Journal of The Lepidopterists' Society

Volume 62 2008 Number 1

Journal of the Lepidopterists' Society
62(1), 2008, 1–17

A CHARACTERIZATION OF NON-BIOTIC ENVIRONMENTAL FEATURES OF PRAIRIES HOSTING THE DAKOTA SKIPPER (*HESPERIA DACOTAE*, HESPERIIDAE) ACROSS ITS REMAINING U.S. RANGE

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ABSTRACT. Within the United States, the Dakota Skipper now occurs only in Minnesota, North Dakota, and South Dakota. In these states it has been associated with margins of glacial lakes and calcareous mesic prairies that host warm-season native grasses. Preliminary geographic information system (GIS) analysis in North Dakota has indicated a close congruency between historic distribution of the Dakota Skipper and that of specific near-shore glacial lake features and related soil associations. This study analyzed humidity-related non-biotic microhabitat characteristics within three remaining occupied Dakota Skipper sites in each state during the larval growth period in 2000. Measured parameters included topographic relief, soil compaction, soil pH, moisture, and temperature at various depths, soil bulk density, soil texture, and temperature and humidity within the larval nest zone. Results of these efforts reveal two distinctive habitat substrates, one of relatively low surface relief with dense but relatively less compact soils, and another of relatively high relief with less dense but more compact soils. In the low-relief habitat, grazing appears to compact soils unfavorably in otherwise similar prairies in the more xeric western portion of the range, potentially by affecting groundwater buffering of larval nest zone humidity.

Additional key words: Dakota Skipper, habitat, climate, soils, management.

Numerous survey efforts have clearly defined present limits of distribution for the Dakota Skipper (*Hesperia dacotae* Skinner, 1911) (McCabe 1979, 1981; Dana 1991; Royer 1988a, 1988b, 2003; Royer & Marrone 1992; Orwig 1995, 1996; Schlicht 1997; Royer & Royer 1997, 1998; Skadsen 1997, 1999, 2000). Some recent work also has characterized this species' habitat floristically at selected sites (Dana 1997, ND Parks and Recreation Department 1999). However, there has been no systematic attempt to define physiographic or other non-biotic features of habitat across the species' entire U. S. range. A primary intention of this project was to identify and characterize non-biotic features that might help habitat managers better understand and more easily recognize favorable sites in areas where the species remains, has recently suffered decline, or is believed historically to have occurred but is now absent.

The original range of the Dakota Skipper is believed to have extended from Illinois northwestward as far as southeastern Saskatchewan (Royer 2003) and Manitoba (Klassen *et al*. 1989). It is known to occur within the U.S. now only in the states of Minnesota, North Dakota, and South Dakota, and a few populations still exist in Canada. The U. S. range originally included Iowa and Illinois, in both of which the species is now believed to have been extirpated (Scott 1986, T. Orwig, Morningside College, pers. comm.). In parts of this range the Dakota Skipper has been specifically associated with the margins of glacial lakes (McCabe & Post 1977, McCabe 1981). Many workers have also associated it with calcareous mesic prairies (McCabe 1981), such indicator plants as smooth camas (*Zygadenus elegans* Pursh., Liliaceae) (Royer & Marrone 1992), and warm-season native grasses (ND Parks and Recreation Department 1999).

Recently a very close relation has been noted in McHenry County, North Dakota, between recorded distribution of the Dakota Skipper, glacially related surface geology, and soil associations defined by the United States Department of Agriculture (USDA) (Royer & Royer 1998, Lord 1988, see Fig. 1). Subsequent preliminary GIS analysis has suggested a statewide congruency of known distribution of the Dakota Skipper with these soil associations (Tom Sklebar, retired USGS NPWRC, pers. comm.). McCabe (1981) proposed that precipitation/evaporation ratios may be an important defining feature of this species' habitat requirements. Presence of "hydrofuge glands" on larval segments 7 and 8 (McCabe 1981) suggests a historic or present need of the species for protection from inundation. This led to our hypothesis that factors limiting Dakota Skipper populations may have more to do with such non-biotic habitat elements as temperature and local humidity during sensitive larval and pupal stages than with such biotic factors as host plant or nectar source availability or predation during the adult flight period, when this species has been most extensively studied.

Specifically, we hypothesized that such edaphic features as soil moisture, soil compaction, and soil bulk density, as well as related non-biotic factors such as temperature and relative humidity at and near (within 2.0 cm of) the soil surface, where several authors have noted that early stages abide in a silken nest during most of the summer (cf. McCabe 1981, Dana 1991), may be significant factors in larval survival potential. Microtopography substantially affects soil evaporation rates in the north-central United States (Cooper 1960). Soil compaction and vegetation removal (whether by herbivory, hay mowing, or fire) substantially alter soil water movement and evaporation, thereby altering near-surface humidity (Frede 1985, Miller & Gardiner 1998, Hausenbuiller 1985). Livestock grazing has been shown to increase bulk density (Zhao *et al*. 2007) and soil compaction (Greenwood *et al*. 1997), which are correlated with decreased soil water content and hydraulic conductivity (Zhao *et al*. 2007). In summer months these changes are likely to restrict the movement of shallow groundwater to the soil surface, thus preventing groundwater buffering of surface humidity conditions. Water loss from moist soils in contact with dry air occurs rapidly, usually exceeding the rate of upward movement of water through the soil (Hausenbuiller 1985). As a result a dry soil layer forms, inhibiting further evaporation. Formation of a dry soil layer would decrease surface humidity at precisely those times later in the summer when young larvae of the Dakota Skipper are most vulnerable to desiccation.

The principal objectives in this study therefore were (1) to characterize non-biotic features related to hydrology and microclimate (microtopography, soil compaction, soil pH, soil moisture, soil temperature, soil bulk density, soil texture, near-surface humidity) and the variability of those features within and across occupied sites in the context of average summer climate conditions generally, and also (2) to compare those features between grazed and hay-mowed sites within the more xeric portion of the range in North Dakota.

STUDY AREA AND METHODS

Western Minnesota, eastern North Dakota and eastern South Dakota were shaped by Laurentide ice sheets. This shaping profoundly affected the landforms and materials found at the surface in these areas. The Des Moines lobe cut across Minnesota and the eastern margin of South Dakota (South Dakota Geological Survey 1965). Slightly to the west, the James lobe cut through North Dakota and eastern South Dakota. These lobes deposited extensive moraines that contained unsorted clay to boulder sized material (Agnew *et al*. 1962, Hobbs and Goebel 1982). During the last glacial retreat, many areas were submerged under melt water lakes (South Dakota Geological Survey 1965, Hobbs and Goebel 1982, Lord 1988). Thus our study area contains relatively level areas with sorted sediment typical of lake bottom and near shore deposits, as well as rolling hills composed of poorly sorted sediment typical of glacial moraine deposits. Original Dakota Skipper habitat across the region ranged from tall-grass to mixed-grass native prairie. Much of the remaining habitat is now privately owned and managed either as hay meadow or pasture. Within this context, we specifically sought sites that were under public ownership or at which conservation is a management goal.

