

BUTTERFLY COMMUNITY AND BEHAVIORAL RESPONSES TO RESTORED
DISTURBANCE REGIMES

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Butterfly Community and Behavioral Responses to Restored Disturbance
Regimes

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North Dakota State University's regulations and meets the accepted
standards for the degree of

MASTER OF SCIENCE

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ABSTRACT

Grassland organisms evolved alongside the interaction of fire and grazing, but modern management often decouples these disturbances. In order to analyze the effects of reintroducing this interaction, we implemented four treatments. Two of these treatments were variations of patch-burn grazing, one was modified rest-rotation grazing, and one was season-long grazing. We chose to monitor the butterfly response to these treatments because butterflies have short generations, require a wide variety of resources, and are easily identifiable as adults. We quantified both the butterfly community and the behavioral time budgets of two species. We found that the butterfly community is more species-rich and abundant in treatments including fire than in treatments without fire. We found no difference in time budgets between treatments. Overall, we suggest that managers implement a carefully-planned patch-burn grazing regime in order to support grassland butterflies and other organisms.

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TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
CHAPTER 1: BUTTERFLY COMMUNITIES ARE MORE DIVERSE IN GRASSLANDS WITH RESTORED DISTURBANCE REGIMES.....	1
Abstract.....	1
Introduction.....	2
Methods.....	5
Results.....	11
Discussion.....	21
References.....	24
CHAPTER 2: BEHAVIORAL TIME BUDGETS OF REGAL FRITILLARIES (<i>SPEYERIA IDALIA</i>) AND MONARCHS (<i>DANAUS PLEXIPPUS</i>).....	31
Abstract.....	31
Introduction.....	32
Methods.....	35
Results.....	39
Discussion.....	46
References.....	48

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.1. List of all butterfly species codes.....	16
1.2. Further detail on species' density models and results.....	19
2.1. Behavioral ethogram.....	36
2.2. All the combinations of behaviors and vegetation composition variables that were indicated as significant in the two ordinations (Figures 4 & 5).....	45

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1. Examples of layouts in all four treatments.	7
1.2. Butterfly total abundance and species richness compared across treatments.....	12
1.3. NMDS ordination of butterfly abundance data from 2017-2019.....	13
1.4. Density estimates for 6 species meeting a minimum of ≥ 60 detections and displaying differences between treatments.....	15
1.5. Density estimates for 11 species meeting a minimum threshold of ≥ 60 detections and displaying no differences between treatments.....	16
2.1. Mean percent time in each behavior for all monarch butterflies.....	41
2.2. Mean percent time in each behavior for regal fritillaries.....	42
2.3. Ordination plot displaying monarch behaviors and explanatory vegetation variables ($p \leq 0.1$).....	43
2.4. Ordination plot displaying regal fritillary behaviors and explanatory vegetation variables ($p \leq 0.1$).....	44

CHAPTER 1: BUTTERFLY COMMUNITIES ARE MORE DIVERSE IN GRASSLANDS WITH RESTORED DISTURBANCE REGIMES

Abstract

Grassland organisms evolved with the interaction of fire and grazing. However, recent management often decouples these disturbances. Such changes can lead to woody encroachment, invasive species expansion, and homogenization of the landscape. Since grassland organisms are adapted to the interaction of fire and grazing, conservation plans for these species may benefit from the reintroduction of this interaction. We conducted a study in the northern Great Plains of North America to determine the influence of restoring fire and grazing to mixed-grass prairie on the butterfly community. Specifically, we used line-transect distance sampling to quantify butterfly species richness, abundance, and community composition across four cattle management treatments. Our four treatments included two variations of patch-burn grazing—a management framework in which a portion of the landscape is burned each year and cattle are allowed to select from burned and unburned areas for grazing, season long grazing without fire, and modified twice-over rotational grazing with no fire. We found that both species richness and abundance were higher in the two patch-burn grazing treatments than in the grazing without fire treatments. Communities across the four treatments overlapped marginally, with generalist species largely causing this overlap. Additionally, the two patch-burn grazing communities overlapped almost entirely, and the modified twice-over rest-rotation treatment community completely contained within the season-long grazing community. We quantified detection-corrected densities for 17 species, six of which showed differences among the four treatments. Three had higher densities in the patch-burn grazing treatments, and three had higher densities in the grazing without fire treatments. Eleven other species, including regal fritillaries (*Speyeria*

