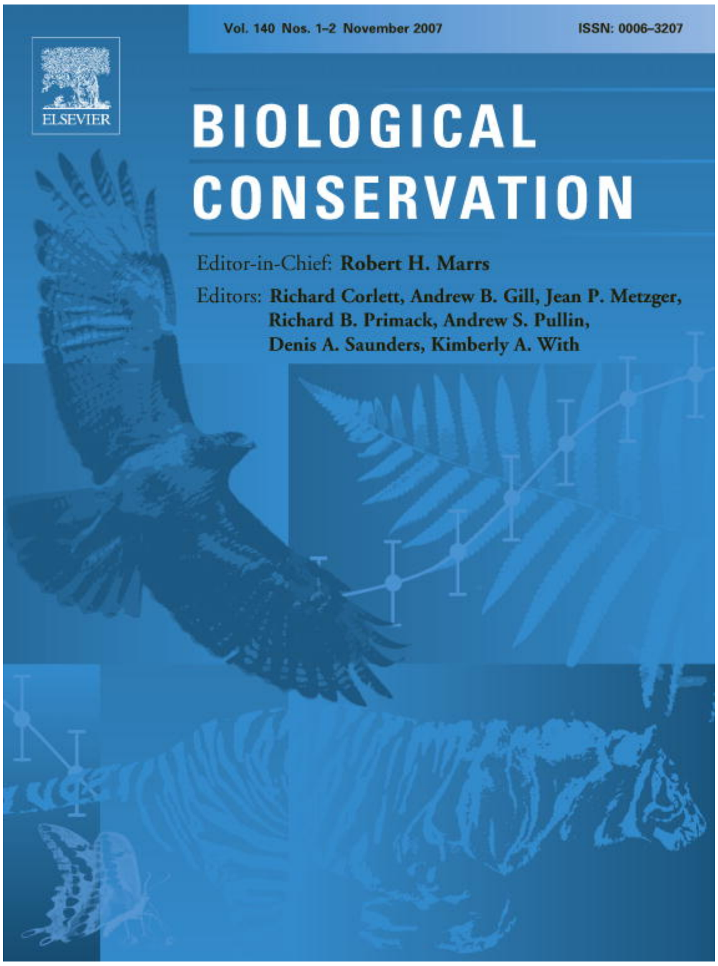
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Butterfly responses to prairie restoration through fire and grazing

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ABSTRACT

The development of land for modern agriculture has resulted in losses of native prairie habitat. The small, isolated patches of prairie habitat that remain are threatened by fire suppression, overgrazing, and invasion by non-native species. We evaluated the effects of three restoration practices (grazing only, burning only, and burning and grazing) on the vegetation characteristics and butterfly communities of remnant prairies. Total butterfly abundance was highest on prairies that were managed with burning and grazing and lowest on those that were only burned. Butterfly species richness did not differ among any of the restoration practices. Butterfly species diversity was highest on sites that were only burned. Responses of individual butterfly species to restoration practices were highly variable. In the best predictive regression model, total butterfly abundance was negatively associated with the percent cover of bare ground and positively associated with the percent cover of forbs. Canonical correspondence analysis revealed that sites with burned only and grazed only practices could be separated based on their butterfly community composition. Butterfly communities in each of the three restoration practices are equally species rich but different practices yield compositionally different butterfly communities. Because of this variation in butterfly species responses to different restoration practices, there is no single practice that will benefit all species or even all species within habitat-specialist or habitat-generalist habitat guilds.

1. Introduction

Destruction of habitat is the most prevalent threat to butterfly and insect populations around the world (New et al., 1995). Habitat losses across the globe have resulted from the conversion of land for agriculture and development (Saunders et al., 1991; Stoner and Joern, 2004). Grassland ecosystems are especially vulnerable to losses from agricultural development and, in fact, the tallgrass prairie region of North America is one of the most endangered ecosystems on Earth (Smith, 1981; Noss et al., 1995). Given these extensive losses of habitat, the preservation of remaining habitat is of great concern. Overall conservation strategies should not only include preservation of existing habitat but also habitat restoration (Jordan, 1997).

In addition to habitat loss, grassland ecosystems have been degraded by the disruption of their natural disturbance regimes. Studies of butterflies and insects from different regions of the globe have indicated that populations respond differently to disturbances and that many species have different habitat requirements at each life stage (New et al., 1995;

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Samways, 2007). In North American grasslands, as in grasslands around the world, methods used to restore habitats have included reintroducing natural disturbances such as fire and grazing.

The effects of grazing on butterflies may be moderated by the effects of grazing on their host plants. Long term studies of the skipper *Hesperia comma* in the UK have illustrated how grazing influences their grass host plant, *Festuca ovina* (Thomas et al., 1986; New, 1997). Over time, reduced grazing led to taller host plants and reduced oviposition site suitability for the species. A more recent reintroduction of grazing in the area has returned many areas to suitable habitat for *H. comma* (Thomas et al., 1986; New, 1997). Another European grassland butterfly, *Lysandra bellargus*, had larger populations on sites where grazing kept vegetation height between 1 cm and 4 cm (Thomas, 1983). In contrast, studies of many other European grassland butterflies have indicated that species richness tends to be higher where vegetation is taller from reduced disturbance intensity (Ockinger et al., 2006; Poyry et al., 2006). For one threatened butterfly in Belgium, the bog fritillary (*Procossiana eunomia*), grazing decreased butterfly populations by an estimated 74% compared to un-grazed sites (Schtickzelle et al., 2007). Differences in microclimate requirements in conjunction with the relatively small sizes of remaining habitat patches have led to the implementation of single species management in order to preserve rare insects and butterflies.

Large grazing mammals were present throughout the evolutionary history of North American prairies and are an important component of the ecosystem (Mutel, 1989). Grazing can increase plant species diversity when used in a moderate grazing regime (Soleki and Toney, 1986). Intensive grazing could have negative effects on sensitive invertebrate species (Moffat and McPhillips, 1993; Swengel and Swengel, 1999) and many prairies have likely been destroyed or degraded by improper grazing regimes (Williams, 1997).

Fire is an important component of many ecosystems around the world (Sauer, 1950; Huntzinger, 2003; Fleishman, 2000; Vieira et al., 1996) and of grassland ecosystems in particular (Collins and Gibson, 1990; Schultz and Crone, 1998). Following a period of suppression, fire has increasingly been used as a management tool for restoring native habitats (Panzer and Schwartz, 2000; Huntzinger, 2003; Hobbs and Atkins, 1990). However, some researchers have expressed concern about the response of insect species to prescribed fire in small, isolated remnants (Dana, 1991; Swengel, 1996; Panzer, 2002; Samways, 2007). Local populations of insects on fragmented preserves may not survive repeated prescribed burns (Panzer, 2002).

