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ORIGINAL PAPER

Grass-skipper (Hesperiinae) trends in midwestern USA grasslands during 1988–2013

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Abstract We surveyed butterflies in prairies, pine-oak barrens, and degraded grasslands during 1988–2013 in southern Wisconsin, USA. In prairie preserves (primarily managed with frequent fire), both specialist and non-specialist "grassland" grass-skippers declined strongly. Specialists inhabiting the native herbaceous flora of pine-oak barrens that had little management but relatively consistent vegetation over time had large fluctuations but more stable trends. Grassland grass-skippers showed similar more stable trends in barrens and degraded fields with relatively consistent vegetation over time. Significant population trends did not relate clearly to how southerly the species' ranges are. Specialist and grassland grass-skipper persistence after prairie preservation correlated negatively with both number of years since preservation and prairie patch size. We also analyzed grass-skipper abundance during 1977–2012 in midwestern 4th of July Butterfly Counts, an annual volunteer butterfly census. Specialists declined significantly but grassland as well as forest and wetland grass-skippers averaged a non-trend. We hypothesize that the reasons why fire management is adverse are because of direct mortality and also the thick tall grass regrowth, which may be unsuitable for larvae to use. It appears urgent to identify and implement management strategies in prairie preserves that consistently maintain grassland vegetation as required by grass-skippers in ways the grass-skippers themselves tolerate.

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Introduction

North America's tallgrass prairie contains a predominately herbaceous flora. Savanna (trees and brush interspersed with herbaceous patches) mixes with and occurs along the eastern and northern margins of tallgrass prairie (Curtis 1959; Nuzzo 1986). This is usually called "oak savanna" except for more northerly "pine-oak barrens" on sandy soil. Since European contact in North America, about 99 % of tallgrass prairie and oak savanna has been destroyed primarily by conversion to agriculture (Curtis 1959; Nuzzo 1986; Samson and Knopf 1994). Patches of original prairie and oak savanna vegetation remain in preserves, parks, and unintensively utilized or fallow farmland (hay fields, pastures). These remnants are isolated and often degraded. Barrens have also declined but not to the same degree, and occur in less degraded landscapes, including military reservations and timber reserves (Curtis 1959; Borgerding et al. 1995; Wisconsin Department of Natural Resources 2000).

Because of this catastrophic prairie and oak savanna loss, butterflies obligate to these native herbaceous vegetations are now primarily restricted to government and private preserves and are generally rare (Opler 1981; Opler and Krizek 1984; Johnson 1986). In October 2013, the US Fish and Wildlife Service (2013) proposed to list the Dakota skipper *Hesperia dacotae* as threatened and Poweshiek skipperling *Oarisma poweshiek* as endangered. Various prairie and savanna butterflies are also designated as threatened or endangered on state lists (e.g., reviews in

Swengel and Swengel 2007: 265; Schlicht et al. 2009: Online Resource Table 1). Resident in pine-oak barrens, the Karner blue *Lycaeides melissa samuelis* is federally listed as endangered (U.S. Fish and Wildlife Service 2003), and occurs in both conserved land as well as timber reserves.

Many populations of prairie-specialist grass-skippers (Lepidoptera: Hesperiinae) have declined greatly in prairies after they were preserved, as well as in unintensively utilized agricultural lands (Schlicht et al. 2009; Swengel et al. 2011; Swengel and Swengel 2013, 2014; U.S. Fish and Wildlife Service 2013). Other grass-skipper species (termed "grassland" species here) tolerate vegetative degradation more, and have widely occurred in both native herbaceous flora and degraded fields that reverted after agricultural abandonment. Declines of grassland grass-skippers have also been noted in the region (Selby 2006; Dupont 2011; U.S. Fish and Wildlife Service 2013). As a result, there is concern that skipper conservation problems here are broader than merely preserving and maintaining native herbaceous flora, such as a disease or agricultural factor (Dupont 2011; U.S. Fish and Wildlife Service 2013).

In this paper, we analyze two datasets of long-term butterfly surveys to examine patterns of specialist and grassland grass-skipper abundance and trend in midwestern herbaceous vegetations. The first dataset is our butterfly surveying in prairie preserves, barrens, and fields during 1988–2013 in Wisconsin, USA (Swengel 1996, 1998). Second, we obtained data from the annual, volunteer 4th of July Butterfly Count Program for areas surveyed long-term in the northern tallgrass prairie region of the midwestern USA (Swengel 1990). We tested for significant differences in population trend within species-groups (specialist or not) among site types and among species-groups within site type. In prairie preserves, we calculated the number of years after preservation that we recorded the specialist and non-specialist grassland grass-skippers as present. We correlated those measures of persistence to preserve size. These results should be useful for evaluating conservation methods and developing effective conservation strategies for grass-skippers.

Methods

Swengel dataset

We conducted butterfly transect surveys along similar routes in each site on each visit (similar to Pollard 1977), as described in Swengel (1996, 1998). Walking at a slow pace (2–3 km/h) on parallel routes 5–10 m apart, we counted all adult butterflies observed ahead and to the sides, to the limit an individual could be identified, possibly with binoculars after detection, and tracked. Survey dates and locations were selected to study a focal specialist species (Swengel 1996, 1998; Swengel and Swengel 2005), including frosted elfin *Callophrys irus*, listed in Wisconsin as threatened (Bureau of Endangered Resources 1999) and Karner blue *Lycaeides melissa samuelis*, federally listed as endangered (U.S. Fish and Wildlife Service 2003) in barrens; Ottoe skipper *Hesperia ottoe*, recently listed in Wisconsin as endangered (Wisconsin Department of Natural Resources 2014) in prairies; or regal fritillary *Speyeria idalia*, listed in Wisconsin as endangered (Bureau of Endangered Resources 1999) in prairies and fields, and Leonard's skipper *H. leonardus* in barrens and fields.

