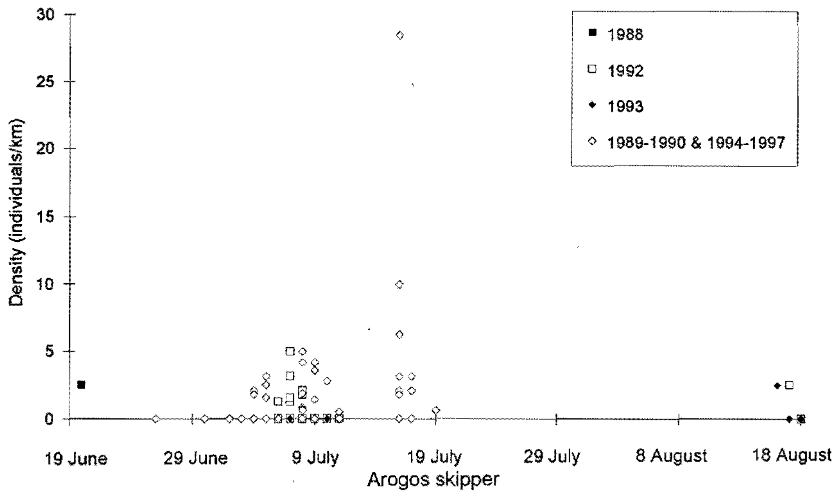

Figure 5. Relative Arogos skipper density (individuals/km per unit survey) at sites where the species was ever recorded during these surveys.

plot their observation rates (individuals/km, per unit survey) by date (Figs. 3–5). We recorded 290 Pawnee skippers only during 16–20 August.

The 27 Ottoe skippers (sex recorded for 14; all were males) observed on formal surveys were at Hole-in-the-Mountain (see App. 1 for site locations) during 1989–1992. We also informally observed two individuals (sex not noted) at Freda Haffner Kettlehole on 1 July 1989. Others recorded this species at a third study site, Prairie Coteau, during the study period (D. Schlicht, pers. comm.). To provide more insight into the flight period of this species, we compared the dates when we did or did not observe the Ottoe skipper at these three sites to the span of dates in which we observed adults of this species in southern Wisconsin in the same years (Fig. 6). Our span of observations in Wisconsin averaged 28.3 days (range 10–55) per year. Our observations of Ottoe skipper in Iowa and Minnesota occurred before or during the period when we observed the species in Wisconsin in the same year.

Sex ratio. Only 30 of 81 Arogos skipper individuals were sexed; these were evenly divided between males and females. The number of sexed individuals was adequate for analysis for Dakota Skipper (252 males and 214 females, which is 85% of the total individuals observed) and Pawnee skipper (88 males and 30 females; 41% of total observed). On later dates in the flight period, female Dakota skippers proportionately increased but the sex ratio (expressed as percent males of sexed individuals) was also quite variable among unit surveys (Fig. 7). The time span in which Pawnee skippers was observed was too narrow (16–20 August) for such analysis. With increasing observation rates (total individuals/km, per unit survey), the Dakota skipper sex ratio became a bit less variable and less skewed to either extreme (Fig. 8). Data for the Pawnee skipper were insufficient to determine whether it showed a similar pattern (Fig. 9).

Geography, timing, weather. Too few Ottoe skippers were observed to support analysis. Observation rates (individuals/km per unit survey) of

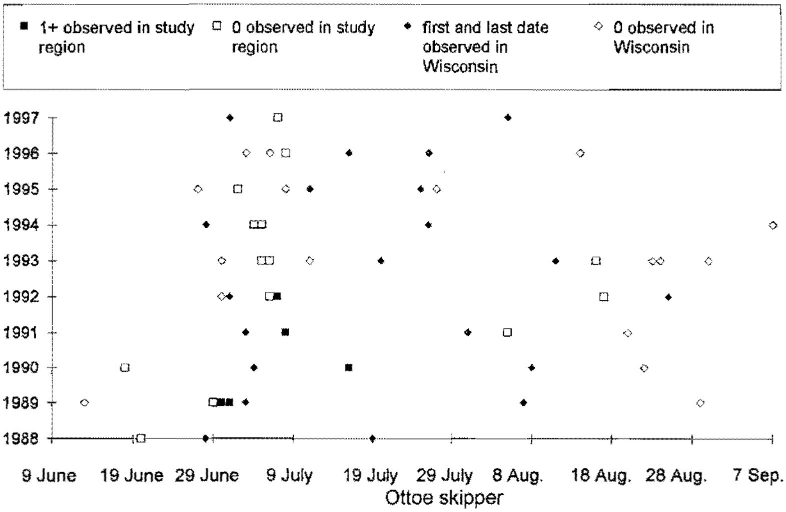

Figure 6. Dates of visits to study sites known to support Ottoe skippers during the study period (Freda Haffner Kettlehole, Hole-in-the-Mountain, Prairie Coteau, locations listed in App. 1), with indication whether any individuals were recorded or not. Included for comparison of flight periods are the first and last dates we recorded the Ottoe skipper each year at six prairies in southwestern Wisconsin (Crawford, Grant, Green, and Sauk Counties), and dates of visits to these sites outside the observed flight period.

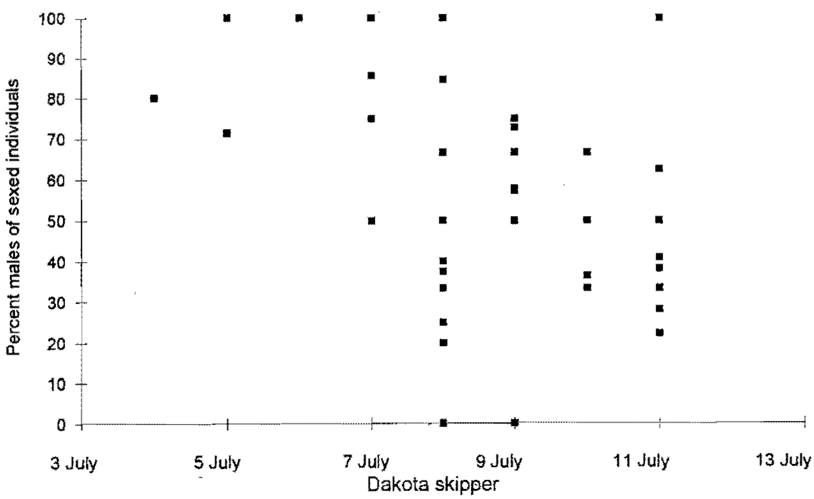

Figure 7. Percent male of sexed Dakota skippers by date, on unit surveys with >1 individual sexed.