Climatically, the study area crosses a transition zone from humid, middle latitude with severe winter type in western Minnesota to mid-latitude steppe in central North and South Dakota (Ackerman 1941). This transition can be seen in summer average monthly temperatures and precipitation for the period of record (1895–2003) and the data collection year (2000, Table 1). South Dakota has average monthly temperatures that exceed Minnesota and North Dakota average monthly temperatures by 1–2°C. Minnesota's average monthly precipitation exceeds North and South Dakota average monthly precipitation by 20–50mm. Despite these differences in statewide values, temperature patterns are similar at climate stations near the study sites. Precipitation, however, is far more variable throughout the summer season and the region. State averages show that monthly precipitation declines from June through September, and that Minnesota has the largest average precipitation for each month of the

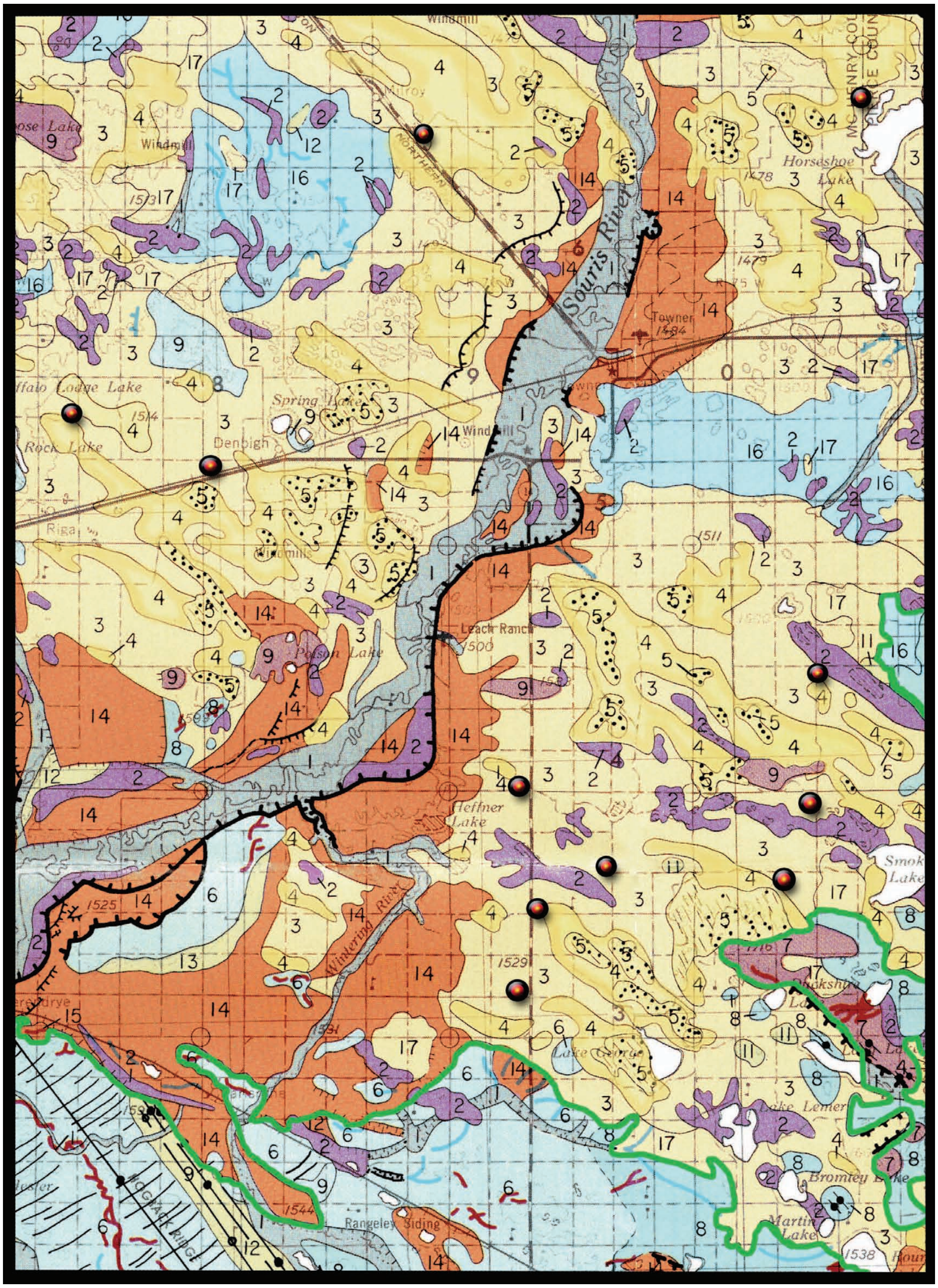

Fig. 1. Superimposition on a surface geology map (Lord 1988) of recently confirmed occurrence sites for *Hesperia dacotae* in McHenry County, North Dakota (dots) indicating close congruency with distribution of windblown soil units (#3 and #4) in the near-shore environment of glacial Lake Souris. Unit #3 was described by Lord as "silt and sand, fine to medium grained, moderately to well sorted…, gradational to unit 4." Unit #4 was described as "Sand, fine to medium grained, well sorted… (with dunes) as high as 5 metres." Both of these were characterized as having been reworked from unit 17, "nearshore lake sediment … up to 30 metres thick." The green line represents putative glacial lake margin, and the background map grid indicates square miles. (After Royer and Royer 1998.)

TABLE 1. Monthly mean temperatures (°C) and precipitation (mm) during summer months for Minnesota, North Dakota, and South Dakota (data from National Climatic Data Center, 2004).

	Average Temperature (°C)		Average Rainfall (mm)	
	1895–2003	2000	1895–2003	2000
Minnesota				
June	17.8	16.6	163.4	192.5
July	20.6	20.4	142.5	150
August	19.4	19.8	136.2	135.8
September	14.1	13.7	113	65.7
North Dakota				
June	17.1	15.7	136.2	129.9
July	20.4	20.3	103.1	74.4
August	19.2	20.1	82.7	102.8
September	13.4	13.7	64.2	55.9
South Dakota				
June	18.8	18.9	130.3	107.9
July	22.6	22.8	94.5	99.2
August	21.5	22.8	82.7	58.3
September	16.7	15.8	63.8	25.2

summer (Table 1). Climate stations near the study sites show that in addition to having greater average summer rainfall, the Minnesota site experiences its peak precipitation later in the summer than the North Dakota site and the South Dakota site. In 2000, however, average precipitation patterns were not experienced. North Dakota experienced higher precipitation during August than July in 2000 and South Dakota had much less than average precipitation during both August and September. Because of this variability in precipitation, onsite recording of humidity was deemed necessary.

Field sites. Field sites selected for this study all had an extensive history of involvement in earlier work on the Dakota Skipper (McCabe 1979, 1981; Royer 1988a, 1988b; Royer & Marrone 1992; Royer & Royer 1997, 1998; Dana 1991, 1997; Skadsen 1997, 1999). Involving three states, these sites spanned the known remaining U. S. range of the Dakota Skipper (Table 2, Fig. 2).

Sampling methods. We first developed a three-state map depicting all known U. S. populations of the Dakota skipper as points (Fig. 2). We then both sampled and monitored habitats at three specific sites in each state that were known to be hosting viable Dakota Skipper populations. (We here use the term "sample" to denote data from a point in time and the term "monitor" to denote continuous data collection with HOBO® loggers.) Sampling was conducted to determine spatial variability within Dakota Skipper habitat; monitoring was conducted to determine temporal variability throughout the most vulnerable period of the larval growth season (eclosure to onset of winter diapause).

At all study sites, sampling was conducted in four randomly oriented 50m by 40m gridded plots (Fig. 3), each centered on a monitoring point determined in the field by either (i) directly observing oviposition or (ii) using locations of documented skipper activity within the past three years (Royer & Royer 1997; Schlicht 1997; Skadsen 1997, 1999). Treating each plot as a rectilinear set of five parallel 50m transects, we took

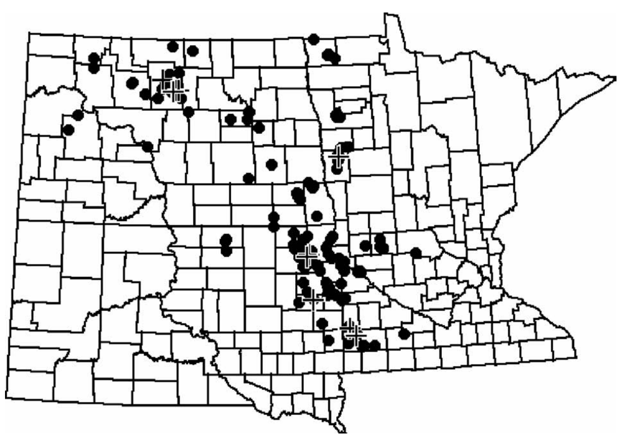

FIG. 2. Distribution of all known Dakota Skipper (*Hesperia dacotae*) records from the three states in which the species is known to persist. Site locations for this project are designated as crosses.