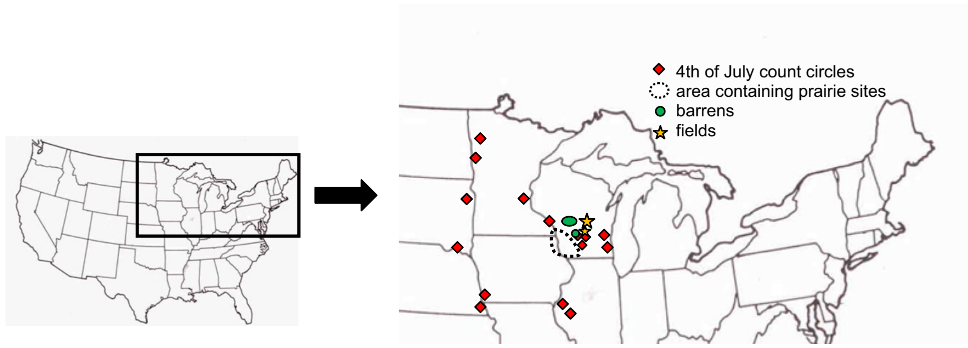
Study sites (Fig. 1) were deliberately selected for conservation interest, i.e., those known or thought to have specialist butterflies. All sites could not be visited each year but most were visited more than once both within and among years. We consistently surveyed a subset of Wisconsin sites in most or all years (Online Resource Table 1). Annual surveys occurred from early spring to late summer in barrens, mid-summer in prairies, and early to late summer in fields.

The ten native prairie sites were preserves. Most were managed primarily with cool-season fire typically in a rotation of 2–5 years, with some mowing, brush-cutting, or spot-herbiciding in addition. Four prairies were analyzable only for the non-native European skipper *Thymelicus lineola* (Online Resource Table 1). The other skipper species were not analyzable because <7 individuals were recorded on the sum of all annual peak counts of the species at the site.

The eight barrens (Online Resource Table 1) occurred in a context of forest cover, primarily in timber reserves (-some burned by wildfire in 1977 or 1988) as well as conservation land. As a result, the habitat patches are not as discretely defined. All barrens in this analysis except Mirror Lake State Park have supported Karner blue and thus were covered by federal regulation requiring protective effort for this butterfly (as described in Swengel and Swengel 2005).

The six field sites were degraded reversions from intensive agriculture, with non-native plants prevalent, as well as some common native plants (Curtis 1959). Five sites were at Buena Vista Grassland Wildlife Area, which contains ca. 5,000 ha of public land within a 16 km × 13 km area in several discrete areas of permanent grassland cover. Units for management (fire, season-long grazing, haying, localized brush-cutting or herbiciding, tilling) were relatively small (8–49 ha) in a context of nearby longer unmanaged units. No more than 10 % of the site per year received any broadcast management treatment. The 200 ha area surveyed at Pine Island Wildlife Area had no management evident at the start of the study period and became

Fig. 1 Map of the northeastern USA (*right*) showing locations of the 15 4th of July Butterfly Count circles (4JCs) and *ovals* encompassing Swengel long-term study sites in Wisconsin prairies, fields, and barrens



rotationally burned fire, with localized mowing. Only one species (Delaware skipper *Anatrytone logan*) was analyzable at this site as it was the only grassland species with >6 individuals recorded on the sum of all annual peak counts of the species at the site.

For each study species (Table 1), we identified the highest count on a single survey along the same route each year to represent that butterfly's abundance at each long-term survey site (Online Resource Table 1), if obtained during the main flight period that year. We surveyed sites multiple times per year both to verify the timing of the main flight period and to survey different target species. However, a "collated" index (e.g., sum of weekly counts throughout a species' flight period in a year) was not possible because the number of visits per flight period varied both among sites and among years. Using one survey during the main flight period avoids pseudoreplication (counting the same individual in more than one value in the dependent variable) and has been adequate for producing representative indices for comparisons of relative abundance within and among sites (Thomas 1983; Swengel and Swengel 2005; Schlicht et al. 2009). It was not necessary to standardize the Swengel data as observation rates for trend calculation at each site because effort was similar within site among years.

4th of July Butterfly Counts

Patterned after the Christmas Bird Count, the 4th of July Butterfly Count Program was founded in 1975 as an annual, volunteer, international census of butterflies and skippers at selected sites (Swengel 1990). The count period extends several weeks before and after this holiday. People initiating a count establish a 15-mile (24-km) diameter count circle, which remains the same each year the count is conducted, although actual count sites within the circle may vary from year to year. On a single date, participants keep track of the number of each species of butterfly and skipper seen, weather, number of observers in how many field parties, and how much time each party spent in the field (called "party-hours"). Results are published annually (citations provided in Online Resource Table 2). Although this program was intended to be recreational, midwestern count compilers have treated it seriously as a way to study, conserve, and educate about butterflies (Swengel 1990). Although count results are relatively informal, they have been cross-validated to other data sources (e.g., Swengel 1995; Walton and Brower 1996; Vandenbosch 2007). As a result, count results can be scientifically useful for a variety of biogeographical topics (e.g., Koenig 2006; Ries and Mullen 2008; Meehan et al. 2013).

For this analysis, we identified 4th of July Count circles (4JCs) in the northern tallgrass prairie zone: Illinois, Iowa, and southern and western Minnesota as in Wendt (1984); far eastern Nebraska and South Dakota as in Risser et al. (1981); and southern Wisconsin as in Curtis (1959). We started by selecting 4JCs (Fig. 1; listed in Online Resource Table 3) that were started in 1995 or earlier and reported results in 2012, the most recent available published report at the time of analysis (Online Resource Table 2). We added one more 4JC (McDonough County, Illinois), even though it was last reported in 2011, because its dataset extended back the furthest in time.

Collectively for all these 4JCs in all years, count dates occurred from 5 June to 13 August (range of 69 days). Count date on individual 4JCs varied among years by 11–46 days. It was not possible to determine the flight period for each species in each year in each 4JC. Instead, if a grass-skipper was ever reported on a 4JC, we included all years reported for that 4JC in analysis of that species. We are treating variation in count date relative to seasonal phenology as a confounding factor in this analysis, with the assumption that there is not an overall directed trend over time for the count dates of these 4JCs to be timed earlier or later in seasonal phenology.