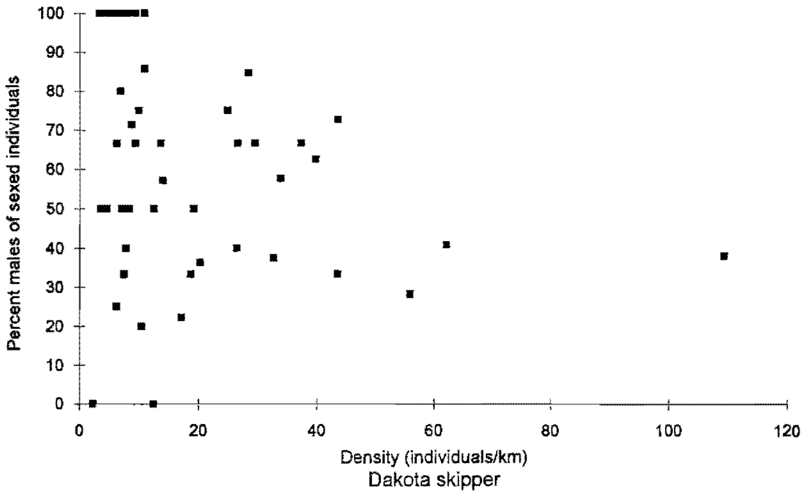

Figure 8. Percent male of sexed Dakota skippers by total Dakota skipper density (individuals/km per unit survey, including unsexed), on unit surveys with >1 individual sexed.

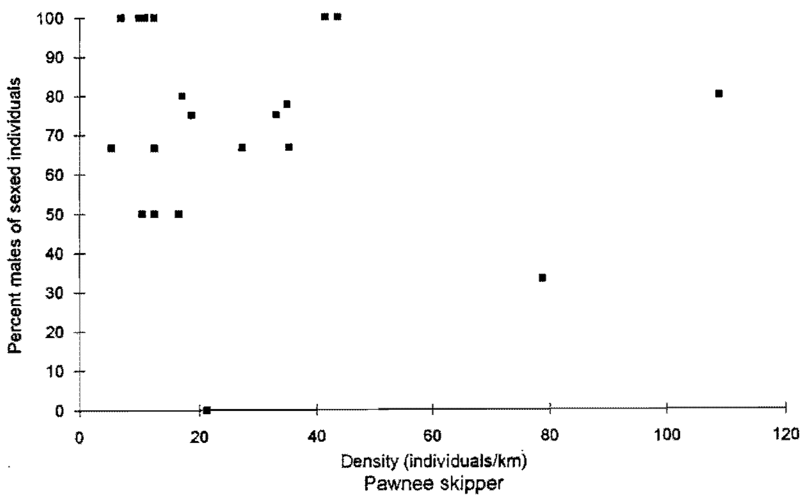

Figure 9. Percent male of sexed Pawnee skippers by total Pawnee skipper density (individuals/km per unit survey, including unsexed), on unit surveys with >1 individual sexed.

Table 2. Spearman rank correlation coefficients of the study species' relative density (individuals/km per unit survey) with geography, timing, and weather factors. Analyses include only unit surveys during the species' flight period in each year at sites where the species was ever recorded during this study's surveys.

	Poweshiek	Dakota	Pawnee	Arogos
Number of unit surveys (N)	482	338	44	151
Geography				
Latitude	–0.202 **	+0.080	–0.508 **	–0.138
Longitude	–0.163 **	+0.260 **	+0.178	+0.153
Timing				
Crepuscularity[1]	–0.056	–0.008	–0.373 *	–0.176 *
Time of day	–0.050	+0.042	+0.046	+0.032
Weather				
Percent cloud cover	+0.019	+0.076	+0.175	–0.070
Percent sunshine	–0.014	–0.075	–0.061	+0.054
Temperature	+0.109 *	+0.027	+0.218	+0.155
Wind speed	–0.103 *	–0.033	+0.174	–0.188 *

* P<0.05

** P<0.01

[1]Nearness to morning/evening (i.e., as opposed to nearness to noontime CST).

Poweshiek skipperling correlated negatively and significantly with latitude and longitude, Dakota skipper rates correlated positively with longitude, Pawnee skipper rates correlated negatively with latitude, while Arogos skipper had no significant correlations with geographical factors (Table 2).

The only significant correlations with diurnal timing were negative for Pawnee and Arogos skipper rates with crepuscularity (Table 2). All analyzed species were active in a wide range of times of day, from 0633–0657 h to 1724–1745 h out of a possible 0628–0644 to 1742–1745 h CST, except Pawnee skipper was observed during 0823–1630 h CST, which was the full range of survey timings at sites where this species was ever recorded. The proportion of unidentified grass skippers (out of total grass skippers, per unit survey) correlated significantly with later times of day (r=+0.133, N=438 unit surveys, P<0.05, Spearman rank correlation), but not with crepuscularity.