Table 2. Dakota Skipper (*Hesperia dacotae*) study sites by state, county, ownership, approximate extent (ha), and general soil texture classification (TNC=The Nature Conservancy, DNR=Department of Natural Resources, WMA=Wildlife Management Area, USFWS=U.S. Fish and Wildlife Service).

State/Site	County	Ownership	ha	Texture[a]
Minnesota				
Felton Prairie (FP)	Clay	County/TNC	200	L/SL
Hole-in-the Mountain (HM)	Lincoln	DNR/TNC/Private	65	SL
Prairie Coteau (PC)	Pipestone	TNC	25	SL
North Dakota				
Mount Carmel Camp (MCC)	McHenry	ND State School	65	SL/LS
Smokey Lake School Sect. (SLS)	McHenry	ND State School	65	SL
Swearson School Sect. (SSS)	McHenry	ND State School	65	SL
South Dakota				
Scarlet Fawn Prairie (SFP)	Roberts	Sioux Tribal	30	SL
Knapp Pasture (KNP)	Roberts	Private	65	SL
Cox Lake WMA (CXL)	Hamlin	USFWS	30	SL/LS

[a] L=loam, SL=sandy loam, LS=loamy sand.

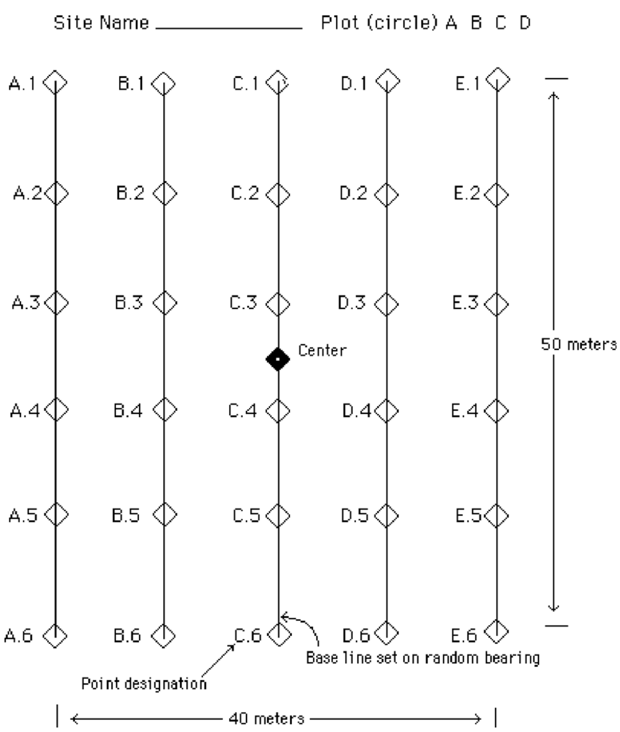

Fig. 3. Grid design for sampling within each plot. Center was determined by (a) observed oviposition or (b) reference to most recent confirmed adult skipper activity. Samples were taken for compaction and pH at all grid points and for other parameters generally at points A1, A3, A5, B2, B4, B6, C1, C2, C5, D2, D4, D6, E1, E3, and E5. Compass bearing for the grid axis (center transect line) was randomized for each sampling period.

probe readings at alternate 10 meter intervals within all four grids in each site. At four points in each grid, soil samples were also taken during one sample period for determining soil texture and bulk density within that grid (a total of 16 samples per site). For possible future GIS reference, precise center-point UTM coordinates (NAD 27) were confirmed during each sampling period. At each of these gridded plots we recorded local surface relief (in meters), soil texture, soil bulk density, and pH; with moisture, temperature, and compaction each measured at three depths (20, 40, 60cm). We also quantified both temperature and humidity within the primary larval nest zone (estimated to be 0–2cm above the soil surface).

Data loggers were used to monitor surface humidity and larval nest zone temperature continuously, in half-hour intervals, at all study sites from time of oviposition (approximately 5 July) through estimated initiation of larval diapause (23 September). A HOBO® Temp/RH data recorder was placed at the center point of at least two plots at each study site. In North Dakota, data recorders were placed at all plot center points except in grazed habitat. At Minnesota and South Dakota sites, data loggers were placed at two of four plots for each site except Scarlet Fawn Prairie (South Dakota), where there was only one plot and hence only one data logger was needed. One data logger failed at the Prairie Coteau site in Minnesota, and loss of another necessitated reducing the total number of useful Minnesota data sets to four. The resulting array of monitoring devices provided a continuous record of both spatial and temporal variability in larval nest zone temperature and humidity across the range of the Dakota Skipper in all three states.

Sampling was conducted at approximately two-week intervals, from the beginning of the mating flight (ca. 1 July 2000) until the estimated beginning of larval diapause in the fall (the first significant frost in North Dakota sites was on 23 September 2000). Each site was subjected to at least four rounds of sample data collection. For the first sampling period at each site, all 30 grid points were sampled for all parameters. For subsequent temperature and moisture readings, half the points were sampled by alternating sample points as follows: A1,3,5; B2,4,6; C1,3,5; D2,4,6; E1,3,5. Soil samples for determining composition, texture, and bulk density were taken similarly at compass-randomized points B2, B4, D2 and D4 within each plot. For relief, we determined the minimum elevation for each plot within each site and then subtracted this minimum from each elevation within the plot to define the response variable "relief," scaled to the minimum elevation value within each plot.

Instrumentation. Equipment included (a) for relief a total station with data logger, (b) for soil compaction a DICKEY-john® Soil Compaction Tester (indicating compaction pressure in lbs/in^2), (c) for soil pH a Kelway® soil pH and moisture meter, (d) for soil moisture content both a Kelway® soil pH and moisture meter (surface moisture) and an Aquaterr® soil moisture, temperature, and salinity probe (moisture at various depths), (e) for soil temperature at various depths an Aquaterr® soil moisture, temperature, and salinity probe, and (f) for temperature, relative humidity, and absolute humidity within the larval nest zone a HOBO® RH data logger programmed to read continuously in 30-minute intervals. To determine soil bulk density samples of known volume were dried to a constant weight. To determine soil texture these same samples were subjected to settling and mechanical analysis in order to define percent sand, silt, and clay. Data were compiled by study site and stored in tabular form in Microsoft Excel®. All were archived electronically at the USGS Northern Prairie Wildlife Research Center in Jamestown, North Dakota.

Data Analysis. To gain an understanding of how variation in the various non-biotic response variables might be partitioned and to take advantage of the completely nested design structure of the study (i.e., 40×50m plots nested within study sites, grid sampling points nested within plots, with repeat sampling considered nested within grid sampling points), we first conducted a variance components analysis using the variance components procedure (PROC VARCOMP) of SAS (1999). This allowed us to compute site-to-site, plot-to-plot, point-to-point, and sampling time-to-sampling time variance components (where applicable) and assess their relative contribution to the total variation for each non-biotic response variable. Variance components are useful descriptive summaries and have their greatest value in planning future studies (e.g., if there is more plot-to-plot variation relative to variation among points within plots for a particular response variable then sampling effort should focus on establishing more plots within sites with less effort focused on the number of grid sampling points within plots to fully characterize Dakota Skipper sites).