In the state of Iowa, USA, less than 0.01% of the original 12 million hectares of prairie remains (Sampson and Knopf, 1994). As a result, the landscape is highly fragmented with small, isolated remnants surrounded by a matrix of agricultural lands. The negative consequences of habitat fragmentation on plants and animals are numerous and have been studied extensively (e.g., Kruess and Tscharntke, 1994; Quinn, 2004; Wilsey et al., 2005; Benedick et al., 2006; Cagnolo et al., 2006). Because smaller fragments have a higher edge-to-area ratio than larger fragments (Webb, 1989; Kiviniemi and Eriksson, 2002; Benedick et al., 2006), they are more susceptible to invasion by non-native species (e.g., Kiviniemi and Eriksson, 2002; Hansen and Clevenger, 2005). In fact, invasive species such as leafy spurge (*Euphorbia esula*) and smooth brome (*Bromus inermis*) are a major threat to biodiversity in the remaining prairies of North America (Fellows and Newton, 1999; Vinton and Goergen, 2006).

The Loess Hills of western Iowa contain some the state's largest unplowed native prairies. This unique landform is composed of fine soil particles, or loess, deposited by wind that has blown over glacial melt-water silt from the Missouri River bottoms (Mutel, 1989). Many of the remaining prairies in the Loess Hills have historically been used as pastures and hay meadows (Mutel, 1989). Remnant prairies in the Loess Hills area are home to almost 100 species of butterflies (Orwig, 1990), including some rare and endangered species. The diversity of butterflies in the state of Iowa has been declining because of habitat destruction and alteration (Schlicht and Orwig, 1998). The invertebrate communities of tallgrass prairies make up a large component of the total biodiversity in the ecosystem and their survival is an important issue for conservation (Dietrich, 1998; Schlicht and Orwig, 1998).

The questions addressed in this study are:

1. How do grazing and burning restoration practices affect butterfly species richness and abundance on prairie remnants managed for biological diversity?
2. Are there distinct butterfly communities associated with burned only, grazed only, or burned and grazed restoration practices?
3. How has the vegetation responded to prescribed restoration practices and how have butterflies responded to the vegetation?

2. Methods

2.1. Study area

We conducted butterfly surveys on prairie remnants located in Plymouth County, Iowa, USA at the northern end of the Loess Hills Landform (Fig. 1). Specifically, survey sites were located on Broken Kettle Grasslands Preserve (more than 1800 ha, owned and managed by The Nature Conservancy), Five Ridge Prairie (approximately 320 ha, owned and managed by the Plymouth County Conservation Board), and on adjacent private land.

We surveyed a total of 69 sites located within 28 management units. The study area was divided into units based on the restoration practices (burned only, grazed only, or burned and grazed) they received. Management units ranged in size from approximately 10 to over 100 ha, with an average size of 40 ha (Appendix A). Burned units were managed with prescribed fires conducted during the fall and spring in 2–6 year rotations (Appendix A). Prescribed burns conducted within a management unit were designed to burn the entire area within that unit. The limited number of burned only units available ($n = 10$) restricted our ability to further divide units into categories by season or frequency of burn. Grazed units received light rotational grazing by domestic cattle with stocking rates of approximately one cow–calf pair (one Animal

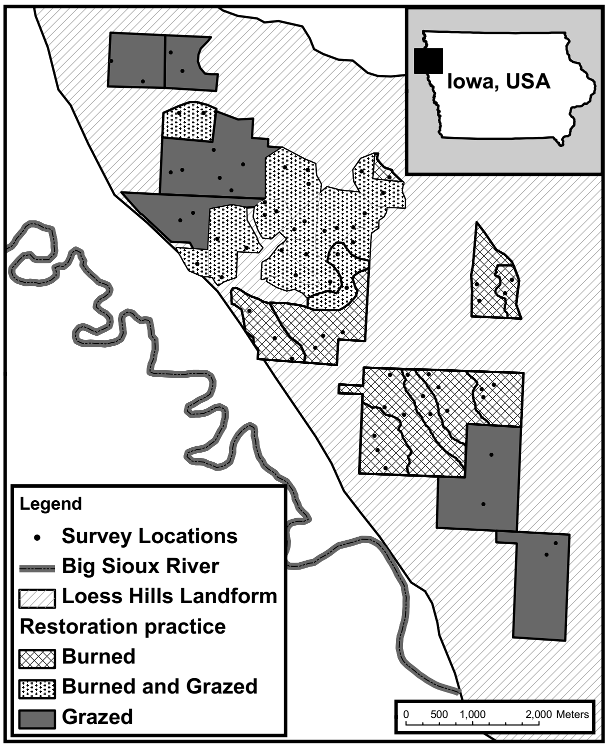

Fig. 1 – Map of study sites with restoration practices, management unit boundaries, and butterfly survey locations. All sites are located in Plymouth County, IA, USA. Study sites include Broken Kettle Grasslands Preserve, Five Ridge Prairie, and privately owned land.

Unit) per four ha (Scott Moats, Director of Stewardship, Iowa Chapter of The Nature Conservancy, personal communication). Grazing in this system is used as an ecological management tool and grazing intensity was much lighter than in a system where grazing is primarily for economic gain. Present restoration practices have been in place at the study area for a minimum of 4 years. We placed survey sites randomly with the restrictions that they were at least 150 m apart and at least 50 m from any unit edge or woody edge. We established at least two survey plots in most of the management units. However, for some management units, size prevented the placement of more than one survey site using the above restrictions. Using the above sampling design, there were 16 survey sites in six grazed only units, 26 survey sites in 10 burned only units, and 27 survey sites in 12 burned and grazed units for a total sample size of 28 management units (Fig. 1).

2.2. *Butterfly surveys*

We conducted two rounds of butterfly surveys each year between 1 June and 15 August of 2004 and 2005. We conducted surveys on warm (21–35 °C), sunny (less than 50% cloud cover), and calm (winds less than 16 km/h) days between 10:00 h and 18:30 h. We recorded weather conditions (temperature, cloud cover, and wind speed) and time of day prior to beginning a survey. We surveyed butterflies in 50 m × 50 m plots at each survey site. Surveys consisted of two observers walking through a plot in a zig-zag pattern while netting individuals observed for 30 min (e.g., Debinski and Brussard, 1994). We placed netted butterflies in glassine envelopes to avoid double counting of individuals. At the end of the survey, we recorded data for each individual, including the species name, activity at the time of capture, and sex (if known). We released all butterflies at the completion of the survey unless their identity could not be confirmed. Unidentified individuals were collected as voucher specimens to be identified in the lab and are housed in D.M. Debinski's laboratory at Iowa State University, Ames, IA, USA.