Poweshiek skipperling rates covaried significantly with increasing temperature (Table 2). Relative densities of that species and Arogos skipper correlated significantly and negatively with wind speed (Table 2). No species correlated significantly with percent cloud cover or sunshine, and Dakota and Pawnee skippers had no significant correlations with weather factors (Table 2). All analyzed species were active in from 0 to 100% sunshine and cloud cover. Poweshiek skipperling and Dakota skipper were active throughout the range of temperatures (14–16 to 32°C) and wind speeds (0–48 km/h) on surveys during their flight periods at sites where we ever recorded these species. The Pawnee skipper was detected in the full range of temperatures (19–30°C) and wind speeds (8–28 km/h) on surveys during its flight period at known sites. The Arogos skipper was observed in temperatures of 19–32°C (out of a possible 18–32°C) and winds of 0–40 km/h (out of a possible 0–48 km/h). The proportion of unidentified grass skippers (out of total grass skippers, per unit survey) correlated significantly with temperature (r=+0.190,

Table 3. Mean ± SD of the study species' relative abundances (individuals/km per unit survey). Data reported are only from unit surveys during the species' flight period in each year at sites where the species was ever recorded during this study's surveys. Means in the same column and habitat factor sharing the same letter are not significantly different by the Mann–Whitney U test (two-tailed $P<0.05$).—indicates a sample too small for statistical testing.

	Poweshiek			Dakota			Pawnee			Arogos		
	N	mean ± SD		N	mean ± SD		N	mean ± SD		N	mean ± SD	
Prairie type												
wetland	4	1.03 ± 2.07	–	3	0.00 ± 0.00	–	0			1	0.00 ± 0.00	–
wet prairie	129	2.99 ± 10.09	B	54	0.08 ± 0.56	B	2	0.00 ± 0.00	–	22	0.00 ± 0.00	B
mesic prairie	55	3.33 ± 9.80	B	60	1.29 ± 5.34	B	1	0.00 ± 0.00	–	9	0.46 ± 1.38	AB
dry prairie	291	13.93 ± 2.62	A	222	4.51 ± 11.61	A	35	15.60 ± 23.30	A	120	1.02 ± 2.98	A
sand prairie	6	0.00 ± 0.00	–	0			6	15.86 ± 9.60	A	0		
Prairie quality												
degraded	28	0.81 ± 3.30	C	16	0.00 ± 0.00	B	0			18	0.23 ± 0.98	A
semi–degraded	120	4.82 ± 12.96	B	75	2.16 ± 12.68	B	18	13.03 ± 14.41	A	29	0.35 ± 1.19	A
undegraded	337	11.94 ± 30.57	A	248	3.71 ± 9.10	A	26	15.63 ± 25.29	A	105	1.07 ± 3.13	A
Site diversity[1]												
uniform	118	2.75 ± 8.61	B	72	0.72 ± 3.52	B	12	4.91 ± 7.57	B	0		
diverse	367	11.72 ± 29.81	A	267	3.86 ± 10.83	A	32	18.19 ± 23.71	A	152	0.83 ± 2.70	–
Site size[2]												
small	11	1.18 ± 2.26	A	0			4	21.18 ± 16.74	–	0		
medium	220	11.25 ± 27.78	A	127	1.08 ± 3.21	B	9	1.84 ± 4.20	B	76	0.38 ± 0.95	B
l arge	254	8.41 ± 25.94	A	212	4.46 ± 12.01	A	31	17.41 ± 23.62	A	76	1.28 ± 3.65	A
Unit management												
idle	24	11.02 ± 22.96	A	20	1.03 ± 2.36	B	2	2.07 ± 2.93	–	16	3.67 ± 7.28	A
grazed	10	0.21 ± 0.66	B	0			11	12.47 ± 9.37	A	0		
hayed	21	7.59 ± 15.97	A	11	23.60 ± 21.46	A	4	58.77 ± 45.14	–	2	1.38 ± 1.95	–
burn+mow/hay	2	0.00 ± 0.00	–	0			0			0		
burned	428	9.81 ± 27.49	AB	308	2.61 ± 8.69	B	27	9.80 ± 12.11	A	134	0.47 ± 1.07	B

[1]Topographic diversity: uniform = only lowland or only upland grassland; diverse = lowland and upland grassland.
[2]Prairie sizes: small <20 ha, intermediate >30 and <130 ha, large >140 ha.

N=438 unit surveys, P<0.01, Spearman rank correlation), but not with the other weather factors.

Habitat. On formal surveys, Poweshiek skipperling occurred in the most sites (20, in all three states) in the widest range of unit and site characteristics (Table 3). We recorded the Dakota skipper at 12 sites in Minnesota, Pawnee skipper in eight sites in Minnesota and North Dakota, and Arogos skipper in nine sites in all three states (Table 3).

Poweshiek skipperling had significantly higher observation rates (individuals/km, per unit survey) in dry, undegraded units in diverse prairies, with no statistical differences by prairie size (Table 3). Significantly higher rates also occurred with idling and haying, and lower densities in grazed units. While the mean rate in burned units was relatively high, these rates were highly variable and showed no statistical patterns. Dakota skipper rates were significantly higher in dry, undegraded units in diverse, large prairies with management by haying rather than burning or idling (Table 3). Pawnee skipper rates were significantly higher in diverse prairies and large vs. medium prairies (Table 3). The mean rate in small prairies was similar to that in large prairies, but the sample was too small for statistical testing. Arogos skipper rates were significantly higher in dry units in large sites with management by idling rather than burning (Table 3). The few Ottoe skipper individuals occurred in dry undegraded prairie, both fire-managed and idle.

The only habitat factors that significantly related to each other in Spearman rank correlations were prairie type and topographic diversity—i.e., drier sites were more likely to have topographic diversity. No significant correlations occurred among prairie quality, type, and size. With respect to habitat differences by management categories, we had analyzable numbers of sites only for grazing and burning. In Mann-Whitney U tests, the grazed sites (i.e., areas in Sheyenne National Grassland) had significantly drier and more degraded vegetation in larger prairie patches, but did not differ significantly by topographic diversity.

Behavior. Table 4 presents nectar visits by species, and by sex if possible. Although many more individuals of Poweshiek skipperling were recorded than Dakota skipper, the latter was observed nectaring on more flower taxa (Table 4). The proportion of nectaring individuals seemingly increased in rough correspondence to increased difficulty in (and closer view required for) identification, with the exception of male Arogos skipper (Table 4). In other words, the more difficult the species was to detect and identify, the more skewed our survey totals tended to be toward nectaring individuals. Two instances of predation were observed, both of a Poweshiek skipperling: by a crab spider (Araneida) hidden in an ox eye [*Heliopsis helianthoides* (L.)] flower on 6 July 1992 at Prairie Marshes and by two ambush bugs (Hemiptera: Phymatidae) on black-eyed Susan (*Rudbeckia hirta* L.) on 11 July 1996 at Bluestem.