Because sampling effort varied within a circle among years, we chose to standardize 4JC data as individuals per party-hour per 4JC, for each species in each year, as frequently done in other studies (e.g., Walton and

Table 1 Total individuals of each study species recorded on all surveys at the study sites, by site type

English name	Scientific name	4JCs	Prairies	Fields	Barrens
Specialist					
C Poweshiek skipperling	*Oarisma poweshiek*	151			
S Ottoe skipper	*Hesperia ottoe*	10	625		
S Leonard's skipper	*Hesperia leonardus*			87	1,615
S Cobweb skipper	*Hesperia metea*				744
C Dakota skipper	*Hesperia dacotae*	7			
N Indian skipper	*Hesperia sassacus*	[1]			433
S Byssus skipper	*Problema byssus*	110	15		
S Dusted skipper	*Atrytonopsis hianna*				863
Grassland					
N European skipper	*Thymelicus lineola*	2,025	250[1]	206	[3]
C Peck's skipper	*Polites peckius*	496	[4]	77	33
S Tawny-edged skipper	*Polites themistocles*	619	417	35	63
S Crossline skipper	*Polites origenes*	177	421	[4]	108
N Long dash	*Polites mystic*	2,003	[3]	965	27
S Delaware skipper	*Anatryone logan*	1,110	306	37	38
Forest					
S Northern broken-dash	*Wallengrenia egeremet*	1,229			
S Little glassywing	*Pompeius verna*	209			
C Hobomok skipper	*Poanes hobomok*	168			
S Zabulon skipper	*Poanes zabulon*	117			
S Common roadside-skipper	*Amblyscirtes vialis*	117			
Wetland					
S Least skipper	*Ancyloxypha numitor*	1,162			
C Mulberry wing	*Poanes massasoit*	423			
S Broad-winged skipper	*Poanes viator*	59			
S Dion skipper	*Euphyes dion*	158			
C Black dash	*Euphyes conspicua*	541			
C Two-spotted skipper	*Euphyes bimacula*	16			
S Dun skipper	*Euphyes vestris*	840			
Immigrant					
S Fiery skipper	*Hylephila phyleus*	68			
S Sachem	*Atalopedes campestris*	120			

Numbers in brackets indicates too small samples to analyze (total individuals <7 for a species). Range categorizations of species: *S* southern range, *C* core range, *N* northern range. C and N lumped for analysis. Forest, wetland, and immigrant species were analyzed only in 4JCs

[1] 176 of the 250 individuals of European skipper were recorded at sites analyzable only for this species (Online Resource Table 1); only 74 individuals occurred in prairies where any specialists were recorded

Brower 1996; Koenig 2006; Vandenbosch 2007). As reported by the 4JC compilers, counters visited a variety of types of sites, including prairie preserves (some larger than in the Swengel dataset analyzed here; e.g., Bluestem Prairie in Minnesota was about 1,000 ha [The Nature Conservancy Minnesota Chapter 1988]), wildlife areas, state parks, and roadside rights-of-way, and counted in a variety of vegetation types, including prairies, fields, forests, and wetlands. One site (Mirror Lake) is represented in both the Swengel and 4JC datasets. However, there is no data overlap between the analyses of the two datasets. Spring and late summer species found at Mirror Lake are analyzed only in the Swengel dataset. The summer species found at Mirror Lake are analyzed only in the 4JC dataset.

Statistics

We classified species as in previous studies (Swengel 1996; Swengel and Swengel 2001) (Table 1): (1) specialist grassland ("specialist," restricted or nearly so to native herbaceous flora), (2) non-specialist grassland ("grassland," occurring widely in open non-forested and non-wetland vegetation, both native and degraded, without strong sensitivity to vegetative quality), (3) forest (including forest edge), (4) wetland, and (5) immigrant (occurring in the study region during the growing season but rarely if ever surviving the winter). All these categories of species were recorded in all site types. Because we biased the Swengel survey sites to target non-wetland undegraded herbaceous vegetation, we did not analyze groups 3–5 in the

Swengel dataset. However, we had no basis to assume that 4JCs had a similar bias in vegetation types counted, and more kinds of forest and wetland species occurred in the 4JCs. Thus, we analyzed species groups 3–5 in the 4JCs as outgroups to the specialist and grassland species analyzed in both 4JCs and Swengel data. Analyses including grassland species were done both including and excluding the non-native European skipper *Thymelicus lineola*, which primarily uses a non-native grass for caterpillar food (Opler and Krizek 1984; Scott 1986).

All analyses were done with ABstat 7.20 software (Anderson-Bell 1994). All tests were two-tailed, with statistical significance set at $P < 0.05$. We used non-parametric tests for all analyses because they do not require data to be distributed normally. The Spearman rank correlation was used for all correlations and the Mann–Whitney U test to test for significant differences between samples.

We calculated trend by correlating each time series (one abundance value per site per year, by species) with year. We then tested the resulting correlation coefficients (r) for significant differences by species group (e.g., specialist and grassland) and site type (4JCs; prairies, barrens, and fields in the Swengel dataset). Because of the number of population declines in the prairies, it was possible to calculate an index of population persistence after preservation as the difference between the year the species was last recorded and the year the site was preserved. We correlated skipper population persistence at the scale of the individual species to prairie patch size.

We classified the study species based on their published range (Opler and Krizek 1984; Scott 1986) (Table 1). Most species are "southern" species with the northern edge of their range in the study region or nearby to the north. A few are "core" species because they have a rather narrow latitudinal range that does not extend much north or south of the study region, if at all. A few are "northern" species because more of their range is north than south of the study region. For analysis, we combined core and northern species into one group because of the limited number of species in these categories.

We performed all trend analyses at the scale of individual species at individual sites because we wanted to retain local variation in the statistical tests. Butterfly survey totals can lack a normal distribution, so that the mean may be skewed toward the high abundance of a few sites when most other sites had few or no individuals found (e.g., as in Swengel and Swengel 2014). By analyzing at the scale of the site, rather than the region, each site was represented equally in statistical tests. For analogous reasons, we did not aggregate results of the three grassland skippers in a site prior to analysis of persistence.