We were also interested in isolating specific differences in the various non-biotic response variables among the nine study sites, and if applicable, how those differences might vary with soil depth (20, 40, and 60cm for soil compaction, temperature, and moisture only). To do so, we used analysis of variance (ANOVA) techniques using the mixed linear models procedure (PROC MIXED) of SAS (1999). For the ANOVAs, and as with the variance components analysis described above, we considered the 40×50m plots to be a random factor nested within study sites, with grid sampling points also as a random factor nested within plots. Repeat sampling effort, where applicable, was also considered as a random factor and nested within grid points. We compared not only mean responses among the nine study sites but also mean variances, where variances were calculated across the sampling grid points within each plot, and mean variances then computed by averaging across plots within sites. We examined these mean variances because variation in abiotic response variables may be as important as or more important than mean responses for characterizing Dakota Skipper habitat. For the responses soil compaction, soil temperature, and soil moisture measured at three depths the ANOVA design structure was considered to be a split-plot with depth being the sub-unit (Littell *et al*. 1996). All other ANOVAs were considered to be one-ways, and where applicable, with sub-sampling (Steel and Torrie 1980). For those response variables measured in the "larval nest zone" as described earlier, we did not conduct an ANOVA because of the small sample sizes for most of the sites, but we do report the mean responses for each plot and site, where the means are seasonal means. In North Dakota we also compared these characteristics at three known Dakota Skipper sites (two hay meadows and one grazed site with a similar plant community and topography) in order to assess possible differing effects of hay mowing and grazing on these features. All means reported, unless stated otherwise, are least squares

Table 3. Summary statistics for selected physical response variables (RV) measured at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (see Table 2 for study site descriptions and abbreviations).

		Minnesota			North Dakota			South Dakota		
RV[a]	Metric[b]	FP	HM	PC	MCC	SLS	SSS	SFP	KNP	CXL
Relief	Mean	0.38	3.99	4.36	0.38	0.37	0.45	2.02	3.16	3
	SD	0.21	2.2	2.37	0.34	0.25	0.31	1.48	2.27	1.86
	Min.	0	0	0	0	0	0	0	0	0
	Max.	0.76	8.68	9.01	1.26	0.98	1.29	4.28	8.67	8.19
	n	3	3	4	4	4	4	1	4	4
BD	Mean	0.86	0.86	0.91	1.04	1.14	1.28	0.78	0.96	0.92
	SD	0.13	0.09	0.1	0.16	0.18	0.23	0.05	0.21	0.13
	Min.	0.65	0.68	0.76	0.73	0.7	0.77	0.73	0.53	0.74
	Max.	1.12	1	1.14	1.21	1.35	1.55	0.84	1.41	1.23
	n	4	4	4	4	4	4	1	4	4
pH	Mean	6.26	6.28	6.61	6.4	6.73	6.39	6.45	6.66	6.4
	SD	0.25	0.22	0.3	0.55	0.58	0.46	0.22	0.27	0.28
	Min.	5.4	5.8	6	4.9	5.6	5.5	6	5.9	5.8
	Max.	7	7	7.4	7.8	8	7.6	6.80	7	7
	n	4	4	4	4	4	4	1	4	4
Clay	Mean	8.3	9.2	7.7	6.9	9	11.7	5.8	4.8	3.7
	SD	4.6	6.3	4.3	5.2	5.9	4	3.2	4.2	3.2
	Min.	3.3	0	3.3	0	0	3.3	3.3	0	0
	Max.	16.7	23.3	16.7	20	23.3	20	10	16.7	10
	n	4	4	4	4	4	4	1	4	4
Sand	Mean	53.3	61.7	60.8	65.6	61	74.4	56.7	56.2	61.5
	SD	8	8.3	11.1	12.7	8.6	5.9	8.6	9.8	8.8
	Min.	40	46.7	40	33.3	46.7	60	46.7	40	50
	Max.	66.7	80	76.7	86.7	73.3	80	66.7	80	86.7
	n	4	4	4	4	4	4	1	4	4
Silt	Mean	38.3	29.2	31.5	27.5	30	14	37.5	38.9	34.8
	SD	5.2	6.1	9.2	11.8	6.7	5.1	6.9	8.3	7.8
	Min.	30	16.7	20	6.7	16.7	6.7	30	20	10
	Max.	46.7	40	46.7	60	40	26.7	46.7	53.3	43.3
	n	4	4	4	4	4	4	1	4	4

[a]RV=response variable; relief in meters above lowest elevation, BD=bulk density (g/cm^3), texture (clay, sand, silt) as percent composition.
[b]Mean=arithmetic mean of all data (as distinguished from least squares means reported in later tables), SD=standard deviation, n=number of 40×50 meter plots within each site

means (LSMEANS) with separations among LSMEANS done using Fisher's protected least significant value (LSD) as recommended by Milliken and Johnson (1984) and only for significant site effects at α=0.05. All statistical tests were considered significant at the 0.05 level.

Because of the correlated nature of many of the response variables, we also conducted a principal components analysis (PCA) (McCune and Grace 2002) to help visualize separations among the study sites along the principal component gradient variables. For the PCA, we did not include any of the responses measured in the "larval nest zone" because of small sample sizes and because no data were collected on the Swearson School Section study site. Although no soil compaction data were collected at the Prairie Coteau (PC) site, and

TABLE 4. Variance components for site-to-site, plot-to-plot within sites, point-to-point within plots, and sampling time-to-sampling time across the season at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (see Table 2 for study site descriptions and abbreviations); values in parentheses are within row percents of total variation attributed to that variance component.

Response Variable	**Site (%)**	**Plot (%)**	**Point (%)**[a]	**Sampling (%)**[a]
Total relief (m)	10.39 (91)	1.06 (9)	nm	nm
Mean relief (m)	2.91 (55)	0.03 (1)	2.32 (44)	nm
Bulk density (g/cm3)	0.021 (43)	0.000 (<1)	0.028 (57)	nm
pH	0.023 (13)	0.027 (15)	0.126 (72)	nm
Clay (%)	5.24 (18)	0.00 (<1)	24.11 (81)	nm
Sand (%)	29.71 (25)	20.01 (17)	70.13 (58)	nm
Silt (%)	55.81 (47)	12.07 (10)	50.42 (43)	nm
Compaction 20 cm (kg/cm^2)	18.39 (47)	5.74 (15)	7.23 (19)	7.43 (19)
Compaction 40 cm (kg/cm^2)	26.02 (51)	8.96 (17)	8.79 (17)	7.64 (15)
Compaction 60 cm (kg/cm^2)	30.03 (52)	9.62 (17)	10.28 (18)	8.02 (14)
Temperature 20 cm (°C)	2.51 (14)	0.21 (1)	0.00 (<1)	15.40 (84)
Temperature 40 cm (°C)	2.00 (17)	0.14 (1)	0.00 (<1)	9.83 (82)
Temperature 60 cm (°C)	1.12 (13)	0.19 (2)	0.00 (<1)	7.03 (84)
Moisture surface (% sat.)	23.07 (9)	47.21 (18)	196.44 (73)	nm
Moisture 20 cm (% sat.)	28.59 (7)	13.27 (3)	0.00 (<1)	357.57 (90)
Moisture 40 cm (% sat.)	47.70 (14)	11.74 (3)	0.00 (<1)	276.13 (82)
Moisture 60 cm (% sat.)	79.94 (26)	14.59 (5)	0.00 (<1)	213.00 (68)
Larval zone temperature (°C)	0.75 (1)	0.00 (<1)	nm	52.02 (98)
Larval zone dew point (°C)	0.29 (1)	0.24 (1)	nm	29.20 (98)
Larval zone abs. hum. (g/m3)	0.21 (1)	0.19 (1)	nm	18.49 (98)
Larval zone rel. hum. (%)	3.08 (1)	5.50 (1)	nm	314.14 (98)

[a]nm= not measured at that level.

TABLE 5. Analysis of variance results for total relief (i.e., maximum elevation - minimum elevation within plots), relief (all elevations - minimum elevation within plots), and variance in relief within plots at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota; all units are in meters.

	Total relief		Relief		Variance in relief	
SV[a]	df	F[b]	df	F[b]	df	F[b]
S	8	27.41**	8	35.48**	8	10.89**
P(S)	22	--	22	--	22	--
T(P S)	--	--	505	--	--	--
Total	30		535		30	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot.
[b]P(S) served as the appropriate error term for testing significance of S based on expected mean squares; *=significant at α=0.05, **=significant at α=0.01, ns=not significant.

TABLE 6. Least squares means (LSMEAN ± SE) for total relief (i.e., maximum elevation-minimum elevation within each plot), relief (all elevations-minimum elevation within plots), and variance in relief within plots at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota; all units are in meters. LSMEANs within columns followed by the same letter are not significantly different using Fisher's protected LSD value at α=0.05 (see table 2 for study site descriptions and abbreviations).