The Poweshiek skipperling was the only study species observed outside prairie habitat. One individual was seen 300 m east of Prairie Marshes along the access trail (a primitive dirt road) and another 800 m east along the same trail. Habitats east of this site were tilled field and old field.

We recorded only three mating pairs. At 0930 h CST at Bluestem on 9 July 1992 (26°C, 70% sunshine, 45% cloud cover, wind SW 8 km/h), one Dakota skipper pair courted in a brief spiral flight, landed, and in 20 sec coupled, with the female perched above the male on grass. At 1637 h CST at Prairie Coteau on 4 July 1994 (28°C, 90% sunshine, clouds decreasing from 60 to 30%, wind SE 16–24 km/hr), one Dakota skipper pair was found copulating that separated one minute later. At 1228 h CST at the hayed

Table 4. Number of each species observed nectaring at each flower, by sex (m = male, f = female, u = unsexed) if possible, and total of all individuals observed from 1990–1997. Multiple visits by the same individual to different flowers of the same species are excluded. Visits by the same individual to more than one kind of flower are included: one Poweshiek skipperling, three male and one female Dakota skippers, and one unsexed Pawnee skipper each nectared at two kinds of flowers.

		Dakota			Ottoe	Pawnee			Arogos		
	Poweshiek	m	f	u	m	m	f	u	m	f	u
Achillea millefolium L. yarrow		1	0	0							
Agoseris Raf. prairie dandelion	2	1	0	0							
Allium [Tourn.] L. wild onion						4	1	4			
Asclepias speciosa Torr. showy milkweed	2	3	1	1							
Asclepias syriaca L. common milkweed	2	0	2	0							
Aster [Tourn.] L. aster (purple flower)						2	0	0			
Astragalus [Tourn.] L. milk vetch		0	1	0							
Astragalus crassicarpus Nutt. ground plum	4	16	7	5							
Carduus [Tourn.] L. thistle		1	0	1					0	0	1
Carduus nutans L. nodding thistle	1	1	0	4					0	1	5
Chrysopsis Nutt. golden aster	1	1	0	0		1	0	1			
Cirsium arvense L. Canada thistle	1										
Cirsium [Tourn.] Hill. thistle (not Canada)	1	0	4	0					0	1	0
Coreopsis palmata Nutt. coreopsis	41								0	1	0
Echinacea angustifolia (DC.) Heller. pale purple coneflower	115	75	105	10	12				1	3	28
Erigeron L. fleabane	1	3	0	0							
Gaillardia aristata Pursh. blanketflower		30	22	13							
Galium L. bedstraw		2	0	1							
Heliopsis helianthoides (L.) ox eye	129										
Lactuca [Tourn.] L. blue lettuce		1	2	0							
Liatris aspera Willd. rough blazingstar						1	0	0			
Liatris punctata Hook. dotted blazingstar						18	6	22			

Lilium philadelphicum L. wood lily		1	0	0							
Lobelia spicata Lam. pale spike lobelia	7										
Medicago sativa L. alfalfa		1	0	2							
Melilotus alba Desr. white sweet clover	1										
Oenothera L. sundrops		2	1	0							
Oenothera L. sundrops, wilted	1										
Oxytropis lambertii Pursh locoweed	1	1	0	0							
Penstemon [Mitchell] Ait. slender penstemon		1	0	0							
Petalostemum purpureum (Vent.) Rybd. purple prairie clover						0	1	0	0	1	0
Phlox pilosa L. downy phlox	6	2	2	0	1						
Ratibida columnifera (Sims) T. & G. upright coneflower	1					1	0	1			
Rudbeckia hirta L. black–eyed susan	15	3	1	0							
Solidago nemoralis Ait. gray goldenrod						0	1	0			
Solidago rigida L. rigid goldenrod						1	0	0			
Trifolium hybridum L. alsike clover		1	0	0							
Trifolium pratense L. red clover		1	0	0							
Verbena stricta Vent. hoary vervain									0	1	0
Zygadenus elegans Pursh white camass		1	0	0							
Total records (during 1990–1997)	332	149	148	37	13	28	9	28	1	8	34
Total individuals observed during 1990–1997	1973	252	214	79	14	88	30	172	15	15	47
Percent individuals nectaring	17	59	69	47	93	32	30	16	7	53	72

prairie near Bicentennial on 19 August 1992 (28°C, 100% sunshine, 25% cloud cover, wind SE 24 km/h), a copulating Pawnee skipper pair was harassed by a male conspecific; the pair separated one minute later while being photographed.

More often, courtship rejection was observed. The male pursued the female, and when perched, the male stood behind and faced the female while she fluttered her wings rapidly and shallowly. For Poweshiek skipperling, which could not be readily sexed in the field, we considered an interaction of this appearance to be courtship rejection. Courtship rejection by 11 pairs (22 individuals) of Poweshiek skipperling occurred on each date between 4 and 8 July, in 1992, 1994, 1996. For Dakota skipper, this occurred with 15 pairs on each date from 8 to 11 July, in 1992–1993 and 1996–1997 (with another conspecific perched nearby in two instances), and with 2 trios (2 males, 1 female) on 9 July 1993 and 10 July 1997. Ten Pawnee skipper pairs behaved in this way on 18–19 August 1992 and 17 August 1994. We recorded one Arogos skipper pair in courtship rejection on 5 July 1994.

In our surveys in the study region, the Ottoe skipper occurred only in sites with much topographic relief, but the other four skippers were in sites of both little or great relief. We did not note a particular tendency for hilltopping (i.e., concentration of individuals on ridgetops) in any of these species.

We observed oviposition only by Arogos skipper, at Hole-in-the-Mountain on 17 August 1992 at 1534–1547 h CST (28°C, 35% sunshine, 75–65% cloud cover, wind W 16 km/hr), on big bluestem (*Andropogon gerardii* Vtm.). At 1715 h CST on 6 July 1992 (24°C, 0% sunshine, 100% clouds, light wind), on a small, semi-degraded prairie ridge uphill from campsite 79 in Camden State Park, Minnesota, an Arogos skipper laid one egg on the upperside of a big bluestem blade.