2.3. *Vegetation and floral resource surveys*

We measured the vegetation at each survey site twice each year in June and July of 2004 and 2005. Variables included vegetation height, litter depth, percent cover of warm season grasses, percent cover of cool season grasses, percent cover of native forbs, percent cover of exotic forbs, percent shrub cover, percent cover of litter, and percent cover of bare ground. Most of the cool season grasses in the study area were one of two exotic species, smooth brome (*B. inermis*) and Kentucky bluegrass (*Poa pratensis*). All of the warm season grasses in the study area were native species. The most commonly occurring warm season grasses included big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schisachyrium scoparium*), and side oats grama (*Bouteloua curtipendula*). We measured vegetation height in dm using a Robel pole and a modified version of the Robel method (Robel et al., 1970) at 5 m and 25 m from the center of the 50 m × 50 m plot in each cardinal direction. Similarly, we measured litter depth in mm using a ruler at 5 m and 25m from the center of the plot in each cardinal direction. We measured the percent cover variables by placing a 0.5 m × 0.5 m Daubenmire frame (Daubenmire, 1959) on the ground at locations 5 m and 25 m away from the center of the plot in each cardinal direction. We determined the percent cover of each vegetation type visually within the sampling frame. For all of the vegetation variables, we averaged the measurements taken at each of the 8 locations within a plot for each survey site.

Immediately following each butterfly survey, we conducted a floral resource survey on each plot to assess the availability of floral resources. One observer walked a one-half meter wide transect diagonally across the survey plot counting the number of flowering ramets of all nectar species within the transect.

2.4. *Data analysis*

We categorized butterflies into three habitat guilds (habitat-specialists, habitat-generalists, and woodland species) based on their requirements for host plant and floral resources (Appendix B). We considered a species to be a habitat-specialist if it relies on a native prairie plant species for either its larval food or adult nectar resources. As a result, habitat-specialist species are found primarily in high quality prairie habitat. We considered a species to be a habitat-generalist if it did not require a native prairie plant species for either its larval food or adult nectar resources. As a result of this categorization, species we considered to be habitat-generalists use a variety of common plant species (both non-prairie natives and non-natives). Habitat-generalist species are found in a wide variety of open habitats including yards, roadsides, and disturbed areas. Butterfly species that we categorized as woodland species utilize woodland plant species for their host and floral resources. Habitat-specialist species correspond to the "habitat-sensitive" category and habitat-generalist species correspond to the "disturbance-tolerant" category of Ries et al. (2001) and Reeder et al. (2005). Previous uses of the term "disturbance-tolerant" referred to disturbances such as removal of native habitat. We changed the terminology here to prevent misinterpretation of the word "disturbance." Only species in the habitat-specialist and habitat-generalist guilds were included in the analyses.

We compared butterfly species richness, abundance, and diversity (Shannon Diversity Index) among the three restoration practices (burned only, grazed only, and burned and grazed) using Analysis of Variance (ANOVA) in SAS v8.2 (SAS Institute, 1999). For each of these three response variables, we tested a model that included restoration practice as a fixed effect and community type (habitat-specialist vs. habitat-generalist) as a repeated measurement at each site. We also included a term in the model to test for an interaction between restoration practice and community type. Butterfly data were summed over the two rounds for each survey site, averaged for sites within each management unit, and averaged over the 2 years creating an overall average for each management unit ($N = 28$). Abundance data were log transformed when necessary to improve the normality of their distributions. For species that had a total abundance of greater than 50 individuals summed across all sites over both years and were present on at least 40% of all sites, ANOVAs were conducted to test for differences in their abundance among the three restoration practices. Pairwise comparisons were made between practices using Tukey–Kramer adjustments for multiple testing.

To determine whether local vegetation characteristics differed among the restoration practices, we performed ANOVAs for each of the measured vegetation variables. Pairwise comparisons were made between practices using Tukey–Kramer adjustments for multiple testing. Percent cover vegetation variables were arcsin transformed prior to analyses. All local vegetation variables were entered into stepwise linear regressions to determine which of them were important in explaining butterfly species richness and abundance on our sites. A significance level of 0.05 was required to enter into any vegetation model. Models were formed for each of the butterfly community response variables (abundance, species richness, and species diversity). For the most abundant butterfly species, individual species responses to local vegetation characteristics were examined using linear regressions of the mean abundance of each species with the environmental variables.

We used canonical correspondence analysis (CCA) to assess the differences in butterfly species composition among sites and to examine the relationships among the environmental variables and both butterfly species composition and restoration practice (R Development Core Team, 2004). Differences in community composition are represented as the physical distance in two dimensions (CCA1 and CCA2) of each site with respect to the others on the plot. Sites that are near one another have more similar butterfly species compositions than sites that are more distant. The analysis is constrained by environmental variables measured for each site which are indicated with arrows that represent the direction and strength (length of arrow) of their correlations. Prior to analysis, rare species (<10 individuals observed across all sites in both years) were eliminated from the dataset.

We performed a forward stepwise discriminant analysis to determine whether the sites could be classified into a particular restoration practice based on their species composition. Rare species (<10 individuals) were removed prior to analysis. Discriminant analyses were performed using JMP v5.1 (SAS Institute, 2002). Analyses were conducted first using all three restoration practices and then using just the burned only and the grazed only practices.

3. Results

Nearly 4000 individuals of 51 different butterfly species were observed during our surveys in 2004 and 2005. Of the 51 species, 28 were habitat-generalists, 16 were habitat-specialists, and 7 were woodland species (Appendix B). Two habitat-specialist butterfly species, *Speyeria idalia* and *Cercyonis pegala*, and one habitat-generalist species, *Colias eurytheme*, were the most abundant species encountered, making up over 50% of the individuals observed. Three species encountered in the study area (*S. idalia*, *Hesperia ottoe*, and *Atrytonopsis hianna*) are species of conservation concern in the Iowa Department of Natural Resources Draft Conservation Plan (IDNR, 2005).

3.1. *Butterfly responses to restoration practice*

Butterfly abundance differed among the three restoration practices ($F = 8.07$, d.f. = 2, 25, $P = 0.003$, Table 1). The highest mean butterfly abundance occurred in the burned and grazed restoration practice and the lowest in the burned only practice (Table 1). Butterfly species richness did not differ among the three restoration practices ($F = 1.51$, d.f. = 2, 25, $P = 0.226$; Table 1). Butterfly diversity was highest in the burned only restoration practice but did not differ between the grazed only and burned and grazed practices ($F = 7.16$, d.f. = 2, 25, $P = 0.004$; Table 1). Because the P-values for restoration practice by community interactions were greater than 0.05 in all of the above analyses, we did not analyze the habitat-specialist community separately from the habitat-generalist community.