idalia) and monarchs, did not show significant differences across treatments. Based on these results, we recommend that managers implement a variety of grazing strategies to promote a diverse butterfly community, including those that support spatially-discrete fire through the use of patch-burn grazing.

Introduction

Pollinator populations are in global decline (Potts et al. 2010). Many factors are driving this decline, including pesticide-induced mortality (Rortais et al. 2005), climate change (Peterson et al. 2004), habitat fragmentation (Davis et al. 2007), and degradation of remaining natural ecosystems through mismanagement (Potts et al. 2010). Loss of pollinator populations represents a major economic crisis as native pollinators provide up to \$3.07 billion in agricultural pollination services annually in the U.S. (Losey and Vaughn 2006), and contribute to native plant pollination that helps preserve biodiversity (Allen-Wardell et al. 1998). There is a need for proactive conservation and management approaches so society can continue to benefit from the ecosystem services provided by pollinators. Evidence suggests that management focused on restoring ecological processes such as fire and grazing in grassland ecosystems may be the most effective at promoting biodiversity and potentially benefiting pollinator populations (Scasta et al. 2015).

Grasslands evolved with the interacting disturbances of fire and grazing (Anderson 2006), and restoring them is likely to benefit organisms native to these ecosystems. However, traditional management typically focuses on even distribution of grazing and excludes fire (Fuhlendorf and Engle 2004). Grazing or fire applied uniformly across the landscape can lead to landscape homogeneity (Fuhlendorf and Engle 2001), which limits niche availability for many organisms, including pollinators. In contrast, interacting fire and grazing that varies the spatial

and temporal extent of disturbance can create a heterogeneous landscape that promotes greater biodiversity through expanded niche availability (Fuhlendorf and Engle 2001, 2004; Fuhlendorf et al. 2006; Hovick et al. 2014).

Patch-burn grazing is an effective management framework for restoring heterogeneity to grasslands (Fuhlendorf and Engle 2004; McGranahan et al. 2014). In a patch-burn grazing management framework, discrete portions of the landscape are burned and grazers have access to areas across the time since fire gradient. Through a series of positive and negative feedbacks, grazers selectively choose the most recently burned area, which results in vegetation heterogeneity across patches (Fuhlendorf and Engle 2004; Allred et al. 2011). Consequently, forb diversity and density increases in patches that recover post-disturbance, while litter accumulates in patches with greater time since fire (Fuhlendorf and Engle 2004). The resultant heterogeneity supports diversity in many organisms including birds (Hovick et al. 2015; Hovick et al. 2017a; Hovick et al. 2017b), small mammals (Fuhlendorf et al. 2010), and macroinvertebrates (Engle et al. 2008; Doxon et al. 2011). Previous work examining the influence of patch-burn grazing on pollinators has taken place in the central and southern tallgrass prairie of the Great Plains (Debinski et al. 2011; Moranz et al. 2012), but no studies have examined pollinator responses in northern mixed-grass prairie dominated by cool season grasses or across multiple seasons of fire (but see Bendel et al. 2018). These differences in disturbance timing and plant community will likely cause variation in pollinator responses. As a result, understanding the influence of patch-burn grazing on pollinator communities under these novel conditions is of major conservation importance given the current lack of knowledge and worldwide decline in both natural grasslands and pollinators (Sala et al. 2000; Potts et al. 2010).