Pawnee skippers appeared sometimes to make clicking noises while flying, presumably with their wings and apparently under their control, as we did not hear this sound every time an individual was flying near us. The sound seemed associated with flights in pursuit of a skipper or toward us, but not in evasive flight or solitary flight among flowers or perches.

DISCUSSION

Flight period. We recorded relatively high observation rates (densities) of Poweshiek skipperling and Dakota skipper in late June and the first two weeks of July (Figs. 3–4). Dana (1991) reported similar timings for Dakota skipper based on emergence dates in enclosed plots at Hole-in-the-Mountain in 1981 (24 June-1 July for males and 29 June-12 July for females; a span of 18 days) and 1982 (28 June-8 July for males and 30 June-13 July for females; a 15-day span). Some variation in timing among years occurred during our study. In 1988, we recorded both species on 20 June (the Poweshiek skipperling abundantly), while in 1990, we recorded neither species on 18, 25, or 26 June at known sites in warm, sunny weather. McCabe (1981) reported that onset of Dakota skipper flight in his study region (Minnesota and North Dakota) ranged from 16 June to 8 July, due to varying spring weather. The span of dates for adult Poweshiek skipperling in Michigan (24 June-19 July) is similar to what we observed in the study region (Nielsen 1999). For North Dakota, McCabe and Post (1977) reported flight spans of 12 June-30 July for Poweshiek skipperling and 18 June-30 July for Dakota skippers.

It is more difficult to characterize flight periods for the other study species since we observed them on fewer dates in fewer years. For Ottoe skipper, Dana (1991) reported emergence dates in enclosed plots at Hole-in-the-Mountain for 1981 (1–23 July for males and 8–29 July for females; a 28-day span). These started about one week later than Dakota skipper and spanned a longer period, consistent with the flight timing and length we observed in Wisconsin (Fig. 6). Based on comparisons of our Ottoe skipper records in the study region and Wisconsin, it appears likely that our survey dates at the Iowa and Minnesota sites in July 1994 and 1997 were within the Ottoe skipper flight period, even though we observed none. Our observation dates in the study region fall within the cumulative span for our Ottoe skipper records in Wisconsin (28 June to 25 August) (Fig. 6), which is similar in length but a bit later than reports from Michigan (18 June–16 August) and North Dakota (15 June-6 August) (McCabe and Post 1977, Nielsen 1999).

August surveys occurred in only four years (Fig. 2). We recorded the Pawnee skipper in the three years we surveyed during 15–20 August (1992–1994) but not during 5–9 August in 1991. For North Dakota, McCabe and Post (1977) reported a flight span from 8 August to 30 September, with the peak in mid-August.

We observed peak Arogos skipper rates on 16 July 1990 (Fig. 5). This suggests most July sampling dates, which were in the first two weeks of July, were early in the species' flight period, while the August survey dates were late. McCabe and Post (1977) reported a flight span from 25 June to 4 August in North Dakota. We also recorded this skipper in June, July, and August, which implies a longer period of emergence than for Poweshiek skipperling and Dakota skipper.

Sex ratio. The numbers of sexed Ottoe and Arogos skippers were too few for any analysis of sex ratio. The Dakota skipper sex ratio showed the typical butterfly pattern of increasing proportion of females later in the flight period (Opler and Krizek 1984, Scott 1986, Brakefield and Shreeve 1992), but female Dakota skippers nonetheless occurred widely throughout the flight period (Fig. 7). McCabe (1981) reported that, at onset of the flight period, both sexes emerge on the same day. Dana's (1991) emergence enclosures indicated that the first male emerged earlier than the first female, but only by a few days. Dana's emergence enclosures would seem more precise in this regard, since they eliminated the confounding effects of behavior and detectability on observation. These enclosures also indicated a shorter span of days for male than female emergence, which would also contribute to the increasing female proportion later in the flight. The time span in which we observed Pawnee skippers was too narrow for this analysis.

At lower observation rates (relative densities), the Dakota skipper sex ratio varied widely (Fig. 8), likely due to variation in flight period timing (pre- or post-peak) and/or sampling error from low observed numbers. But at the highest densities (corresponding to peak flight in large populations), the sex ratio was roughly equal. The Pawnee skipper showed a somewhat similar but milder pattern (Fig. 9). Dana (1991) reported a range of sex ratios for Dakota and Ottoe skippers in his emergence enclosures, but these did not differ significantly from 1:1. The ready observability of female Dakota skippers early in the flight period, and approximately even sex ratio around peak, contrasts with the higher male proportion observed at comparable times in the flight period of the Karner blue (*Lycaeides melissa samuelis* Nabokov) (Swengel and Swengel 1998). Relative to this blue, our ability to sex skipper individuals seemed biased considerably toward females since female skippers were easier to identify and sex and less active than territorial males, whose flighty behavior was described by McCabe (1981) and Dana (1991). Thus, in interpreting these skipper sex ratios, relative change among dates or densities, rather than actual sex ratio at a given date or density, should be emphasized.

Geography, timing, weather. For the four analyzable species, geographical factors showed the most significant patterns (4 out of 8 tests), followed by timing (2/8, with the expected pattern of higher detection nearer noontime), and lastly weather (3/16, with the expected patterns of positive correlation with temperature and negative correlation with wind) (Table 2). This suggests that biogeography is relatively more important than timing and weather for skipper detection within known sites, during the flight period, and under the conditions of our surveys (which excluded twilight and very inclement weather). Consistent with this, Holzman (1972) reported greater activity, more nectaring, and longer flight distances by the Poweshiek skipperling in warmer, sunnier weather, even until sunset, but in cool, overcast weather, these activities were reduced but did not cease.