For individual butterfly species, most habitat-generalists did not differ in mean abundance or number of butterflies per hectare among the restoration practices (Table 2). However, the mean abundance of *Danaus plexippus* in the grazed only restoration practice was more than twice the abundance in the burned only practice. In addition, *Colias eurytheme* was less than half as abundant in the burned only restoration practice than in burned and grazed practice. Also, *C. eurytheme* abundance in the burned only practice was less than one third as high as in grazed only.

Table 1 – Three butterfly community response variables, total butterfly abundance (abundance), total butterfly species richness (species richness), and Shannon Diversity (diversity), tested using ANOVA for differences among the three restoration practices (d.f. = 2, 25)

Butterfly response	Burned		Grazed		Burned and Grazed		F	P
	Mean	SD	Mean	SD	Mean	SD		
Abundance	20.17	6.28a	27.78	5.67ab	31.48	7.25b	7.65	0.003
Species richness	8.64	1.48	7.44	1.78	8.53	1.19	1.44	0.256
Diversity	2.34	0.22a	1.93	0.31b	2.00	0.32b	0.04	0.004

Different letters following means indicate $P < 0.05$ for Tukey–Kramer adjusted pairwise comparisons.

Table 2 – Total number of individuals summed across both years (*n*), average number of butterflies per hectare (*n*/ha) and mean number of butterflies per unit (mean) for 2004 and 2005 occurring in burned, grazed, and burned and grazed restoration practices

Species name	Common name	Burned			Grazed			Burned and Grazed			Total	
		n/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*	P
Habitat-generalist												
Family Pieridae												
Colias eurytheme	Orange Sulfur	19.20	96	4.80a	64.00	192	16.00b	45.32	272	11.33b	560	0.001
Pieris rapae	Cabbage White	4.40	22	1.10	8.00	24	2.00	10.68	64	2.67	110	0.406
Family Nymphalidae												
Danaus plexippus	Monarch	3.60	18	0.90a	9.00	27	2.25b	4.68	28	1.17ab	73	0.015
Megisto cymela	Little Wood Satyr	8.60	43	2.15	11.00	33	2.75	19.00	114	4.75	190	0.361
Vanessa atalanta	Red Admiral	4.00	20	1.00	2.00	6	0.50	4.00	24	1.00	50	0.593
Euptoieta claudia	Variegated Fritillary	19.80	99	4.95	19.68	59	4.92	8.16	49	2.04	207	0.362
Family Lycaenidae												
Strymon melinus	Gray Hairstreak	13.00	65	3.25	11.32	34	2.83	3.68	22	0.92	121	0.104
Everes comyntas	Eastern Tailed Blue	12.60	63	3.15	7.68	23	1.92	8.00	48	2.00	134	0.528
Echinargus isola	Reakirt's Blue	6.40	32	1.60	2.32	7	0.58	4.16	25	1.04	64	0.574
Family Hesperiidae												
Polites themistocles	Tawny-edged Skipper	5.00	25	1.25	3.00	9	0.75	3.00	18	0.75	52	0.547
Habitat-specialist												
Family Nymphalidae												
Cercyonis pegala	Common Wood Nymph	38.20	191	9.55a	99.68	299	24.92b	83.00	498	20.75b	988	0.021
Speyeria cybele	Great Spangled Fritillary	6.60	33	1.65a	3.32	10	0.83ab	1.32	8	0.33b	51	0.029
Speyeria idalia	Regal Fritillary[a]	22.00	110	5.50a	50.00	150	12.50ab	47.84	287	11.96b	547	0.039
Family Hesperiidae												
Hesperia ottoe	Ottoe Skipper[a]	15.60	78	3.90a	0.68	2	0.17b	2.16	13	0.54b	93	0.002

P-values are given for ANOVA tests for differences among restoration practices for butterfly species (d.f. = 2, 25). Only species with a total abundance of at least 50 individuals and were present on at least 40% of sites are listed. A complete species list is located in Appendix B. Butterflies are separated into habitat-specialist and habitat-generalist habitat guilds based on their habitat requirements for food and host plants.

a Denotes Species of Conservation Concern, Iowa DNR Draft Comprehensive Plan. Different letters following means indicate $P < 0.05$ for Tukey–Kramer adjusted pairwise comparisons.

For habitat-specialists, the responses of individual species were mixed. *C. pegala* was less than half as abundant in the burned only restoration practice than in grazed only or burned and grazed. The abundance of *S. idalia* in the burned only practice was half that of burned and grazed or grazed only. In contrast, the abundance of *Speyeria cybele* was five times higher in the burned only restoration practice than in the burned and grazed practice. *Hesperia ottoe* was more abundant in the burned only practice than in grazed only. We found more than 20 times more individuals of *H. ottoe* in the burned only restoration practice than in grazed only.

3.2. *Vegetation responses to restoration practice*

The vegetation variables we measured had mixed responses with respect to the restoration practices (Table 3). The burned only practice had higher percent cover of both warm season grasses and bare ground and lower percent cover of cool season grasses and lower litter depth and than either of the other two restoration practices (Table 3). The grazed only restoration practice had a higher percent cover of litter than did the burned only or burned and grazed practices (Table 3). The percent cover of all forbs was lower in the burned only

Table 3 – Environmental variables tested using ANOVA for differences among the three restoration practices (d.f. = 2, 25)

Environmental variable	Burned		Grazed		Burned&Grazed		P
	Mean	SD	Mean	SD	Mean	SD	
Floral resources (# flowering ramets)	9.55	5.30	23.31	16.09	14.32	9.32	0.190
Vegetation height (dm)	2.67	2.15	2.13	0.77	2.55	0.62	0.561
Litter depth (mm)	11.79	7.19a	21.49	7.81b	19.41	4.71b	0.003
Warm season grasses (%)	41.55	6.26a	16.88	10.61b	25.26	11.88b	0.001
Cool season grasses (%)	1.98	2.07a	26.27	9.89b	25.76	11.98b	<0.001
Forb cover (%)	12.69	4.21a	23.18	7.89b	23.01	10.39b	0.008
Native forb (%)	12.13	4.00	10.89	6.45	7.92	4.53	0.133
Exotic forb (%)	0.56	0.95a	12.29	7.10b	15.09	12.45b	<0.001
Shrub (%)	7.05	5.11	2.69	1.48	3.95	3.32	0.064
Litter (%)	15.68	5.08a	25.01	7.35b	17.86	4.83ab	0.013
Bare ground (%)	20.49	10.19a	5.97	5.33b	4.37	3.47b	<0.001

Different letters following means indicate $P < 0.05$ for Tukey–Kramer adjusted pairwise comparisons.

restoration practice than in either of the other two restoration practices. This reduced cover of forbs in the burned only restoration practice was driven by exotic forb cover, which was lower in the burned only practice than in the other two restoration practices (Table 3).