Since significant results occurred much more frequently than expected due to Type I statistical errors, we did not lower the critical P value further, as far more Type II errors (biologically meaningful patterns lacking statistical significance) would then be created than Type I errors eliminated. Moran (2003) advised this approach of assessing frequency of significance at $P < 0.05$, rather than lowering the critical P value. As recommended by Nakagawa (2004), we also report effect size through r's and mean values between groups. Per García (2004), the primary situations for critical P reduction are (1) "fishing" to identify relevant independent variables by testing many variables without a priori justification, (2) the dependent variable in a single test containing repeated samples of the same individuals (pseudoreplication), and (3) repeated sampling of the same population divided into more than one test (analogous to the "fishing" in #1). By contrast, the justifications for our tests have been established by prior literature (see "Introduction" and "Discussion" sections), although we made no assumptions about the direction of the pattern and thus used two-tailed tests. We avoided pseudoreplication because our dependent variables all contain only values that represent a single sampling of individuals (one value per generation of each species) at the sites. Furthermore, in a particular type of test (e.g., a table), all years of sampling at a site are contained within a single test.

Results

In 4JCs, numbers recorded for each specialist species were all lower than for any of the grassland grass-skippers (Table 1: 1–151 and 177–2,025 individuals, respectively). Furthermore, fewer 4JCs reported each specialist than for any of the grassland grass-skippers (Fig. 2: 1–3 and 7–15 4JCs, respectively).

Specialists declined in both 4JCs (Fig. 2a, b) and prairies (examples in Fig. 3, Online Resource Fig. 1), with similarly negative mean trends in each site type (Table 2; Fig. 4). The only positive specialist trend (non-significant) in prairies was for Byssus skipper (analyzable at one site). The one specialist species found in fields also declined (example in Online Resource Fig. 2). Specialists in barrens exhibited a wide range of patterns (examples in Online Resource Fig. 3). Grassland species had significantly more negative trends in prairies than in 4JCs, fields, and barrens (Table 2; Fig. 4). Except in prairies, grassland species had correlation coefficients averaging near zero (non-trend).

Specialist and grassland species did not differ significantly in trend in prairie (both negative) or barrens (both stable) (Table 2). Specialist species had significantly more negative trends than grassland species in 4JCs. Specialists were too few to test this in fields but the results suggest a similar pattern of more negative trend for specialist than grassland species. In 4JCs, specialists had