Many butterflies have a paradoxical relationship with fire and grazing because they are simultaneously dependent upon and sensitive to these disturbances (Moranz et al. 2014). Patch-burn grazing is well suited to mediate this paradox, as large portions of the landscape are left unburned in a given season and can act as refugia for sensitive butterflies or other species. Additionally, patch-burn grazing meets the complex vegetation needs of butterflies as it promotes both varied structure and plant expression across a disturbance gradient (Fuhlendorf and Engle 2004; Samways 2007). Moreover, examining the influence of season of fire on butterflies is necessary for informed conservation actions because most species are susceptible to direct mortality (Vogel et al. 2007). However, altering season of fire could mitigate these impacts. Patch-burn grazing should reduce total mortality by burning discrete patches as opposed to entire management units, thus leaving large unburned refuges for larvae (Black et al. 2011; Kral et al. 2017; Swengel 2001). Despite the risk of mortality, butterflies still rely on fire and grazing to maintain treeless grasslands with extensive floral resources (New et al. 1995, Briggs et al. 2002). Understanding the impacts of patch-burn grazing on butterflies will contribute to a growing body of research that seeks to find balance between human land use and conservation.

Grasslands are dependent upon disturbance to prevent woody encroachment or invasion from herbaceous species (Briggs et al. 2002; Toledo et al. 2014), but management actions must consider sensitive pollinators that provide valuable ecosystem services (Losey and Vaughn 2006). Assessing management approaches that mitigate mortality during vulnerable life stages, while still allowing for cattle production, could improve management and conservation for imperiled pollinators (Fuhlendorf and Engle 2004; Kral et al. 2017). To address this conservation need, we assessed the influence of four experimental grazing treatments on butterfly

communities. Specifically, our objectives were 1) quantify overall butterfly richness, abundance, and community composition and 2) calculate individual species' densities while accounting for detection across four treatments that varied the spatial and temporal extent of fire and grazing by domestic cattle. This research will improve the conservation value of managing cattle in working landscapes to promote declining butterfly species and other grassland organisms.

Methods

Site Description

This study took place in the northern Great Plains at the Central Grasslands Research Extension Center (CGREC) near Streeter, North Dakota. CGREC is 2,159 ha and part of the North Dakota State University Agricultural Experiment Station system with the sole mission of extending scientific research to the surrounding rural communities. CGREC is located in the Missouri Coteau ecoregion (USDA-SCS 1981) which receives an average of 39.9 cm of rain per year (NDAWN 2017). Mean low temperature is -15.3 °C in January and mean high temperature is 18.6 °C in August (NDAWN 2017). The plant community is mixed-grass prairie with the most abundant native grasses including green needlegrass (*Nasella viridula*), western wheatgrass (*Pascopyrum smithii*), and blue grama (*Bouteloua gracilis*) (Limb et al. 2018). Common native forbs include goldenrod spp. (*Solidago* spp.), sage spp. (*Artemisia* spp.), milkweed spp. (*Asclepias* spp.), and a violet spp. (*Viola pedatifida*) (Limb et al. 2018). Other common plant species include two non-native, invasive grasses, Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*), and a native, invasive woody shrub, western snowberry (*Symphoricarpos occidentalis*) (Limb et al. 2018).

Experimental Design

We subjected sites to four experimental treatments that included two variations of patch-burn grazing, season-long grazing, and a modified version of rotational grazing (Fig. 1.1). All pastures were stocked with cow-calf pairs of mixed breed cattle at a rate of 1.85 animal unit months (AUMs) per hectare for the duration of the growing season (mid-May to mid-October). We had four different treatments. The first, season long grazing (SLG), received full stocking rate throughout the growing season and had no fire. This treatment represented the “status quo” management in the area and acts as a check or control site. The modified twice-over rest-rotation treatment (MTORG) was intended to create heterogeneity with cattle grazing in the absence of fire. For this treatment, we stocked cattle for varying lengths of time across four separate paddocks per pasture to achieve the desired amount of take. Our stocking durations were 0 days (idle), 27 days (light), 54 days (moderate), and 74 days (heavy). We grazed cattle for these durations in the same paddocks twice during the growing season. These stocking rates rotate through the paddocks each year, with the heavily stocked paddocks becoming idle the following year, and so on. The final two treatments were variations of patch-burn grazing which were intended to maximize heterogeneity while simultaneously promoting cattle production and biodiversity. In one of the patch-burn grazing treatments, we burned 1, 16 ha patch each spring on a four-year fire return interval (PBG40). In the other patch-burn grazing treatment, we burned 1, 8 ha patch each spring, and 1, 8 ha patch each summer or fall, also on a four-year fire return interval (PBG20). However, in 2018 and 2019, summer and fall weather conditions were not conducive to prescribed fire, and we were only able to complete two of the four summer/fall burns. We had four replicates of each treatment type totaling 16 pastures. In total, each pasture was 64 ha, with a total of 1,024 ha included across the four treatments in our study. All