3.3. *Butterfly responses to vegetation*

The abundance of three habitat-generalist butterfly species, *C. eurytheme*, *D. plexippus*, and *Euptoieta claudia*, was positively correlated with floral resources (Table 4). Three species, *H. ottoe*, *Strymon melinus*, and *E. claudia*, had negative associations with litter depth while *S. idalia* and *C. pegala* had positive ones. Total forb cover was positively correlated with just one habitat-generalist species (*C. eurytheme*), but it was negatively correlated with one habitat-specialist species (*H. ottoe*). Species relationships with the percent cover of bare ground were also mixed, two species (*H. ottoe* and *S. melinus*) had positive associations and three species (*C. pegala*, *C. eurytheme*, and *S. idalia*) had negative ones. In addition, warm season grasses and cool season grasses had both positive and negative associations with butterfly species. Species that had positive correlations with cool season grasses (*C. pegala*, *C. eurytheme*, and *D. plexippus*) had negative correlations with warm season grasses and the species (*H. ottoe*) that had a negative correlation with cool season grasses had a positive correlation with warm season grasses. No species had a relationship, positive or negative, with vegetation height.

For butterfly abundance, the best predictive model included the vegetation variables of percent cover of bare ground and percent forb cover (Table 5). In this model, total butterfly abundance was negatively associated with bare ground and was positively associated with forb cover. Neither species richness nor diversity had vegetation variables that met the criteria for entry into the model (Table 5).

3.4. *Butterfly community composition*

Butterfly community composition separated sites according to their restoration practices, especially between burned only and grazed only sites (Fig. 2). In contrast, there was little separation between grazed only and burned and grazed sites

Table 4 – Butterfly species responses to environmental variables

Butterfly species	Habitat guild	Floral	VH	LD	WS	CS	Forb	S	L	BG
Cercyonis pegala	hs		+	+**	–	+*	+	–	+	–***
Hesperia ottoe	hs			–*	+**	–*	–		–	+*
Speyeria idalia	hs	+	+	+*		+	+		+	–*
Colias eurytheme	hg	+*		+	–*	+***	+	–	+	–
Danaus plexippus	hg	+	–		–	+	+	–	+	–
Euptoieta claudia	hg	+*	–	–		–	–			+
Everes comyntas	hg	+		–	+		–	+	–	+
Megisto cymela	hg				+	+	–			–
Pieris rapae	hg			+		+	–		+	–
Strymon melinus	hg	+	–	–	+	–	–	+		+

Correlations of mean butterfly responses with environmental variables. Environmental variables listed are Floral Resources (Floral), Vegetation Height (VH), Litter Depth (LD), Percent Warm Season Grasses (WS), Percent Cool Season Grasses (CS), Percent Forb Cover (Forb), Percent Shrub (S), Percent Litter (L), and Percent Bare Ground (BG). Butterfly habitat guilds are either Habitat-specialist (hs) or Habitat-generalist (hg). Plus and minus signs indicate whether the relationship is positive or negative. Correlations with *R*-square values of <.01 are not reported. Tests were Bonferroni corrected for multiple testing within a species.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 5 – Stepwise linear regression on butterfly response variables with environmental variables measured at each site

Butterfly community response	Variables in model	+ or –	Model R^2
Abundance	Percent bare ground	–	0.49[a]
	Percent forb cover	+	
Species richness	No variables met criteria for entry		
Diversity	No variables met criteria for entry		

Variables required a significance level of <0.05 to enter into the models.
a $P < 0.05$.

(Fig. 2a). The percent variation explained by the first two axes (CCA 1 and CCA2) was 26.1%. When just the burned only and grazed only practices are examined, the CCA ordination plot of site scores shows distinct separation of the two restoration practices (Fig. 2b) and the percent variation explained by the first two axes was 36.1%.

Vegetation variables that were positively correlated with burned sites include percent cover of warm season grasses and bare ground (Fig. 2b). Vegetation components positively associated with grazed sites include percent cover of cool season grasses, forb cover, litter cover, and floral resources (Fig. 2b). Vegetation height did not show correlations with either restoration practice.

Our analyses revealed that some butterfly species were more correlated with sites from a particular restoration practice (Fig. 2c). When the locations of CCA species scores are plotted in the ordination space, the location of each species on the plot indicates its association with particular sites based on its proximity to them on the plot. Several species appear to be more strongly associated with the burned only sites including *Satyrium titus*, *H. ottoe*, *Celastrina ladon*, *Celastrina neglecta*, *Atalopedes campestris*, and *Polites mystic* (Fig. 2c). In addition, several species including *Lycaena dione*, *C. eurytheme*, *Papilio polyxenes*, *D. plexippus*, *Phyciodes tharos*, and *Polites peckius* appear to be associated with sites in the grazed only restoration practice. Most species do not appear to be more closely associated with sites in a particular restoration practice and appear clustered in the center of the plot (Fig. 2b). Habitat-specialist butterfly species were not more closely associated with sites in either restoration practice (Fig. 2d).

Discriminant analysis revealed that the abundance of a small number of butterfly species on each site can differentiate the sites into the correct restoration practice. When all three restoration practices were examined, sites were separated with 96% accuracy (1 site misclassified) using just ten species (Table 6). Looking at sites in just the burned only and grazed only practices, with five species, the misclassification rate was 0%; all sites were correctly classified (Table 7).

4. Discussion

Some researchers have found the practice of burning tallgrass prairie to be detrimental to butterfly communities. For example, Swengel (1998a) found that there were fewer habitat-specialist butterflies in burned areas than in grazed areas and that the combined effects of burning and other management practices were varied. Our analyses indicate butterfly abundance was lowest in the burned only restoration practice. However, we found that butterfly diversity was highest on these burned only sites. Similarly, researchers in a forested system of the western United States found butterfly diversity in burned sites was twice as high as in control sites (Huntzinger, 2003).

We did not find differences in the number of species that each restoration practice supported. In one study, Fleishman (2000) also reported no difference in species richness of butterflies between burned and unburned sites in central Nevada, USA. However, our finding does not suggest that the butterfly communities found at sites with different restoration practices were homogeneous; rather the CCA and discriminant analyses suggested that the composition of butterfly communities differed relative to the type of restoration practice received, especially between the burned only and grazed only restoration practices. These results are consistent with the idea that different restoration practices tend to favor some species and not others even within the same habitat guild.