		Total relief		Relief		Variance in relief	
Site	n[a]	LSMEAN	SE	LSMEAN	SE	LSMEAN	SE
FP	3	0.66 a	0.66	0.38 a	0.31	0.03 a	0.78
HM	3	7.64 c	0.66	3.99 de	0.31	4.68 c	0.78
PC	4	7.89 c	0.57	4.38 e	0.28	5.37 c	0.68
MCC	4	0.96 a	0.57	0.38 a	0.27	0.10 a	0.68
SLS	4	0.79 a	0.57	0.37 a	0.27	0.06 a	0.68
SSS	4	1.02 a	0.57	0.45 a	0.27	0.10 a	0.68
SFP	1	4.28 b	1.14	2.02 b	0.54	2.20 b	1.35
KNP	4	6.35 bc	0.57	3.17 cd	0.27	4.78 c	0.68
CXL	4	6.06 bc	0.57	3.00 c	0.27	3.51 bc	0.68

[a]n=number of 40×50 m plots within each site.

TABLE 7. Analysis of variance results for bulk density (g/m^3), variance of bulk density, pH, variance of pH, surface moisture (% saturation), and variance of surface moisture at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (no surface moisture data were available for study site=HM).

		Bulk density		pH		Surface moisture	
Response	SV[a]	df	F[b]	df	F[b]	df	F[b]
Mean	S	8	13.30**	8	3.26*	7	4.76**
	P(S)	24	--	24	--	18	--
	T(P S)	99	--	956	--	749	--
	Total	131		988		774	
Variance	S	8	1.76 ns	8	4.58**	7	0.86 ns
	P(S)	24	--	24	--	18	--
	T(P S)	--	--	--	--	--	--
	Total	32		32		25	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot.
[b]P(S) served as the appropriate error term for testing significance of S based on expected mean squares; *=significant at α=0.05, **=significant at α=0.01, ns=not significant.

because all other responses were collected there, we chose to include the PC study site in the PCA. We therefore substituted the mean soil compaction values from all of the other study sites for soil compaction at PC. We realize this is not ideal, but for descriptive visualization we believe it suffices. We also conducted a separate PCA for the eight sites using only the "larval nest zone" variables. We used the principal components procedure (PROC PRINCOMP) of SAS (1999) to conduct the PCAs.

RESULTS

General. Table 3 presents the arithmetic means, standard deviations (SD), and ranges (minimum and maximum) for selected physical non-biotic attributes (non-climatic) measured at each of the nine study sites. Table 4 presents the results of the variance component analyses with each of the non-biotic response variable results described below. In general and as would be expected, most of the variation in climatic variables (temperature and moisture) relates to sampling time across the season, with mixed results for the more physical attributes.

Relief. Nearly all of the variation in total relief (maximum elevation minus minimum elevation within each plot) is attributable to site-to-site (91%) differences (Table 4), implying consistency of plot-to-plot total relief within sites (i.e., plots, once established, all had nearly identical total relief within sites but substantial differences among sites). However, relief (all elevations within a plot minus minimum elevation within each plot) from site-to-site accounted for 55%, with less than 1% of the variation in relief being plot-to-plot, and 44% from point-to-point within plots. These results imply that the relief, or "roughness" in microtopography within plots, was consistent from plot-to-plot within sites, while still maintaining substantial variation in relief from site-to-site. Table 5 presents the ANOVA table results for comparing specific differences among the nine sites with respect to total relief, relief, and variance of relief (all *F*-tests for the main effect [site] are highly significant, implying that differences exist among sites). Table 6 presents the LSMEANS and mean separations using Fisher's protected LSD test. In

Table 8. Least squares means (LSMEAN ± SE) bulk density (g/m³), variance of bulk density (g/m³), pH, and variance of pH at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota. LSMEANs within columns followed by the same letter are not significantly different using Fisher's protected LSD value at α=0.05 (see Table 2 for study site descriptions and abbreviations).

	Bulk density		Variance in bulk density		pH		Variance in pH	
Site[a]	LS MEAN	SE	LS MEAN	SE	LS MEAN	SE	LS MEAN	SE
FP	0.86 ab	0.04	0.02 a	0.01	6.26 a	0.09	0.04 a	0.05
HM	0.86 ab	0.04	0.01 a	0.01	6.28 a	0.09	0.05 a	0.05
PC	0.91 ab	0.04	0.01 a	0.01	6.61 bc	0.09	0.06 a	0.05
MCC	1.04 c	0.04	0.03 a	0.01	6.39 ab	0.09	0.27 b	0.05
SLS	1.14 c	0.04	0.04 a	0.01	6.73 c	0.09	0.27 b	0.05
SSS	1.28 d	0.04	0.06 a	0.01	6.39 ab	0.09	0.21 b	0.05
SFP	0.78 a	0.08	0.00 a	0.03	6.45 ab	0.18	0.05 a	0.09
KNP	0.96 bc	0.04	0.04 a	0.01	6.66 bc	0.09	0.06 a	0.05
CXL	0.92 ab	0.04	0.02 a	0.01	6.40 ab	0.09	0.07 a	0.05

[a]n=4 40×50 m plots within each site, n=1 for SFP

general, ND sites had less relief and variation in relief than those in either MN or SD.

Soil Bulk density, pH, and surface moisture. Nearly 60% of the total variation in bulk density, and an even greater percentage of the variation in pH (72%) and surface moisture (73%) is attributable to point-to-point samples within plots, with consistency in this variation from plot-to-plot among all sites (i.e., all plot-to-plot variation < 18%), with some even less so site-to-site (Table 4). This implies high micro-scale variation in these attributes within the plots (e.g., bulk density varies substantially from point-to-point within a plot, and this variation is fairly constant from plot-to-plot, and to a lesser extent, site-to-site). Table 7 presents the ANOVA table results, showing that significant differences occur among site mean responses and for variance in pH (all *F*-tests for the main effect "Site" are significant; no surface moisture data were collected at the Hole-in-the Mountain study site). Specific differences in LSMEANS among the sites using Fisher's protected LSD test are presented in Table 8 for bulk density, variance in bulk density, pH, and variance in pH (mean surface moisture comparisons are presented with other moisture responses below). In general, MN and SD sites had the lowest mean bulk density with ND sites having the highest (no differences were observed among sites with respect to variance in bulk density). While there was no consistent difference in LSMEANS for pH among sites with respect to states, ND sites showed consistently higher variance in pH than the other study sites.

Soil texture (% clay, sand, and silt). Samples across all plots and study sites generally were classified as sandy loams, occasionally as loamy sand, with occasional plot points yielding soils that would be classified strictly as loams. Variance component results (Table 4) show great variation in clay from point-to-point within plots (81%), little to no plot-to-plot variation (<1%), with the remainder variation in clay site-to-site (18%). Sand and silt also show approximately half of the variation attributable to point-to-point comparison (58% and 43% respectively), but with more plot-to-plot variation (17% and 10% respectively) than clay, while much more variation is attributable to site-to-site comparison (25% and 47% respectively). These results imply that while there is substantial variation within each plot with respect to soil texture, there is also substantial variation within sites from plot to plot (sand and silt), and even more from site to site. ANOVA results indicated that mean % clay, % sand, and % silt varied significantly among sites with no significant differences in mean variances (Table 9). Further comparisons among LSMEANS indicated a tendency for SD sites to have lower % clay, whereas ND sites tended to have more sand and less silt (Table 10).

Soil compaction, temperature, and moisture. Variance components analyses were conducted separately for each of these response variables and separately for each depth (20, 40, and 60cm), with results presented in Table 4. As mentioned above, almost all of the variation in the two climatic variables, temperature and moisture, is attributable to sampling time across the season, with the remaining variation mostly attributable to site-to-site differences. However, with increasing soil depth, more and more variation is attributable to site-to-site differences, particularly for moisture, than to sampling time, the latter nevertheless still accounting for 68% of the variation. Nearly half of the variation in soil compaction can be attributable to site-to-site differences, with the other 50% distributed nearly equally among the other variance components,

Table 9. Analysis of variance results for texture composition (clay, sand, silt) and variance in texture composition at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota.