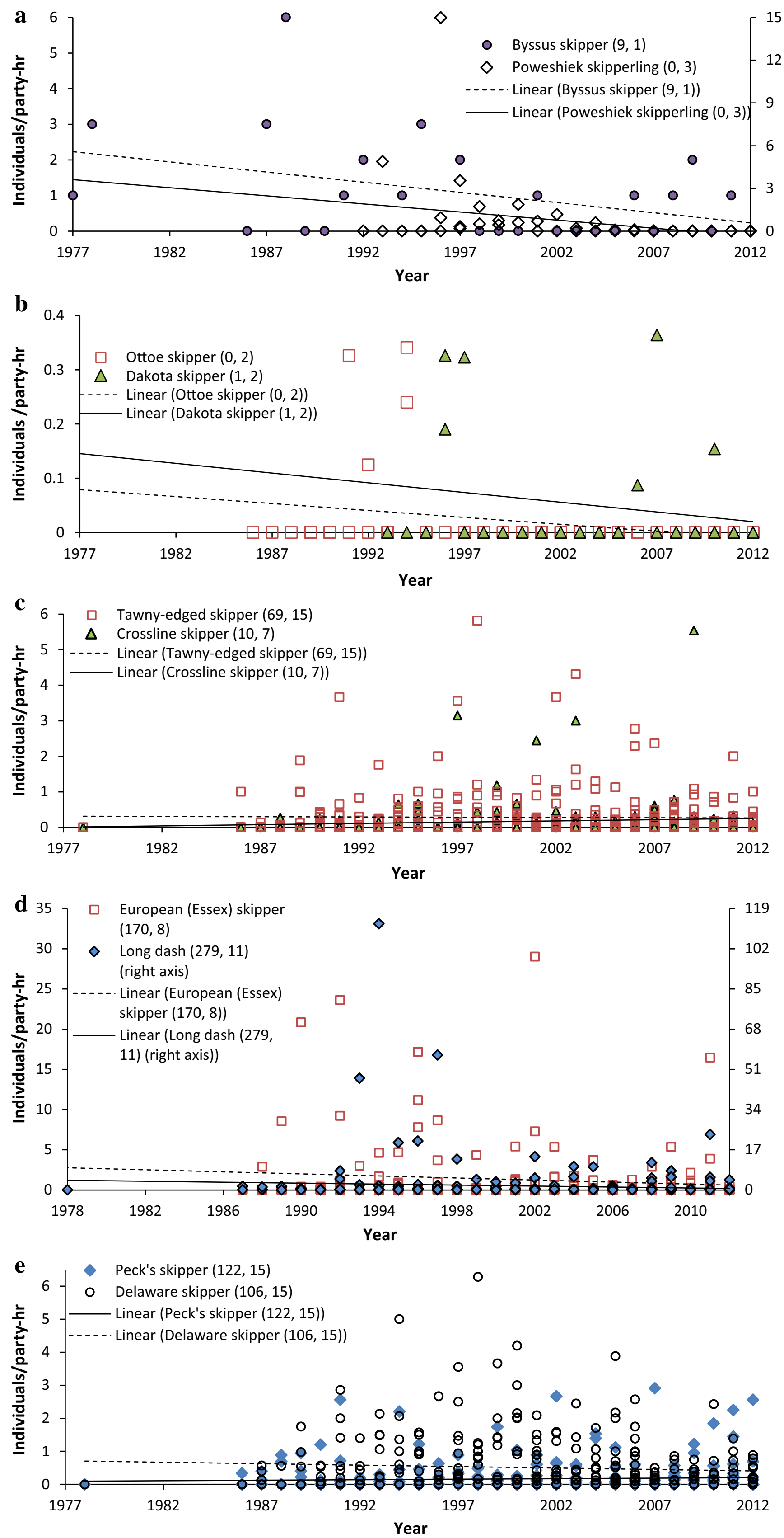


Fig. 2 Individuals per party-hour each year, by individual 4th of July Count circle (4JC) for specialists **a** Byssus skipper and Poweshiek skipperling (*right axis*), **b** Ottoe and Dakota skippers, and six grassland species, **c** tawny-edged and crossline skippers, **d** European (Essex) skipper and long dash (*right axis*), and **e** Delaware and Peck's skippers. Total individuals recorded in 2010–2012, followed by the total number of study circles recording the species since 1985 are in parentheses. Regression lines are by species

Fig. 3 Skipper totals at Hogback Prairie, the only prairie with pre-preservation data. Continuous moderate dairy grazing was removed in 1997 following conservation acquisition. Fire occurred on the east half in 2005, 2010, 2011 (upper slope only)

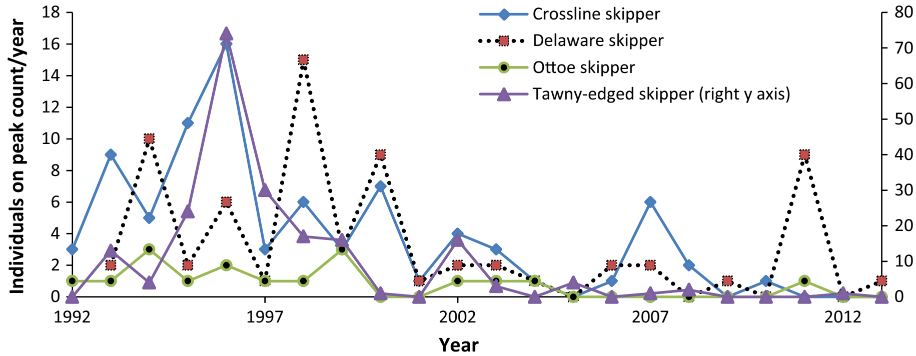


Table 2 Comparison of specialist trends to grassland species trends

	Specialist species			Grassland species			Comparing specialist and grassland
	N	Mean *r*	*P*	*N*	Mean *r*	*P*	*P*
Including European skipper							
4JC	8	−0.3521	B	71	−0.0012	A	0.0010
Prairie	7	−0.5299	B	24	−0.3866	B	0.0620
Field	3	−0.3773	–	13	−0.0807	A	–
Barrens	28	+0.0222	A	13	+0.0945	A	0.5284
Excluding European skipper							
4JC	8	−0.3521	B	63	−0.0216	A	0.0144
Prairie	7	−0.5299	B	18	−0.4017	B	0.1088
Field	3	−0.3773	–	11	−0.0348	A	–
Barrens	28	+0.0222	A	13	+0.0945	A	0.5284

Mean Spearman rank correlation coefficients (r) of trend (year vs. skipper abundance) were calculated from the individual trends of each grass-skipper species at each site. These means are grouped by species type (specialist or grassland) and site type. Two-tailed probabilities (P) are from Mann–Whitney U tests of these coefficients comparing specialist and grassland species within each site type. Within species type (specialist or grassland), means not sharing any letter are significantly different (two-tailed Mann–Whitney U test)

A significantly higher, *B* significantly more negative, – not testable ($N < 4$ coefficients)

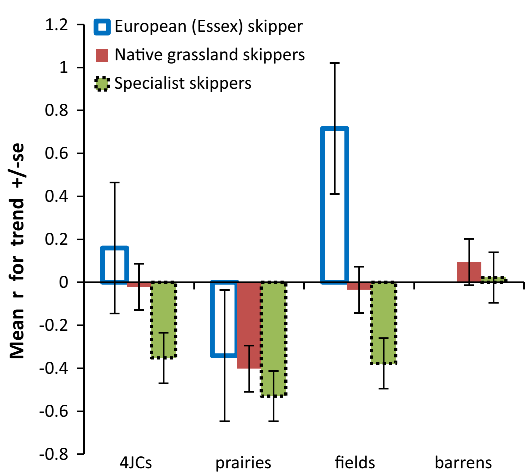


Fig. 4 Mean Spearman rank correlation coefficients (r) of trend (species abundance vs. year) by species type (specialist or grassland) and site type (4JCs; Swengel dataset: prairies, barrens, fields)

significantly more negative trends than all the other species groups (Table 3). Trends of the other species were not statistically distinguishable by group, and averaged a stable trend (absolute value of mean <0.075), except immigrants had a very mildly positive mean r (Table 3).

Four grassland species were individually analyzable for differences in trend among site types (Table 4). Prairies always had significantly more negative trends for these species, and fields and barrens always significantly higher. 4JCs had significantly more positive trends than prairies, but significantly more negative trends for the one species comparable to fields.

The analysis of southern compared to northern species was hampered by the paucity of northern species. For specialist and grassland species, only one test was significant: a northern species (Indian skipper) had significantly more positive trends than southern species in

Table 3 Mean Spearman rank correlation coefficients (*r*) of skipper trend (year vs. skipper abundance) calculated individually for each grass-skipper species at each 4JC, grouped by species type

Species type	Including European skipper			Excluding European skipper		
	N	mean *r*	*P*	*N*	mean *r*	*P*
Specialist	8	−0.3521	B	8	−0.3521	B
Grassland	71	−0.0012	A	63	−0.0216	A
Forest	45	+0.0054	A	45	+0.0054	A
Wetland	62	+0.0727	A	62	+0.0727	A
Immigrant	12	+0.1724	A	12	+0.1724	A

Two-tailed probabilities (*P*) are from Mann–Whitney *U* tests of these coefficients among species types. Means not sharing any letter are significantly different (two-tailed Mann–Whitney *U* test)