Our vegetation models indicated that in terms of overall abundance, butterflies responded positively to the presence of forbs. This is not surprising since most prairie butterfly adults take nectar from a variety of native and non-native forb species. In addition, many species require forbs as their caterpillar host plants. Our models also showed that total butterfly abundance was negatively related to the percent cover of bare ground. The percent cover of bare ground was more than three times higher on burned only sites than on sites that were grazed or grazed and burned. The bare ground parameter in this model reiterated our finding that butterfly abundance was lowest in the burned only restoration practice. Because species richness and diversity did not have any parameters that met the requirements for entry into the models, we did not gain specific insights into their relationships with the vegetation variables we measured.

We found that total butterfly abundance was negatively associated with the percent cover of bare ground, however, the associations of individual species with bare ground were mixed. In a study of the western jewel butterfly (*Hypochrysops halyaetus*) on bushland sites outside of Perth, Australia, males and females within the same species responded differently to the presence of bare ground (Dover and Rowlingson, 2005). Males were positively associated with the amount of bare ground whereas females were not (Dover and Rowlingson, 2005). A high proportion of bare ground potentially increased the ability of males to find mates while sitting on perches where vegetation is sparse (Dover and Rowlingson, 2005). Increased ability to find mates in areas with a high proportion of bare ground may be a possible explanation for the positive relationship between *H. ottoe* and bare ground. Males of this species spend much of the flight period perched on *Echinacea* flowers searching for mates (Dana, 1991).

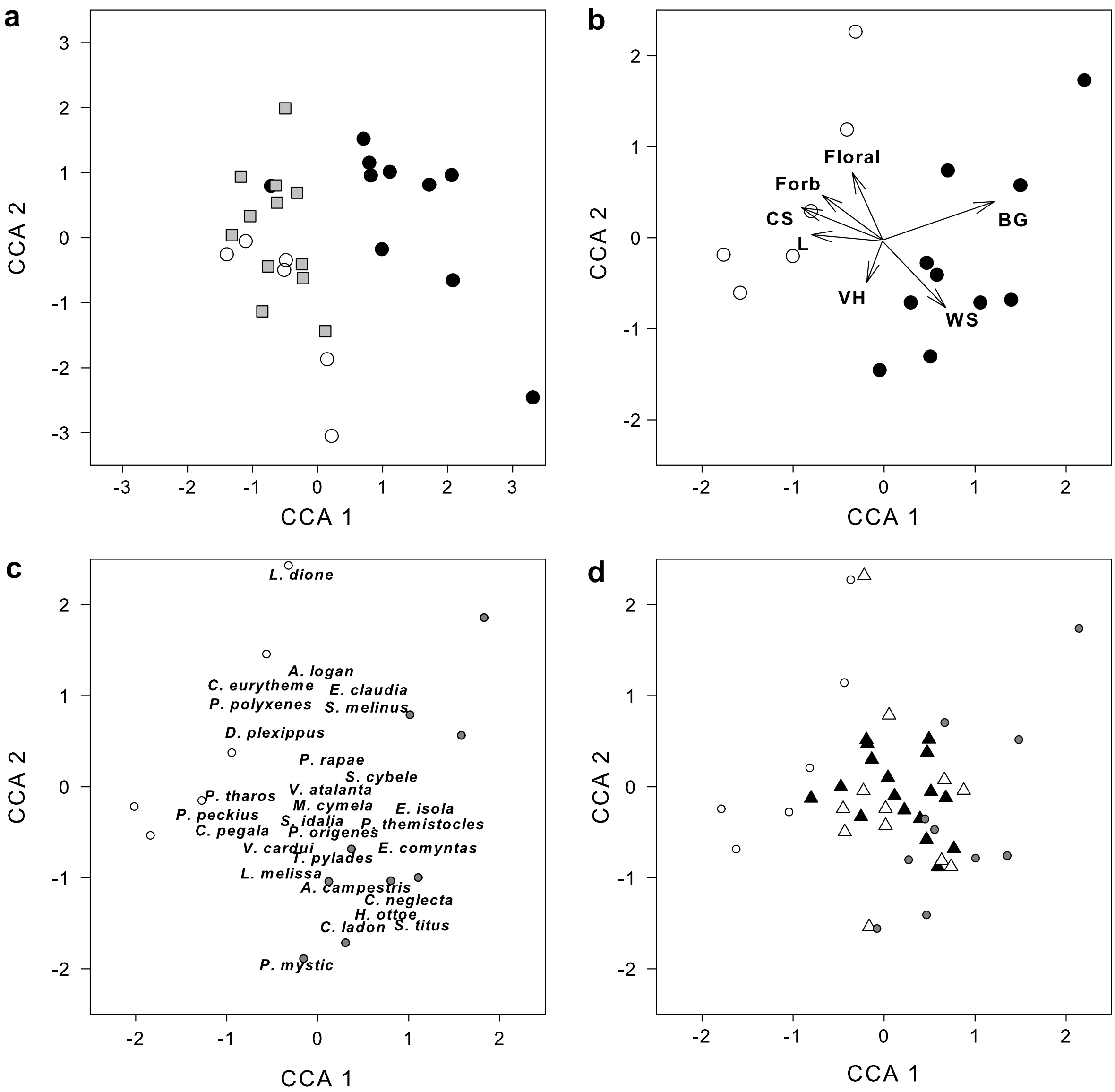

Fig. 2 – Canonical correspondence analysis ordination plots of butterfly community site scores (a, b) and butterfly species scores (c, d). (a) Locations of site scores for all three restoration practices. Burned sites are indicated with solid circles (●), grazed sites with open circles (○), and burned and grazed with shaded squares (▢). (b) Site scores for burned sites and grazed sites only. Burned sites are shown as solid circles (●) and grazed sites are shown as open circles (○). Environmental variables are indicated with arrows that represent the direction and strength (length of arrow) of their correlation with the ordination plot (loadings on each axis). Environmental variables shown are number of flowering ramets (Floral), Vegetation Height (VH), Warm Season Grasses (WS), Cool Season Grasses (CS), Forb Cover (Forb), Litter (L), and Bare Ground (BG). (c) Locations of butterfly species scores. Species names are abbreviated with the first letter of the genus and the specific epithet. Burned sites are shown as small shaded circles (●) and grazed sites are shown as small open circles (○). (d) Locations of butterfly species scores showing habitat-specialist species as open triangles (△) and habitat-generalist species as solid triangles (▲). Burned sites are shown as small shaded circles (●) and grazed sites are shown as small open circles (○).