		Clay (%)		Sand (%)		Silt (%)	
Response	SV[a]	df	F[b]	df	F[b]	df	F[b]
Mean	S	8	3.97**	8	3.64**	8	8.68**
	P(S)	24	--	24	--	24	--
	T(P S)	99	--	99	--	99	--
	Total	131		131		131	
Variance	S	8	1.08 ns	8	0.93 ns	8	0.88 ns
	P(S)	24	--	24	--	24	--
	T(P S)	--	--	--	--	--	--
	Total	32		32		32	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot.
[b]P(S) served as the appropriate error term for testing significance of S based on expected mean squares; *=significant at α=0.05, **=significant at α=0.01, ns=not significant.

regardless of the depth. ANOVA results for comparison among sites and how those differences might vary with soil depth are presented in Table 11, with the interaction of depth and site being significant in all cases (no soil compaction data were available for the Prairie Coteau site where equipment failure precluded collection of data). Because of these significant interactions and the numerous possible pair-wise comparisons, we plotted the LSMEANS (± 1 SE) for soil compaction (Fig. 4), soil temperature (Fig. 5), and soil moisture (Fig. 6), noting in the legend the approximate Fisher's LSD values that can be used for specific pair-wise comparisons.

Pair-wise comparisons of LSMEANS indicated that soil compaction increases with depth at all sites, and that this rate of increase varies depending on site. With the exception of the Swearson School Section study site, ND sites tended to have the lowest soil compaction values, with SD having among the highest at all depths. Although not significant, soil temperatures tended to increase with depth at the MN sites whereas temperatures declined significantly with depth at the ND and SD sites. Minnesota sites tended to have substantially higher soil temperatures on average. In general, soil moisture tended to stay the same at various depths or in some cases to decline with depth, depending on the site. Soil temperature tended to be consistent within depth for all sites, with MN sites tending to have higher soil temperatures for all depths than either ND or SD. We did not compute and compare mean variances using ANOVA among sites for soil compaction, soil temperature, or soil moisture because of the added complexity of incorporating soil depths, and because we did not think it would add substantially to understanding these response variables.

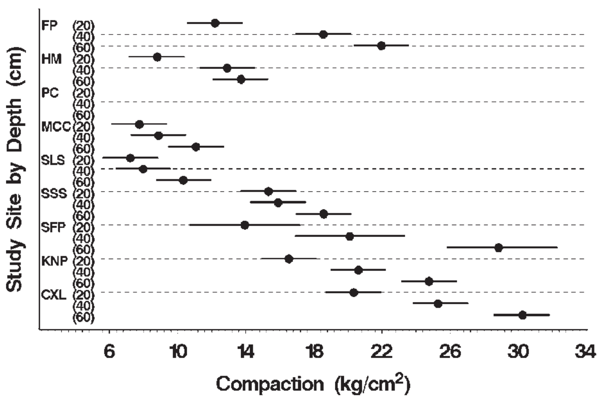

Fig. 4. Least squares means (LSMEAN ± SE) for soil compaction (kg/cm^2) at depths of 20, 40, and 60cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (Fisher's LSD≈4.5 for n=n=4 and LSD≈7.1 for n=4, n=1; see Table 2 for study site descriptions and abbreviations, no compaction data were collected at PC, n=1 for SFP, n=4 for all other sites).

Principal component analysis (PCA). Table 12 presents the results of the PCA using the listed 15 response variables. The first two principal components accounted for 66% of the variation, with the first three principal components accounting for 80%. Examination of the principal component variable coefficients, or "loadings," reveals that the first component variable (PC-1) can be considered a physical-moisture gradient, the second component variable (PC-2) a temperature-relief gradient, and the third component variable (PC-3) a textural gradient. Figure 7 is a plot of the mean principal component values illustrating separation among sites along PC-1 and PC-2. All sites separate out well along the PC-1 axis, with ND sites to the far right and SD sites to the far left, and the MN sites centered (note: the Prairie Coteau study site lies at zero, most

TABLE 10. Least squares means (LSMEAN ± SE) for texture composition (clay, sand, silt) and variance in texture at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota. LSMEANs within columns followed by the same letter are not significantly different using Fisher's protected LSD value at α=0.05 (see Table 2 for study site descriptions and abbreviations).

		Clay (%)		Sand (%)		Silt (%)	
RV[a]	Site[b]	LS MEAN	SE	LS MEAN	SE	LS MEAN	SE
Mean	FP	8.3 cd	1.2	53.3 a	3.1	38.3 c	2.5
	HM	9.2 cd	1.2	61.7 ab	3.1	29.2 b	2.5
	PC	7.7 bc	1.2	60.8 ab	3.1	31.5 bc	2.5
	MCC	6.9 abc	1.2	65.6 bc	3.1	27.5 b	2.5
	SLS	9.0 cd	1.2	61.0 ab	3.1	30.0 b	2.5
	SSS	11.7 d	1.2	74.4 c	3.1	14.0 a	2.5
	SFP	5.8 abc	2.4	56.7 ab	6.2	37.5 c	5.1
	KNP	4.8 ab	1.2	56.2 a	3.1	38.9 c	2.5
	CXL	3.7 a	1.2	61.5 ab	3.1	34.8 bc	2.5
Var.	HM	47.5 a	12.3	66.2 a	39.1	34.7 a	42.1
	FP	16.2 a	12.3	53.4 a	39.1	28.3 a	42.1
	PC	18.8 a	12.3	48.7 a	39.1	22.9 a	42.1
	MCC	26.7 a	12.3	163.3 a	39.1	149.0 a	42.1
	SLS	42.2 a	12.3	63.4 a	39.1	40.1 a	42.1
	SSS	18.5 a	12.3	34.1 a	39.1	23.9 a	42.1
	SFP	10.3 a	24.5	74.1 a	78.3	47.4 a	84.1
	KNP	14.7 a	12.3	48.4 a	39.1	38.3 a	42.1
	CXL	11.6 a	12.3	82.3 a	39.1	67.0 a	42.1

[a]RV=response variable, Var.=variance in texture (clay, sand, and silt).
[b]n=4 40×50 m plots within each site, n=1 for SFP.

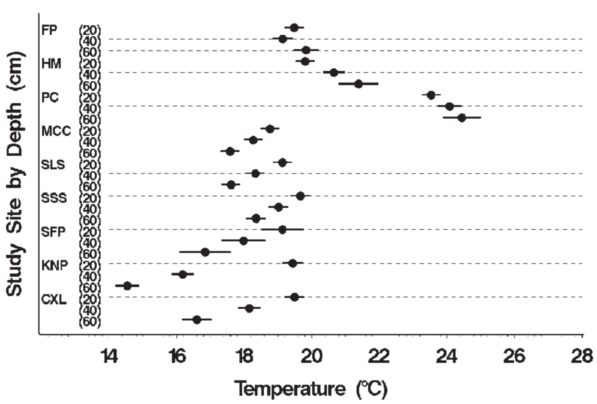

FIG. 5. Least squares means (LSMEAN ± SE) for soil temperature (°C) at depths of 20, 40, and 60cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (Fisher's LSD ≈ 1.1 for n=n=4 and LSD ≈ 1.7 for n=4, n=1; see Table 2 for study site descriptions and abbreviations, n=1 for SFP, n=4 for all other sites).