treatments provided fresh water access, and in the season-long grazing and both of the patch-burn grazing treatments, we allowed cattle full access to the pasture, with no interior fences.

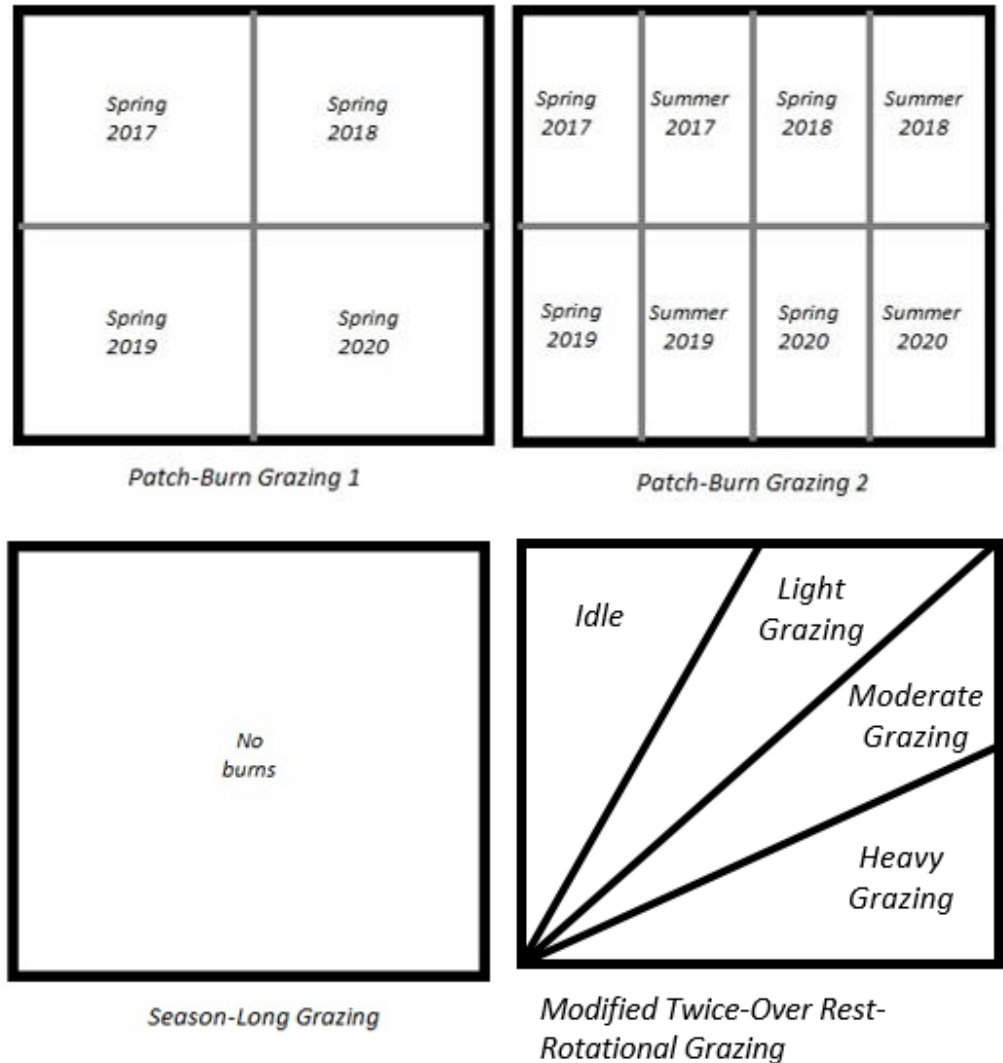


Figure 1.1. Examples of layouts in all four treatments. Gray lines indicate separations between patches for prescribed burning and black lines indicate fences. All treatments allowed for constant access to fresh water and salt/mineral blocks.

Data Collection

Butterfly Surveys

We sub-divided each pasture into eight, eight ha sub-patches and placed a single transect in each sub-patch to ensure even survey effort across each replicate pasture when monitoring the

butterfly community. We placed our 150 m transects at least 200 m apart to avoid duplicate detections and transects remained permanent throughout the study. Each transect was centered within its sub-patch to avoid edge effects. In total, we surveyed 32 transects per treatment for a total of 128 transects.

We surveyed the butterfly community using line-transect distance sampling methodology (Buckland et al. 2010). As an individual observer walked a transect, they recorded each butterfly by species and its perpendicular distance to the transect line. In the event that we could not identify a butterfly in the field, we photographed the individual for later identification. We surveyed each transect three times throughout the butterfly flight season, defined here as approximately June 1st to September 1st. Each set of surveys occurred in a discrete two-week period (approximately June 1st to 15th, July 1st to 15th, and August 1st to 15th). We chose these three survey periods to capture complete phenology. We conducted surveys between 10 a.m. and 6 p.m., when butterflies are most active (Clench 1966). Additionally, we surveyed when temperatures were at or above 21° C, cloud cover was < 50%, and winds were < 20 kilometers per hour (Debinski et al. 2011; Swengel and Swengel 2009). We collected temperature and wind speed data from a North Dakota Agricultural Weather Station located in a treatment pasture, and we visually estimated cloud cover at the beginning of each survey.

Vegetation Surveys