Habitat. Direct comparisons of our observed densities among species (Table 3) are inappropriate, since they differed considerably in detectability and identifiability (see Methods). Within species, these analyses should also be interpreted with caution, since they are based only on adult observations and do not directly address habitat requirements of immatures. Furthermore, we limited each species' analyses to sites where the species was ever recorded on our surveys. This increased the rigor of tests for habitat preferences, since we were comparing results only from units with the greatest plausibility that the skipper could occur there, because the species was known to occur recently somewhere in the site. But this narrow analytical approach also eliminated the strongest possible negative response by a species to a habitat characteristic, namely absence from the entire site, and so reduced the chance of demonstrating a statistically significant difference. Thus, significant results are more meaningful in suggesting a preference than lack of significance is in indicating a lack of preference.

Nonetheless, the four analyzable species showed many significant differences in relative density by habitat factors (Table 3), much more so than to daily timing and weather conditions on the surveys (Table 2). Three species were significantly denser in dry prairie (excluding sand prairie) and the fourth (Pawnee) only occurred in dry and sand prairie. Two species were significantly denser in undegraded prairie. Of the two other species, one had mean densities that consistently but non-significantly increased with increasing prairie vegetative quality while the other was found only in sites of greater quality. Three species were significantly denser in diverse than uniform sites, and the fourth only occurred in diverse sites; this may relate to the significant correlation of diverse sites with drier prairie vegetation types. Site size had three significant results, with higher densities in large prairies. But for one of these (Pawnee skipper), significantly higher densities occurred in large vs. medium prairies while the sample was too small to test densities in small prairies. However, the Pawnee skipper's mean density in small prairies was so high as to suggest that other factors besides size might account for this species' lowest mean density in medium sites. The fourth species had by far its lowest mean density in small prairies.

These significant relationships with prairie size do not appear simply attributable to vegetative characteristics, since the prairie patch sizes of our 40 study sites did not correlate significantly with vegetation type, quality, or topographic diversity. The occurrence of more and/or denser populations of these skippers in larger prairie patches is consistent with research on other habitat-restricted butterflies which are more likely to occupy sites that are larger, among other characteristics (Thomas et al. 1992, Thomas and Jones 1993, Dennis and Eales 1997, 1999).

Holzman (1972) described Poweshiek skipperling habitat in Michigan as wet marshy meadow or wet prairie, with ovipositions on spike-rush (*Eleocharis elliptica* Kunth) and sedges (Cyperaceae). In Wisconsin, the species occurs in wet-mesic prairie, with larval feeding on prairie dropseed [*Sporobolis heterolepis* (Gray) Gray] and little bluestem (*Schizachyrium scoparium* Michx.); when these grasses occur in drier adjacent areas, the skipperling does also (Bureau of Endangered Resources 1999). However, both hosts are more prevalent in Wisconsin in drier prairie (Henderson 1995). In Manitoba, the species primarily occupies areas of transition between mesic and drier prairie, with occasional individuals in extensive dry or wet areas (Catling and Lafontaine 1986). McCabe and Post (1977) reported Poweshiek skipperling from both wet and dry prairie vegetation, with feeding by one larva on a *Carex* sedge. We never found the species in prairie drier than mesic if in sites of uniform topography (i.e., containing no grassland wetter than mesic). However, our highest observed densities consistently occurred in prairie drier than mesic (primarily uphill from the transition from mesic or wetter prairie) when in sites with topographic diversity (i.e., also containing grassland wetter than mesic). The species also occurred in lower densities in mesic and wetter prairies, in sites both containing and lacking drier prairie. This suggests that some obligatory habitat condition(s) occur only in wetter grassland but some factor(s) in adjacent drier prairie allow the highest densities to develop.

The study species varied in patterns of density relative to unit management (Table 3). Poweshiek skipperling and Arogos skipper were significantly denser with idling, while Dakota skipper was significantly lower there. Most species had relatively low densities with burning, while the Poweshiek skipperling had a mean density there that was both relatively high and highly variable—so variable that Poweshiek densities in burning were not statistically distinct from the managements with the significantly lowest (grazing) or highest (idle, haying) densities. Densities in haying were often but not always at the higher end, and never significantly lowest.

Catling and Lafontaine (1986) reported that in southeastern Manitoba, tallgrass prairies occupied by Poweshiek skipperling were grazed and rotationally burned. Bureau of Endangered Resources (1999) reported that Poweshiek skipperling eggs are laid near grass tips, with overwintering by an intermediate larval stage on the host. As a result, immatures are above ground and vulnerable to fire, which should be infrequent for small or isolated populations, and selective cutting and mowing (of only a portion of the habitat) may be better management practices in occupied patches. While the location of Poweshiek skipperling immatures in the herb layer seems to make them vulnerable to mowing/haying as well, this management (occurring every year or every other, in late summer or fall) had significantly high Poweshiek skipperling densities (Table 3). Likewise, the regal fritillary [*Speyeria idalia* (Cramer 1773)] has significantly denser populations in hayed than similar burned prairie (Swengel 1996). These results do not eliminate the possibility of negative effects of mowing/haying on immatures (a particular concern in small or very localized populations), but does suggest that these negative effects may be readily overcome.

McCabe (1981) advised against burning areas where most Dakota skipper ovipositions occurred the previous year. Dana (1991) studied effects of management fires on both Dakota and Ottoe skippers in large populations at Hole-in-the Mountain in the first area preserved there at the inception of fire management. He conducted four experiments, each performed once in consecutive years, to test larval survivorship in early vs. late spring fires under two different fuel loads, in comparison to unburned controls. He reported some variation in results among experiments and varying degrees of confidence about how well his different experimental apparatuses corresponded to conditions in the larger landscape. Nonetheless, several general patterns consistently occurred. Dakota and Ottoe skippers had similar responses, with higher mortality in burned than unburned plots and gradients of increased fire mortality from early spring (when larvae were in semi-subterranean burrows) to late spring (when larvae and pupae are on or above ground), and between moderate and higher fuel loads. Similar results would be expected later in the summer and fall after adult flight, when eggs and younger larvae would be more vulnerable until winter diapause (Dana 1983).