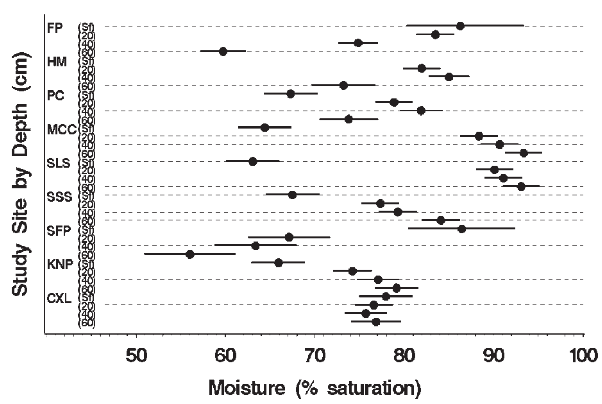

FIG. 6. Least squares means (LSMEAN ± SE) for soil moisture (% saturation) at depths of 20, 40, and 60cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (Fisher's LSD ≈ 1.6 for n=n=4 and LSD ≈ 2.5 for n=4, n=1; surface moisture, denoted as Sf, is only presented for comparative purposes but was not included in analysis of variance, separate ANOVA yielded an LSD ≈ 9.9; see Table 2 for study site descriptions and abbreviations, n=1 for SFP, n=4 for all other sites).

TABLE 11. Analysis of variance results for soil compaction (kg/cm^2), temperature (°C), and moisture (% saturation) at depths of 20-, 40-, and 60 cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (no compaction data were collected at PC, see Table 2 for site descriptions and abbreviations).

	Compaction		Temperature		Moisture	
SV[a]	df	F[b]	df	F[b]	df	F[b]
S	7	13.73**	8	50.80**	8	12.32**
P(S)	21	--	24	--	24	--
T(P S)	808	--	924	--	925	--
D	2	250.17**	2	46.44**	2	9.61**
D*S	14	10.37**	16	16.82**	16	17.01**
D*P(S)	42	--	48	--	48	--
D*T(P S)	1365	--	1383	--	1388	--
R(D T P S)	4071	--	3539	--	3539	--
Total	6330		5944		5950	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot, D=depth at each point within plot, R=up to five readings at each point across the season (here considered as sub-sampling in time, not repeated measures).
[b]P(S) served as the appropriate error term for testing significance of S, D*P(S) served as the appropriate error term for testing significance of D and D*S interaction based on expected mean squares; *=significant at α=0.05, **=significant at α=0.01, ns=not significant.

TABLE 12. Summary of principal component analysis and associated principal component variables; the first two principal components accounted for 66% and the first three principal components accounted for 80% of the variation (PC-1 could be considered as a physical structural component-moisture gradient, PC-2 could be considered as a temperature-relief gradient, with PC-3 as a textural gradient).

	Principal component variable coefficients		
Response Variable	PC-1	PC-2	PC-3
Relief (m)	-0.18	0.33	0.01
Bulk density (g/cm3)	0.29	-0.20	0.32
pH	0.05	-0.05	-0.14
Clay (%)	0.28	0.12	0.22
Sand (%)	0.24	-0.06	0.49
Silt (%)	-0.28	0.01	-0.46
Compaction 20 cm (kg/cm^2)	-0.28	-0.09	0.38
Compaction 40 cm (kg/cm^2)	-0.35	-0.03	0.23
Compaction 60 cm (kg/cm^2)	-0.37	-0.05	0.19
Moisture 20 cm (% sat.)	0.32	0.01	-0.29
Moisture 40 cm (% sat.)	0.34	0.04	-0.18
Moisture 60 cm (% sat.)	0.30	-0.18	0.02
Temperature 20 cm (°C)	-0.02	0.48	0.13
Temperature 40 cm (°C)	0.08	0.53	0.08
Temperature 60 cm (°C)	0.10	0.52	0.03

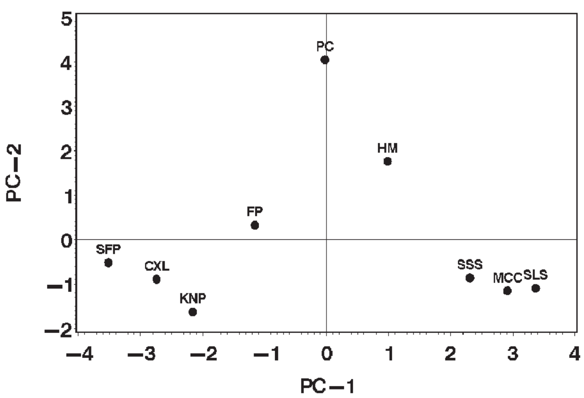

FIG. 7. Plot of the means of the first two principal components illustrating separation among study sites for all response variables except those quantified in the larval zone; PC-1 can be considered a physical structural-moisture gradient with PC-2 considered a temperature gradient (see Table 2 for study site descriptions and abbreviations).

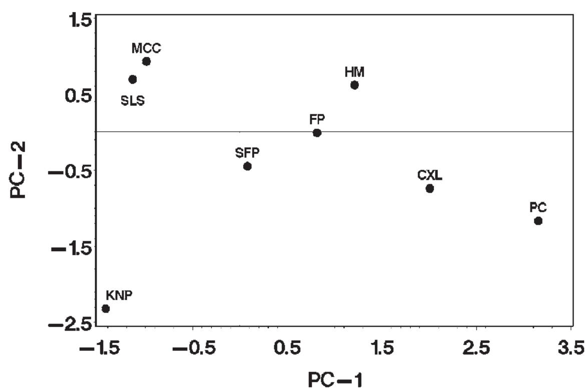

FIG. 8. Plot of the means of the first two principal components illustrating separation among study sites for response variables quantified in the “larval zone” (see table 13, no data were collected at study site=SSS); PC-1 can be considered a dew point-absolute humidity gradient with PC-2 considered a temperature-relative humidity gradient (see Table 2 for study site descriptions and abbreviations).

Table 13. Seasonal mean temperature (°C), dew point (°C), absolute humidity (g/m³), and relative humidity (%) in the "larval zone" (between the soil surface and 2.0 cm) at the center of monitored plots at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (see Table 2 for study site descriptions and abbreviations; values were taken in 30-minute intervals continuously between the beginning of oviposition and at the approximate time of onset of larval diapause in September).

Site	Plot	Temp. (°C)	Dew pt. (°C)	Abs. hum. (g/m³)	Rel. hum. (%)
FP	1	19.14	16.24	13.85	83.81
	3	19.13	15.36	13.11	80.20
HM	1	18.73	15.84	13.75	83.50
	3	18.96	15.93	13.83	83.45
PC	3	20.53	16.77	14.47	81.16
MCC	1	17.76	14.65	12.52	81.74
	2	18.05	14.46	12.40	80.66
	3	17.95	15.25	13.16	84.07
	4	17.94	15.34	13.22	85.11
SLS	1	17.96	14.73	12.67	82.23
	2	17.83	15.08	13.04	84.20
	3	18.41	14.71	12.68	80.28
	4	17.96	14.85	12.82	82.45
SFP	1	19.03	15.44	13.14	80.79
KNP	1	19.45	13.90	12.05	72.51
	3	19.68	15.27	13.04	78.41
CXL	3	19.95	16.41	14.10	82.53
	4	19.90	16.16	13.78	80.90

likely due to using the mean compaction values from the other sites). The axis for PC-2 separates the MN sites from ND and SD sites along this temperature gradient.

Larval nest zone temperature, dew point, and humidity. Table 13 presents the seasonal means for temperature, dew point, absolute humidity, and relative humidity in the zone between the soil surface and 2.0 cm above (the "larval nest zone") at the center of monitored plots at each site. Note that since Swearson School Section site was under intermittent grazing during the study, loggers were not placed and that site is therefore not represented in the table. As expected, nearly all of the variation in temperature, dew point, absolute humidity, and relative humidity can be attributed to sampling time across the season (Table 4). Although not compared statistically, ND tended to have lower mean responses for each of these variables than either MN or SD sites. Table 14 presents the results of the PCA using only the four response variables from Table 13. The first principal component accounted for 64% and the first two principal components accounted for 99% of the variation. Examination of the principal component variable coefficients, or "loadings," reveals that the first component variable (PC-1) can be considered a dew point – absolute humidity gradient while the second component variable (PC-2) can be considered a temperature – relative humidity gradient. Figure 8 is a plot of the mean principal component values illustrating separation among study sites along PC-1 and PC-2. Using these somewhat limited data, no clear pattern emerged when comparing sites from a state perspective.