Although we found no relationship between butterflies and vegetation height in our study, others have reported significant positive associations with the height and vertical density of vegetation (Reeder et al., 2005). In their study of butterflies in filter strips in Minnesota, USA, Reeder et al. (2005) found two habitat-specialist species (*S. idalia* and *C. pegala*) had positive relationships with the height and vertical density of vegetation. Although they proposed that these species may need tall vegetation to provide adequate shelter and habitat structure, we did not find this relationship in our study. The differences in our findings may be a result of differences in the variation of vegetation height between the two studies. Our study had much lower mean vegetation heights than did Reeder et al. (2005).

Previous research suggests that butterfly responses to different restoration practices can be highly variable and no one restoration practice has been found to be optimal for all species within a habitat type (Schlicht and Orwig, 1990; Swengel,

Table 6 – Results of forward stepwise discriminant analysis on all three restoration practices (burned only, grazed only, and burned and grazed)

Order of selection	Species name	Misclassification rate (%)
1	*Danaus plexippus*	54
2	*Hesperia ottoe*	29
3	*Speyeria cybele*	21
4	*Cercyonis pegala*	18
5	*Lycaeides melissa*	14
6	*Vanessa cardui*	7
7	*Polites themistocles*	4
8	*Megisto cymela*	4
9	*Polites peckius*	7
10	*Papilio polyxenes*	4

Butterfly species with abundance of less than 10 individuals across all sites were excluded from the analysis. Butterfly species are listed in the order they were selected. Using all 10 species listed, one site was misclassified.

Table 7 – Results of forward stepwise discriminant analysis on burned only and grazed only restoration practices

Order of selection	Species name	Misclassification rate (%)
1	*Danaus plexippus*	13
2	*Echinargus isola*	13
3	*Celastrina neglecta*	6
4	*Vanessa cardui*	6
5	*Satirium titus*	0

Butterfly species with abundance of less than 10 individuals across all sites were excluded from the analysis. Butterfly species are listed in the order they were selected. Using just five species, all sites were classified correctly.

1998b). The results of our study are consistent with this finding. Within the habitat-specialist guild, individual species responses varied. Two species (*C. pegala* and *S. idalia*) were least abundant in the burned only practice while two others (*S. cybele* and *H. ottoe*) were most abundant in the burned only practice (Table 2). Because specialist species respond to management in different ways, Swengel (1998b) has advocated the use of varied management practices in order to conserve them.

One habitat-specialist and species of conservation concern in Iowa, *S. idalia*, was less abundant in the burned only restoration practice. Although rare throughout the state of Iowa, *S. idalia* was one of the most abundant species encountered in our study area. Previous studies have also found the abundance of *S. idalia* to be lower in burned sites than in sites with alternate management regimes (Swengel, 1996; Swengel, 1998b) and that moderate grazing could potentially have a positive effect on populations due to higher host plant (*Viola pedatifida*) densities on grazed sites (Debinski and Kelly, 1998). In contrast to what we found for *S. idalia*, a similar habitat-specialist species, *S. cybele*, was most abundant in the burned only restoration practice. Although these species are similar in size, coloration, and use similar host plants, *S. cybele* is able to use additional woodland host plants (*Viola* sp.) that *S. idalia* does not use. The woodlands in our study area were not burned potentially allowing *S. cybele* larvae to survive where *S. idalia* larvae could not.

Interestingly, we found another habitat-specialist species, *H. ottoe*, to have higher abundance on sites that were only burned. In one study on *H. ottoe*, Dana (1991) discovered that when fuel levels are moderate/low, fires conducted in early spring did not cause significant larval mortality and that skipper populations assessed after an early spring burn were not lower than pre-burn levels. *H. ottoe* larvae are known to build underground buried shelters where they remain through the winter into spring, potentially increasing their ability to survive during fires (Dana, 1991). However, burns conducted at other times of the year (i.e., late spring, fall) had more significant negative impacts on *H. ottoe* larvae because they were no longer protected in buried shelters (Dana, 1991). In addition to direct mortality, indirect mortality of larvae from exposure to harsh environmental conditions can occur when the litter layer is reduced after a fire (Dana, 1991).

4.1. *Conclusions and implications for management*

Because of the great diversity in butterfly species responses to different restoration practices, we do not recommend a single type of management that would benefit all species or even all species of a particular habitat guild. We found that not all habitat-specialist butterfly species were negatively affected by burning. In addition, the effects of fire on butterflies may be affected by particular aspects of a species natural history, such as over-wintering sites or location of host plants. Managers should be aware of which butterfly species are present on a particular site and which species may be negatively affected by burning prior to implementing management. Further exploration of the habitat preferences of some habitat-specialist species may be necessary to confirm our findings.

Although we found that sites managed with both fire and grazing had the highest overall abundance of butterflies, these sites did not have a higher total number of species compared with other restoration practices. Butterfly abundance was lowest on sites that were burned only, however, butterfly diversity was greatest on these sites that were managed with fire only. Our findings indicated that the butterfly communities supported by sites managed by each of the practices we examined are supporting a different suite of butterfly species. Managers seeking to maximize the number of butterfly species could achieve this goal by using multiple types of management wherever possible to provide the different microhabitat types utilized by different butterfly assemblages.

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Appendix A – Burn history and area of Loess Hills management units

Management unit	Treatment type	Unit area (ha)	Year							
			1997	1998	1999	2000	2001	2002	2003	2004
12	B	10						X		
13	B	58				X			X	X
15	B	73				X			X	
S2	B	10				X			X	
Z	B	10					X			X
R4	B	56							X	X
JC	B	102					X			
R2	B	41					X			X
R5	B	64							X	
R3	B	62							X	X
1	B&G	44					X			
2	B&G	11					X			
3–4	B&G	60					X			
5	B&G	21		X		X		X		
6	B&G	59				X				
7	B&G	20	X	X		X		X		
8	B&G	27			X					
9	B&G	64			X		X			
10	B&G	26						X	X	X
11	B&G	31						X		
B1	B&G	63							X	
B2	B&G	20							X	
KA	G	167								
KB	G	66								
KC	G	135								
L	G	158								
SA	G	84								
SB	G	43								

For burned only (B) and burned and grazed (B&G) restoration practices, an X in the column for a particular year indicates that a prescribed burn was conducted. For grazed only management units (G), no prescribed burns were conducted in the known land history and only area is indicated for these units. Study sites include Broken Kettle Grasslands Preserve, Five Ridge Prairie, and privately owned land.