A significantly higher, *B* significantly more negative

Table 4 Comparison of grassland skipper trends among site types

	4JC		Prairie		Field		Barrens	
Crossline skipper	+0.1212	A	−0.4489	B	–		+0.1343	A
European skipper	+0.1596	A	−0.3411	B	+0.7159	–	–	
Long dash	−0.1076	B	–		+0.3735	A	+0.0348	–
Tawny-edged skipper	−0.0191	A	−0.4277	B	−0.2598	–	+0.1272	A

Mean Spearman rank correlation coefficients (*r*) of skipper trend (year vs. skipper abundance) calculated for each grass-skipper species at each site. Within a species, means from different site types not sharing any letter are significantly different (two-tailed Mann–Whitney *U* test)

A significantly more positive trend, *B* significantly more negative trend, – not testable ($N < 4$)

barrens (Table 5). A similar pattern in fields was nearly significant ($P = 0.0538$) when including European skipper (a northern species) in the analysis. In 4JCs, forest species' trends were significantly more negative for the one northern species (Hobomok skipper) than for southern species. But trends of wetland species showed no statistical difference between northern and southern species, and averaged about a stable trend. Immigrants were not testable in this analysis because both were southern species.

The number of years that Ottoe skipper was still recorded at each of the six prairie sites after becoming a preserve correlated significantly with the number of years the grassland grass-skippers were still recorded in these preserves (Fig. 5). These measures of persistence had a significant negative correlation with prairie size (Fig. 6).

Discussion

Summary

Specialists on average had significant declines in native prairies, degraded fields, and 4JCs, but an approximately stable trend in native barrens (Table 2; Fig. 4). Grassland species declined significantly in native prairies but averaged approximately stable trends in degraded fields, native barrens, and 4JCs. In 4JCs, three other skipper groups (forest, wetland, immigrant) averaged approximately stable trends (Table 3).

Expected outcomes

It is not surprising when specialists are rare and declining (Table 2; Fig. 4), because declines of localized butterflies have been documented widely here and elsewhere (e.g., van Swaay et al. 2006; Schweitzer et al. 2011; Forister et al. 2010; Krämer et al. 2012). The prairies and barrens were biased toward high-quality native flora and thus, supported many specialist populations. But in the 4JCs, located for a variety of reasons such as proximity to where the counters live (Swengel 1990), specialists occurred in lower numbers and fewer locations compared to the grassland grass-skippers (Table 1; Fig. 2). Thus, prairie specialists have been both rare and declining for decades throughout the region (Schlicht and Orwig 1998; Schlicht et al. 2007, 2009; Bouseman et al. 2010; Swengel et al. 2011).

It is also unsurprising when grassland species (tolerant of vegetative degradation) have more favorable trends than specialists in anthropogenically altered landscapes (Table 2; Fig. 4). Numerous other studies have shown that

Table 5 Mean Spearman rank correlation coefficients (*r*) of skipper trend (year vs. skipper abundance) calculated for each grass-skipper species at each site, grouped by range category (southern or northern) and site type

	Southern		Northern		
	N	mean *r*	*N*	mean *r*	*P*
Specialist					
4JC	3	−0.2894	5	−0.3898	–
Prairie	7	−0.5299			
Field	3	−0.3773			
Barrens	23	−0.0702	5	+0.4469	0.0048
Grassland					
4JC	37	−0.0394	34	+0.0404	0.4040
Prairie	18	−0.4017	6	−0.3411	0.6648
Field	4	−0.2909	9	+0.2459	0.0538
Barrens	10	+0.0746	3	+0.1609	–
Grassland excluding European skipper					
4JC	37	−0.0394	26	+0.0037	0.7114
Prairie	18	−0.4017			
Field	4	−0.2909	7	+0.1115	0.1082
Barrens	10	+0.0746	3	+0.1609	–
Forest—4JC	34	+0.0748	11	−0.2091	0.0046
Wetland—4JC	44	+0.0943	18	+0.0198	0.3894
Immigrant—4JC	12	+0.1724			–

Two-tailed Mann–Whitney *U* test probability (*P*) is calculated between southern and northern species by site type. Forest, wetland, and immigrant species were analyzed only in 4JCs

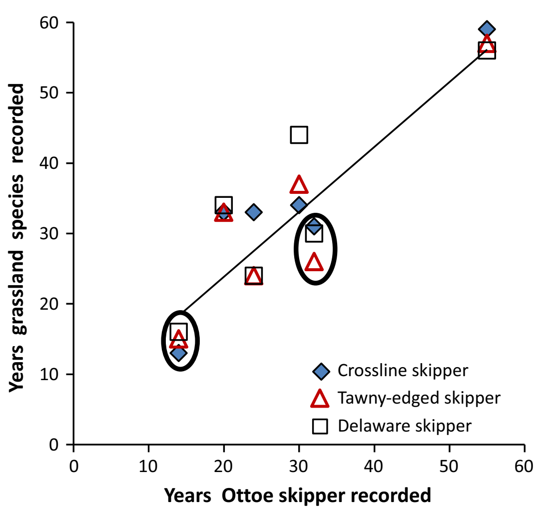


Fig. 5 Correspondence of *N* years after preservation the species has been recorded, between Ottoe skipper and native grassland grass-skippers (Crossline, Tawny-edged, Delaware), in the six prairie study sites, with regression line relating Ottoe skipper persistence to grassland species' persistence at the site for each of the sites ($N = 18$). Spearman $r = +0.6698$ ($N = 18$; $P < 0.01$). *Circles* identify sites where Ottoe skipper was recorded in the last 6 years: 2011 at Hogback (16 ha) and 2013 at Rush Creek (38 ha)