Discussion

Objective 1: Characterization of non-biotic habitat parameters. A review of the above information leads us to two observations. First, there appear to be two relatively distinctive types of habitat substrate for the Dakota Skipper. These were earlier proposed by Royer and Marrone (1992) as "Type A" and "Type B" habitats. The sites in this study that would be designated Type A are topographically of low relief (<1m), with more nearly saturated soils at greater depths (40–60cm), and with soil bulk density exceeding 1.0g/cm³. At least to a depth of 60cm, soils may be sandy but are relatively free of gravel. This is the habitat that McCabe (1979, 1981) associated with the margins of glacial lakes and that Royer and Royer (1998) restricted in ND to glacial lake near-shore Oahe Formation geology (Fig. 1). The ND study sites designated Mount Carmel Camp and Smokey Lake School Section are typical of this habitat, and most historical sites in the Devils Lake and other glacial lakes areas within North Dakota appear to be as well. Soils in these situations are classified as sandy loams, occasionally as loamy sands. These environments have a high water table and are subject to intermittent flooding in the spring, but they offer sufficient relief to provide segments of non-inundated habitat during the spring larval growth period within any single season. Their position in the western part of the historical range of the Dakota Skipper may relate to a larval need of humidity in an otherwise more xeric climate, as earlier noted by McCabe (1981).

The second habitat type (Type B) is associated with more gravelly glacial landscapes of relatively higher relief, more variable soil moisture, and somewhat higher soil temperatures. Mean bulk density was in all Type B study sites below 1.0g/cm^3, but soils in these environments were found to be considerably more compact at all depths (Fig. 4). (It should be noted that higher soil compaction findings may relate to the presence of gravel and its effect on accuracy of the instrument, particularly at depths below 20cm.) Again, these soils were classified predominantly as sandy loams, occasionally as loamy sands.

Given that all study sites were known to harbor viable populations of the Dakota Skipper, analysis of logger readings from within the "larval nest zone" across all plots and sites helps to define acceptable levels for the studied microclimatological variables temperature, dew point, and humidity. For example, the mean season-long larval nest zone temperature for all sites ranged between a low of 17.8°C at Mount Carmel Camp and Smokey Lake School Section plots in North Dakota and a high of 20.5°C at the Prairie Coteau site in Minnesota. The range-wide season-long mean was 18.79°C. The season-long mean larval nest zone dew point ranged across sites from 13.9°C at Knapp Ranch in South Dakota to 16.8°C at Prairie Coteau in Minnesota. Within this context, relative humidity in the larval nest zone remained basically consistent across all sites, with the lowest recorded season-long means being 72.5 percent and 78.4 percent at the Knapp Ranch site in South Dakota and the highest being 84.2 percent at Smokey Lake School Section and 85.1 percent at Mount Carmel Camp in North Dakota. The season-long mean for South Dakota sites was 78.8 percent, for Minnesota sites was 82.2 percent, and for North Dakota sites was 82.6 percent relative humidity.

Table 14. Summary of principal component analysis and associated principal component variables for response variables quantified in the "larval zone;" the first principal component accounted for 64% and the first two principal components accounted for 99% of the variation (PC-1 can be considered a dew point-absolute humidity gradient with PC-2 considered a temperature-relative humidity gradient).

	Principal component variable coefficients	
Response Variable	PC-1	PC-2
Temp. (°C)	0.41	-0.63
Dew pt. (°C)	0.62	0.05
Abs. hum. (g/m^3)	0.62	0.07
Rel. hum. (%)	0.24	0.77

Objective 2: Grazing vs. hay-mowing in North Dakota. Review of bulk density values revealed that, in support of the above-noted two-habitats distinction, LSMEANS for two ND study sites (Smokey Lake School Section and Swearson's School Section) were statistically different from those for all study sites in SD and MN except Knapp Ranch (see Table 8). Mean bulk density measurements for all study sites indicate both that all North Dakota sites exceed 1.0g/cm^3, and that Swearson's School Section, the only site that was under active grazing during the study, had the highest mean bulk density of all sites. (Knapp Ranch had been grazed, but was not under grazing during the study.) It should also be noted, however, that within ND the LSMEANS for Mount Carmel Camp and Swearson's School Section are themselves also statistically different. Swearson's School Section produced a bulk density LSMEAN that was significantly higher than those from any of the eight other study sites. This site has a history of leased grazing, and Dakota Skippers are rare in the grazed portion of the site, although often quite common in adjacent (contiguous) private, ungrazed hayland habitat.

This difference is even more apparent when soil compaction data for the North Dakota ("Type A") sites are considered alone. Figure 4 illustrates that Swearson's School Section soils were significantly different from those from either Mount Carmel Camp or Smokey Lake School Section. All three of these sites are part of the Towner-Karlsruhe Habitat Complex, which has been proposed (Royer & Royer 1997) as the only potentially secure Dakota Skipper habitat area remaining in ND.

Swearson's School Section also contained lower percent moisture at all depths than the other two ND sites (Fig. 6). These findings are consistent with decreased soil water content found in grazed areas (e.g., Pietola *et al*. 2005, Donkor *et al*. 2005, Zhao *et al*. 2007). Higher bulk density values likely result from the loss of porosity, which decreases water movement through the soil (Warren *et al*. 1986, Greenwood *et al*. 1997). Decreased water movement through the soil would readily explain both the slightly higher surface moisture values and lower subsurface moisture values at SSS compared to those in other North Dakota sites. However, the texture of the soil also affects water movement through the soil; sandy soils tend to allow water to pass through them readily, whereas clayey soils impede water movement. The grazed site (SSS) contains a greater percentage of sand than the two hayed sites (MCC and SLS), although for MCC the difference is not significant at the 95% level. Regardless of the cause, the lower moisture at all depths at the SSS site suggests that a dry layer may be formed at this site during years when normal summer precipitation patterns occur.

CONCLUSIONS

Two habitat types were distinguished by the study. One ("Type A") is found in near-shore glacial lake deposits, the other ("Type B") in glacial moraine deposits. The most obvious difference between these habitat types is topographic relief, Type A habitat being relatively flat and featureless, Type B being rolling or hilly. Soil textures in both habitat types are generally classified as sandy loams, but those in moraine deposits are gravelly, whereas the deposits associated with glacial lakes are not.

Soil compaction, presumably a result of long-term cattle grazing, appears to be affecting vertical water distribution in soils within Type A habitat in North Dakota, although minor differences in soil texture may also be a contributing factor. Altered vertical distribution of water may render Dakota Skipper larvae vulnerable to desiccation during the drier late summer months, thus stressing a population.

ACKNOWLEDGEMENTS

This project was funded by USGS cooperative agreement 00HQAG00331, under that agency's 2000 Species at Risk (SAR) program, and by the Division of Science at Minot State University. Northern Prairie Wildlife Research Center (NPWRC), of the U.S. Geological Survey (USGS), contributed both GIS and statistical support. The formal contact there was Thomas Sklebar. Guy A. Hanley conducted the bulk of Minnesota fieldwork. Karew Schumaker and Heidi Richter, undergraduate students in the MSU Division of Science, assisted in both fieldwork and analysis of soil samples. Jeremy Horrell contributed significantly to mapping. A substantial portion of remaining Dakota Skipper habitat in North Dakota is on state-owned public school trust land for use of which formal permission was granted by the state land department and lessees Vernon Kongslie, Daniel Kuntz, and Terry Bailey. In Minnesota, permission was granted by both the Department of Natural Resources (DNR) and The Nature Conservancy (TNC). In South Dakota permission was granted by TNC, the U. S. Fish and Wildlife Service, and a private landowner, Roger Knapp. These permissions are all gratefully acknowledged. We thank R.A. Gleason, G.A. Sargeant, P. Scherr, and two anonymous reviewers for comments on earlier drafts.

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Received for publication 2 December 2005; revised and accepted 17 December 2007.