Appendix B – List of all butterfly species found in study area

Species name	Common name	Guild	Burned			Grazed			Burned&Grazed			Total
			n/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*
Family Papilinidae												
Papilio polyxenes	Black Swallowtail	G	0.80	4	0.20	2.00	6	0.50	0.52	3	0.13	13
Papilio cresphontes	Giant Swallowtail	W	2.00	10	0.50	1.68	5	0.42	0.68	4	0.17	19
Papilio glaucus	Tiger Swallowtail	W	7.80	39	1.95	5.32	16	1.33	4.00	24	1.00	87
Family Pieridae												
Colias eurytheme	Orange Sulfur	G	19.20	96	4.80	64.00	192	16.00	45.32	272	11.33	560
Colias philodice	Clouded Sulfur	G	0.40	2	0.10	0.32	1	0.08	0.16	1	0.04	4
Phoebis sennae	Cloudless Sulfur	G	0	0	–	0.32	1	0.08	0	0	–	1
Eurema lisa	Little Yellow	G	0.20	1	0.05	0.32	1	0.08	0	0	–	2
Pieris rapae	Cabbage White	G	4.40	22	1.10	8.00	24	2.00	10.68	64	2.67	110
Pontia protodice	Checkered White	G	0.40	2	0.10	0.68	2	0.17	0.32	2	0.08	6
Family Nymphalidae												
Danaus plexippus	Monarch	G	3.60	18	0.90	9.00	27	2.25	4.68	28	1.17	73
Megisto cymela	Little Wood Satyr	G	8.60	43	2.15	11.00	33	2.75	19.00	114	4.75	190
Cercyonis pegala	Common Wood Nymph	S	38.20	191	9.55	99.68	299	24.92	83.00	498	20.75	988
Asterocampa celtis	Hackberry Emperor	W	1.20	6	0.30	0.32	1	0.08	0	0	–	7
Limenitis archippus	Viceroy	S	0.20	1	0.05	0	0	–	0.32	2	0.08	3
Limenitis arthemis	Red-spotted Purple	W	0.60	3	0.15	0	0	–	0.32	2	0.08	5
Junonia coenia	Common Buckeye	G	0.80	4	0.20	0.32	1	0.08	0.16	1	0.04	6
Vanessa atalanta	Red Admiral	G	4.00	20	1.00	2.00	6	0.50	4.00	24	1.00	50
Vanessa cardui	Painted Lady	G	1.80	9	0.45	3.32	10	0.83	4.52	27	1.13	46
Vanessa virginiensis	American Lady	G	0.20	1	0.05	0.68	2	0.17	0.16	1	0.04	4

Appendix B – *continued*

Species name	Common name	Guild	Burned			Grazed			Burned&Grazed			Total
			n/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*
Polygonia comma	Eastern Comma	W	0.20	1	0.05	0	0	–	0	0	–	1
Chlosyne gorgone	Gorgone Checkerspot	G	0.40	2	0.10	0.68	2	0.17	0.32	2	0.08	6
Phyciodes tharos	Pearl Crescent	G	0.20	1	0.05	1.00	3	0.25	1.52	9	0.38	13
Boloria bellona	Meadow Fritillary	S	0.20	1	0.05	0	0	–	0	0	–	1
Speyeria aphrodite	Aphrodite Fritillary	S	0.20	1	0.05	0	0	–	0	0	–	1
Speyeria cybele	Great Spangled Fritillary	S	6.60	33	1.65	3.32	10	0.83	1.32	8	0.33	51
Speyeria idalia	Regal Fritillary [a]	S	22.00	110	5.50	50.00	150	12.50	47.84	287	11.96	547
Euptoieta claudia	Variegated Fritillary	G	19.80	99	4.95	19.68	59	4.92	8.16	49	2.04	207
Family Lycaenidae												
Satyrium titus	Coral Hairstreak	S	1.20	6	0.30	0	0	–	1.16	7	0.29	13
Callophrys gryneus	Olive Hairstreak	G	0.80	4	0.20	0	0	–	0	0	–	4
Strymon melinus	Gray Hairstreak	G	13.00	65	3.25	11.32	34	2.83	3.68	22	0.92	121
Lycaena hyllus	Bronze Copper	S	0	0	–	0	0	–	0.16	1	0.04	1
Lycaena dione	Gray Copper	S	0	0	–	0.32	1	0.08	1.84	11	0.46	12
Everes comyntas	Eastern Tailed Blue	G	12.60	63	3.15	7.68	23	1.92	8.00	48	2.00	134
Celastrina ladon	Spring Azure	G	1.80	9	0.45	0	0	–	0.52	3	0.13	12
Celastrina neglecta	Summer Azure	G	7.20	36	1.80	0	0	–	1.84	11	0.46	47
Lycaeides melissa	Melissa Blue	S	1.00	5	0.25	1.68	5	0.42	0.16	1	0.04	11
Echinargus isola	Reakirt's Blue	G	6.40	32	1.60	2.32	7	0.58	4.16	25	1.04	64
Family Hesperiidae												
Hesperia ottoe	Ottoe Skipper [a]	S	15.60	78	3.90	0.68	2	0.17	2.16	13	0.54	93
Polites peckius	Peck's Skipper	G	0.20	1	0.05	2.68	8	0.67	1.16	7	0.29	16
Polites mystic	Long Dash	S	0.20	1	0.05	0	0	–	1.16	7	0.29	8
Polites themistocles	Tawny-edged Skipper	G	5.00	25	1.25	3.00	9	0.75	3.00	18	0.75	52
Polites origenes	Crossline Skipper	S	1.00	5	0.25	1.84	2	0.46	0.68	11	0.17	18
Pompeius verna	Little Glassywing	W		0	–	0.32	1	0.08	0	0	–	1
Atalopedes campestris	Sachem	G	1.40	7	0.35	0.32	1	0.08	0.32	2	0.08	10
Atrytone logan	Delaware Skipper	S	1.40	7	0.35	3.32	10	0.83	1.68	11	0.42	28
Poanes hobomok	Hobomok Skipper	G	0.20	1	0.05	0	0	–	0	0	–	1
Atrytonopsis hianna	Dusted Skipper [a]	S	0.60	3	0.15	0.44	1	0.11	0.32	3	0.08	7
Lerodea eufala	Eufala Skipper	G	0	0	–	0.32	1	0.08	0.16	1	0.04	2
Thorybes pylades	Northern Cloudywing	S	1.20	6	0.30	0	0	–	1.16	7	0.29	13
Erynnis horatius	Horace's Duskywing	W	5.00	25	1.25	0	0	–	6.84	41	1.71	66
Pyrgus communis	Common-checkered Skipper	G	0.80	5	0.20	0	0	–	0.68	4	0.17	9

The total number of individuals (*n*) is summed across both years. The mean number of butterflies per unit and number of butterflies per hectare (*n*/ha) are averaged across both years. Butterflies are separated into habitat-specialist (S), habitat-generalist (G), and woodland (W) habitat guilds based on their habitat requirements for food and host plants.
a – Species of Conservation Concern Iowa DNR Draft Comprehensive Plan.

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