Dakota skippers are consistently absent from sites in heavy grazing for an extended period (McCabe 1981, Dana 1983). McCabe (1981) found the Dakota skipper in only one grazed site, out of many surveyed, and that site had only recently been converted to grazing. McCabe and Post (1977) also reported the species to decline quickly even with the lightest grazing. However, Dana (1983) suggested that brief episodes of grazing, even heavy, might not harm the skipper. Dakota and Ottoe skippers were abundant at Hole-in-the-Mountain in Dana's (1991) study area right after grazing ceased, implying that the previous grazing regime could not have been that adverse. Our data do not add more insight on this issue, because grazing occurred in our study only at Sheyenne National Grassland. We did not find the Dakota skipper there, but we also did not record it in nearby hayed or idled sites either. It is unclear whether and how much management, and which kinds of managements, contributed to this lack of observation.

By contrast, mowing/haying in September or later, on an annual or preferably biennial basis, appears consistently and highly favorable for the Dakota skipper (McCabe 1981, Dana 1983, this study). Mowing before or during the adult flight period is disruptive, causing early death or emigration of adults (McCabe 1981, Dana 1983).

In comparison to burning, grazing at Sheyenne National Grassland appeared unfavorable for Poweshiek skipperling but not Pawnee skipper (Table 3). Since these grazed sites were significantly larger, lower quality, and drier than burned sites, it is possible that these other habitat characteristics contributed to these skippers' apparent management responses. McCabe and Post (1977) reported the Pawnee skipper to be more sensitive (averse) to grazing than our observations suggest.

Some research has suggested that the spatiotemporal scale (i.e., dosage) of an ecological disturbance (e.g., stand-replacing fire) or a comparable management treatment (e.g., clearcut) may matter as much or more in effects on the plant community than the type of disturbance/management (Hobbs and Huenneke 1992, Turner et al. 1994). But in this study, haying occurred on rotations of 1–2 years while fire was rotated over 2–5 or more years, yet haying was associated with higher densities of the study skippers than burning (Table 3). This suggests that suitable ranges of treatment dosage for the skippers must be determined individually for each management type.

Behavior. In Michigan in 1970, Holzman (1972) observed preferential nectaring by Poweshiek skipperling on pale spike lobelia (*Lobelia spicata* Lam.) and secondarily only on black-eyed Susan (*Rudbeckia hirta* L.), which were also nectar flowers in this study (Table 4). Yet in 1971 at same site, at least one individual fed at all types of nectar flowers in bloom (Holzman 1972). For Dakota skipper, McCabe (1981) listed seven acceptable nectar sources, five of which we also recorded. The other two, which bloomed in proximity to Dakota skippers in this study, he ranked first and sixth in preference. Of the six sources he listed as unacceptable (i.e., never visited), we recorded three as nectar sources, but always minor, with a maximum of three visits. Dana (1991) reported 21 nectar species for the Dakota skipper, and 11 for the Ottoe skipper, at Hole-in-the-Mountain. We recorded nectaring by the Dakota skipper at 13 of his 21 flowers while he recorded 12 of our 25 flower taxa. The dominant nectar choice by Ottoe skipper in our study was also so in his. For *Hesperia leonardus* (including *leonardus*, *pawnee*, and the blend of these two subspecies), Spomer et al. (1993) reported that dotted blazingstar (*Liatris punctata* Hook.) was preferred, as in our study, and that three alternates were used in that flower's absence. We recorded nine nectar taxa for this skipper, including two of their four species.

These various studies show some agreement in nectar selection within species, but also a fair degree of discordance. An obvious source of variation derives from differences in sites among studies, which would affect what types of nectar were available. Flowers can also vary among years in abundance and timing relative to a particular species' flight period. Annual fluctuations in skipper abundance might also affect nectaring behavior. At higher densities, the skippers may use alternate sources because of crowding at preferred sources.

Of the two Dakota skipper mating pairs we recorded, the one at 0930 h CST was within the span of daily timing reported by Dana while the one after 1630 h CST extended the period he reported later in the afternoon. As in our observations, McCabe (1981) and Dana (1991) found more courtship rejections than courtships leading to mating.

Conservation conclusions. Factors beyond the presence of larval host limit the distribution and abundance of the study species, which are all localized species documented to use prevalent prairie grasses as larval hosts (Opler and Krizek 1984, Scott 1986, Dana 1991, Bureau of Endangered Resources 1999). McCabe (1981) speculated that soil pH and humidity might affect larval survival in their overwintering sites at the soil surface. The strong preference for site diversity in this study (Table 3) may be symptomatic of these additional limiting factors as well.

Beyond the obvious general consequences of prairie habitat destruction, it is difficult to assess the status and trend of these study species because of the lack of systematic monitoring data over the decades and centuries. However, Schlicht and Orwig (1998) reviewed the decline of these prairie skippers in Iowa over the past century or more. For example, in the 19th century, the Arogos skipper was considered one of the state's most abundant skippers, but now they categorize it as "threatened" (defined as 21–100 known populations), along with the Ottoe skipper. The Dakota skipper is considered extirpated from Iowa, while the Poweshiek skipperling and Pawnee skipper are considered endangered (6–20 known sites). Decline is also apparent since the 1980 Loess Hills (Iowa) Hesperiidae Survey, when prairie-restricted skippers were more readily findable in the remnants of their habitat that had been made (and still are) preserves (Schlicht and Orwig 1999).

Dana (1991) and we surveyed adult Dakota and Ottoe skippers in the same site, he during 1979–1981 and we during 1988–1997. Since our study methods differed considerably, only crude comparisons are possible. Dana (1991: Fig. 15, with corrigendum) reported overall observation rates of about 3.9/h. Since his rates would have been higher if all his time were devoted to counting (as we do) rather than also to his mark-release-recapture effort, he conservatively estimated his observation rate at about 20/h, counting only effort at/near the species' peak (R. Dana in lit. 5 March 1993). Our overall rate during 1990–1997, only in our units corresponding to his sampling areas surveyed during the Dakota skipper flight, was 2.4/h, which is much lower in the more appropriate comparison to his adjusted rates. We recorded much higher Dakota skipper rates elsewhere, ones comparable to or exceeding Dana's adjusted rates (e.g., Bicentennial hay: 52/h)—evidence that our surveys occurred at appropriate times and that high-density populations still existed in the region.