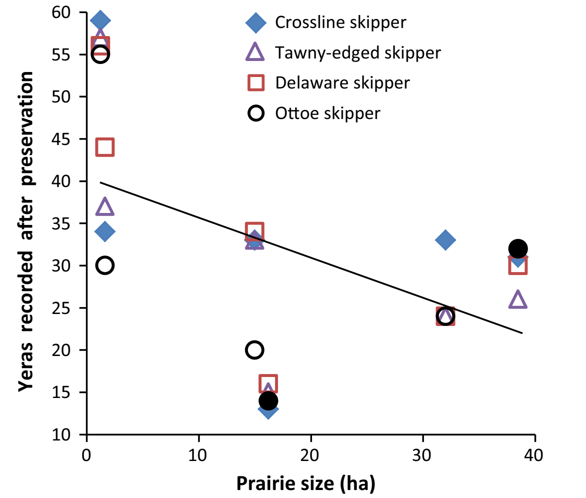


Fig. 6 Correlation of prairie size (ha) and *N* years after preservation the grass-skipper species were recorded in the six prairie sites, with regression line relating each species' persistence at each site to that site's size ($N = 24$). Spearman rank correlation $r = -0.6411$ ($N = 24$, $P < 0.01$). The dark Ottoe skipper markers indicate sites where this species was recorded in the last 6 years: 2011 at Hogback (14 years) and 2013 at Rush Creek (32 years)

less specialized species have more favorable trends than the most specialized species (e.g., Warren 1993; Wenzel et al. 2006; Schlicht et al. 2009; Forister et al. 2010; Filz et al. 2013).

Furthermore, specialists had their most favorable overall trend (a non-trend) in barrens (Table 2; Fig. 4), where the matrix had the least anthropogenic degradation from agriculture (see Introduction) and urbanization and conservation measures for an umbrella butterfly species came into effect during the study period (Wisconsin Department of Natural Resources 2000; U.S. Fish and Wildlife Service 2003; Swengel and Swengel 2007). The fields, prairies, and 4JCs were embedded in similarly highly degraded landscapes (Curtis 1959; Samson and Knopf 1994). Numerous studies have documented greater declines for localized butterflies in smaller and more isolated habitat patches, with benefit from nearer, larger, and/or more connected habitat patches (e.g., Swengel and Swengel 1999; CD Thomas et al. 2002; Hanski and Pöyry 2007; Severns 2008c). Analyses of midwestern 4JCs show that increasing amounts of natural and semi-natural habitat greatly enhance the butterfly faunas, especially of rare species, relative to urbanized and intensively farmed areas (Meehan et al. 2013).

Unexpected outcomes

There is great concern about the negative effects of non-native species on native ones (e.g., Severns 2008a, b;

Severns and Warren 2008), including whether the one non-native grass-skipper (European skipper, a "grassland" species) might negatively affect native grass-skippers in prairies (Dupont 2011). However, the non-native European skipper had similar trends (either increasing or decreasing) as the native grassland grass-skippers within site type (Table 2; Fig. 4) and European skipper was relatively uncommon in prairies with specialist grass-skippers (Table 1). We did not measure its host abundance in the prairie sites to examine whether control of its non-native host is implicated in the declines on preserves. But this non-native grass-skipper did not appear to be directly affecting the outcomes for other grass-skipper species, as would be evidenced by the non-native grass-skipper increasing while native grassland grass-skippers declined. Furthermore, an adverse influence by European skipper does not appear to explain prairie specialist trends, since both European skipper and specialists declined in prairie preserves.

These grass-skippers showed a relatively weak and mixed signal with regard to differences in trend between southern and northern species (Table 5). This is against expectation that southern species would expand and increase while northern species retreat in response to warmer climatic conditions (Parmesan 1996; Forister et al. 2010). In Breed et al. (2013), four of four northern and two of four southern grass-skippers had negative trends. Most grass-skippers declined, although not as many of the southern species. This suggests that other factors besides climate, such as habitat quality and landscape conditions, contribute to these trends, both in that study and in ours (Warren et al. 2001). Likewise, some field studies and models have produced unexpected results, such as alpine species expanding downhill (Franzén and Öckinger 2012), cooler areas increasing in butterfly richness more so than warmer places (Isaac et al. 2011), and species from both the warm and cold ends of their range declining more compared to core-range species (Filz et al. 2013). Since non-negative abundance trends facilitate butterfly species' range adjustments in response to climate change (Mair et al. 2014), the many negative population trends in this study may contribute to these unexpected patterns relative to southern or northern ranges.

It is also surprising when specialist and grassland species have similarly negative trends, as occurred in prairies (Table 2; Fig. 4). Others have also reported broad declines of grassland grass-skippers in prairie preserves (Selby 2006; Schlicht et al. 2007; U.S. Fish and Wildlife Service 2013). The converse of this is the similarly favorable trends of specialist and grassland grass-skippers in the less intensively managed barrens (Table 2; Fig. 4).

Even more surprising are the significantly more favorable trends for grassland grass-skippers in 4JCs and fields compared to prairie preserves (Fig. 4; Tables 2, 4), since all of these site types occur in the same northern tallgrass prairie region. Prairie preserves appeared to become more unsuitable as habitat for these species compared to the variety of other sites selected by counters to survey in 4JCs. The predominant management in these preserves is intensive burning (often 2–6 year rotations), which associates with significantly unfavorable outcomes for specialist Lepidoptera (Swengel 1996, 1998; Shepherd and Debinski 2005; Schlicht et al. 2009; Vogel et al. 2010; Swengel et al. 2011; Rigney 2013) as well as other invertebrates, such as leafhoppers (Wallner et al. 2012) and land snails (Nekola 2002). Specialist populations would be most vulnerable to the direct effects of fire mortality because relatively more of the population is affected and relatively less rescue is available from the surrounding landscape. However, the unfavorable grassland grass-skipper trends in prairie compared to fields and 4JCs suggest that preserve management is a negative factor for grass-skippers more generally. Grassland grass-skipper populations appear to obtain little advantage in recovering from fire mortality by occurring in the surrounding landscape. Thus, direct mortality from fire appears only partially to explain poorer skipper trends in preserves compared to 4JCs and fields.