We found so few Ottoe skippers that we cannot directly distinguish whether this was due to a population much reduced since Dana's (1991) study period or seasonal timing of our surveys. However, Dana's (1991) reported emergence dates, their timing relative to Dakota skipper flight, and our comparison to Ottoe skipper observations in Wisconsin (Fig. 6) suggest that some dates during 1993–1997, when we found no Ottoe skippers in favorable weather in his study area, were within the flight period.

Since this is the only site known to us where a quantitative comparison is possible, cause(s) of apparent decline(s) cannot be proved. However, this does corroborate Schlicht and Orwig's (1998) point that successful conservation of prairie butterflies requires more than habitat preservation and abundant host plants. Specific information on the species' timing and activity patterns is useful for implementing effective population monitoring, and data on the species' habitat and management associations are necessary for designing and managing habitat preserves.

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Appendix 1. Name (with alternate name in parentheses), ownership, and county of the study sites, by state, and years in which each site was visited. See Fig. 1 for map of study region. Each part of Sheyenne National Grassland that was surrounded by non-prairie and/or non-government land was counted as a separate site. X = formal survey, x = informal observations only.

			Years surveys conducted (19..)									
State, site	Ownership[1]	County	88	89	90	91	92	93	94	95	96	97
Iowa												
Anderson (Emmet Co.)	state	Emmet							x	x	X	X
Cayler	state	Dickinson		x				X	X	X	X	X
Crossman	TNC	Howard		x		X	X	X				
Freda Haffner Kettlehole	TNC	Dickinson		x				X	X			X
Hayden	state	Howard		x		X	X	X				
Hoffman	TNC	Cerro Gordo						X				
Kalsow	state	Pocahontas				X	X	X				
Stinson	county	Kossuth		x		X		X	X			

Minnesota												
Audubon (Margherita)	TNC	Clay			X	X	X	X			X	X
Bicentennial (preserve)	county	Clay	x		X	X	X	X	x	X	X	X
nr. Bicentennial (hayed)	county	Clay					X	X	x	X	X	X

Appendix 1. Continued.

State, site	Ownership[1]	County	88	89	90	91	92	93	94	95	96	97
			Years surveys conducted (19..)									
Blazing Star	TNC	Clay	x		X	X	X	X	x	x	X	X
Bluestem	TNC	Clay	x		X	X	X	X	x	x	X	X
Chippewa	TNC, private	Chippewa, Swift	x			X	X	X	X	X	X	X
Foxhome	TNC	Wilkin				X	X	X	X			
Frenchman's Bluff	TNC	Norman					X	X	x	x	X	X
Hole-in-the-Mountain	TNC	Lincoln	X	X	X	X	X	X	X	X	X	X
Kettledrummer	TNC	Wilkin				X	X	X	x		x	
Lundblad	TNC	Murray		x			X	X				
Ordway	TNC	Pope			X	X	X	X	X	X		
Prairie Marshes	state	Lyon		x			X	X	X	X	X	X
Prairie Coteau	state	Pipestone					X	X	X	X	X	X
Seven Sisters	TNC	Otter Tail			X	X	X	X	X		x	x
Staffanson	TNC	Douglas			X	X	X	X	X	X	X	X
Strandness	TNC	Pope							X			
Town Hall	TNC	Wilkin				X	X	X	X	x		x
Twin Valley	TNC	Norman			X	X	X	X	x	x		x
Western North (Elliot)	TNC	Wilkin				X	X	X	x	x		
Western South (Western)	TNC	Wilkin				X		X	x			
Zimmerman	TNC	Becker			X	X	X	X	x	x		
North Dakota												
Brown (hayed)	private	Ransom								X	X	X
Hartleben	USFWS	Richland									X	X
Sheyenne, middle	NFS	Richland							X	X	X	X
Sheyenne, north	NFS	Ransom							X	x	X	X
Sheyenne, north central	NFS	Ransom							X	x	X	X
Sheyenne, northeast	NFS	Richland							X	x	X	X
Sheyenne, northwest	NFS	Ransom								X	X	X
Sheyenne, south	NFS	Richland							X	X	X	X
Sheyenne, southeast	NFS	Richland							X	X	X	X
Sheyenne, southwest	NFS	Ransom							X	X	X	X

[1]TNC=The Nature Conservancy; USFWS=U. S. Fish and Wildlife Service (waterfowl production area); NFS=National Forest Service (national grassland).

Appendix 2. Grass skipper (Hesperiinae) individuals recorded on surveys during this study.

	Iowa	Minnesota	North Dakota
Poweshiek skipperling *Oarisma poweshiek* (Parker 1870)	27	2318	58
Common branded skipper *Hesperia comma* (Linnaeus 1758)			1
Ottoe skipper *H. ottoe* W. H. Edwards 1866		27	
Pawnee skipper *H. leonardus pawnee* Dodge 1874		220	70
Dakota skipper *H. dacotae* (Skinner 1911)		547	
unidentified *Hesperia* Fabricius		7	
Peck's skipper *Polites peckius* (W. Kirby 1837)		10	1
Tawny-edged skipper *P. themistocles* (Latreille [1824])	5	53	19
Crossline skipper *P. origenes* (Fabricius 1793)	4	28	2
Long dash *P. mystic* (W. H. Edwards 1863)	2	316	23
unidentified *Polites* Scudder		6	5
Northern broken-dash *Wallengrenia egeremet* (Scudder 1864)		7	
Satchem *Atalopedes campestris* (Boisduval 1852)	13		
Arogos skipper *Atrytone arogos iowa* (Scudder 1869)	1	79	1
Delaware skipper *A. logan* (W. H. Edwards 1863)	9	38	1
Mulberry wing *Poanes massasoit* (Scudder 1864)		1	
Broad-winged skipper *P. viator* (W. H. Edwards 1865)	3		2
Two-spotted skipper *Euphyes bimacula* (Grote and Robinson 1867)	3		
Dun skipper *E. vestris* (Boisduval 1852)		2	4
unidentified Hesperiinae	5	371	16

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