Fire management appears to have a compounding adverse indirect effect on grass-skippers through changes in grass growth structure over time. As discussed by Dana (1991), long-term fire management can result in grasses increasing and becoming thicker and taller, which leads to less favorable structures for Ottoe and Dakota skippers as well as heavier fuel loads associated with higher fire mortality. Since grassland grass-skipper persistence correlated with Ottoe skipper persistence in preserves (Fig. 5), shorter, thinner grass growth may be more generally preferred by many grass-skippers. Further support for this comes from the barrens, where the sandy soil naturally facilitates a short sparse grass structure (Curtis 1959) and where both specialist and grassland grass-skipper populations had non-negative trends (Table 2; Fig. 4). Others have noted a preference by a variety of grass-skippers for shorter or sparser or finer grass growth (e.g., Summerville and Clampitt 1999; Runquist 2011; Rigney 2013). Such vegetative structures may be more suitable as forage for larvae, especially in the smaller instars.

Furthermore, patch size did not appear to be a buffer against other unfavorable habitat factors. The larger the patch, the significantly faster the declines of grass-skippers in the prairie preserves (Fig. 6), as also found for Ottoe skipper declines in an analysis of more midwestern preserves (Swengel and Swengel 2013). An equal mix of positive and negative area effects (Davis et al. 2007) and a lack of positive area effects (Öckinger et al. 2010), respectively, were also evident in two Iowa datasets and in a cross-continental meta-analysis (Hambäck et al. (2007). Sometimes edges provide better habitat or thermal conditions for a species (e.g., Batáry et al. 2009), so that a smaller site could be more favorable than a larger site, depending on the shape or nature of the edge of the larger site. However, patch size can also be a positive influence as in the barrens and fields, which tended to be larger than the analyzed prairie preserves and had more favorable trends (Fig. 4). Öckinger et al. (2010) reported a positive influence of patch size in most regions or taxa, as also found in barrens (Swengel and Swengel 1996) and even tallgrass prairie preserves for moths (Summerville 2008) and specialist butterflies (Swengel and Swengel 1999). As a result, patch size appears to have a synergistic component. It may intensify either positive or negative aspects of "habitat quality" defined in the species-specific sense as the particular vegetative compositions and structures and conditions necessary for the survival and successful breeding of these butterfly species (Dennis 2010; Thomas et al. 2011). Site size might also sometimes function as a mitigation (counteracting other negative factors), along with sometimes synergistically amplifying either a positive or negative factor. If so, it would be useful to figure out how to maximize the benefit of site size, by obtaining all the mitigation and only the positive synergy.

Conservation implications

Specialist skippers are highly restricted to native prairie flora, which is both rare and highly concentrated in preserves (Curtis 1959; Wendt 1984; Samson and Knopf 1994). Thus, outcomes in preserves strongly affect the future of these species. Idling (long-term non-management) does not appear optimal, as evidenced by the decline of grass-skippers between the cessation of grazing (1997) and the inception of fire in 2005 in part of the Hogback site (Fig. 3). Idling is not necessarily significantly more favorable than fire for specialist butterflies (Swengel 1998; Swengel and Swengel 1999).

As described by McCabe (1981), skipper populations experience two independent factors in the transition from the agricultural to the conservation sector: the cessation of unintensive agricultural management prior to or at preservation and often the inception of a new management (usually fire). A parallel progression combining abandonment of light agriculture with land-use intensification has eroded grassland butterfly diversity in Europe (e.g., van Swaay et al. 2011; Nilsson et al. 2013). Certain types of unintensive agricultural practices, such as rotational haying and light cattle grazing (McCabe 1981; Swengel 1996, 1998; Rigney 2013), have associated with significantly more favorable specialist butterfly outcomes. Dakota skipper is now disproportionately reported on ranch lands in the Dakotas and Manitoba compared to the dearth of recent records for historical populations on sites that had been preserved (Rigney 2013, U.S. Fish and Wildlife Service 2013). However, not all haying and grazing regimes are suitable for maintaining specialist skippers and/or the native vegetation they require (Vogel et al. 2010). Thus, it is urgently needed to determine which light agricultural regimes are suitable and to implement these findings.

This study also indicates that degraded grasslands can be remarkably valuable for conserving grassland grass-skippers (Table 2; Fig. 4, Online resource Fig. 2). As a result, unintensive active management to maintain open grassland vegetation, even if degraded, in ways tolerated by grass-skippers is valuable for butterfly conservation. Specialist insect biodiversity is richest in high-quality native flora (Panzer and Schwartz 1998; Krämer et al. 2012), which needs to be maintained as such in ways that the insect populations tolerate. But already thoroughly degraded grasslands may be more valuable to butterflies as such than as venues for efforts to re-create or restore more native flora. Others have found that conservation efforts to eradicate already existing stands of non-native plants can directly disfavor specialist insects of conservation concern (Severns and Warren 2008; Severns and Moldenko 2010; Severns 2011; Richter et al. 2013).

Although some skipper trends appeared stable in this study (specialists in barrens, grassland species in fields, barrens, and 4JCs), it should not be assumed that these populations are in fact secure. Protection from development is not sufficient to ensure conservation actions are beneficial for grass-skippers. Furthermore, in 4JCs, actual survey sites need not be kept the same, so that it is possible for turnover in survey sites to be masking skipper declines in some sites by replacing them with different sites. All data analyzed in this study are biased to come from areas that have vegetative compositions and land uses more favorable than average in the midwestern landscape as a whole. Even the 4JC data cannot be assumed to be representative of the "wider countryside" since 4JC circles, and survey sites within those circles, are not randomly selected or held constant. Van Dyck et al. (2009) documented relatively better trends for common butterfly species in vegetation types targeted for conservation than in the wider countryside.

Volunteer recording programs are essential for obtaining the geographic and temporal scale of monitoring data needed on enough species so as to evaluate butterfly population trends (Swengel 1990; Thomas 2005; van Swaay et al. 2006; Forister et al. 2010; Brereton et al. 2011). Better conservation outcomes should occur when more volunteers are participating in more kinds of surveying in more kinds of midwestern sites, and when conservation programs incorporate the messages in these datasets.

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