We recorded every flowering ramet in bloom within 1 m of butterfly transects, and maintained counts of each individual species' abundances along each transect to estimate floral resource richness and abundance (Szigeti et al. 2016). We collected vegetation structure and species composition data along two transects that paralleled butterfly transects (15 m offset on each side), recording vegetation characteristics every 15 m. Observers recorded cover types

within a 0.5 m² frame, using Daubenmire cover classes (0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, 96-100%; Daubenmire 1959). Vegetation cover types included Kentucky bluegrass, smooth brome, and both native and non-native groups of: cool season grasses, warm season grasses, legumes, forbs, and woody plants, as well as bare ground and litter. We recorded litter depth in millimeters in all four corners of the frame. Surveyors also collected visual obstruction data at these points using a Robel pole which was observed from 4 m at an eye height of 1 m above ground, recording the highest strata that was at least 50% obscured by vegetation. We conducted Robel readings at each quadrat location in all four cardinal directions (Robel et al. 1970).

Statistical Analyses

Community

To quantify the butterfly community, we started by calculating species richness and abundance by treatment. We used the mean species total and total individuals per transect for each year by averaging the three surveys together. Different species are active at different times, and using totals per survey would have ignored this important factor. After calculating the means per transect across all treatments, we performed an analysis of variance (ANOVA) followed by a Tukey's post-hoc test. We followed the same method to analyze the floral community.

To assess butterfly community composition, we used the function *metaMDS* from the *vegan* package in the R statistical environment (3.3.1, release 2016; Dixon 2003). We used the maximum count of each species on each transect in each year to assess communities across the four treatments. By using maximum count instead of mean or sum, we accounted for any individuals that may have been observed in multiple surveys. We used the Bray-Curtis similarity index, which weighs all species equally (Bloom 1981). We used 4 dimensions for this ordination,

and our maximum allowable stress was 0.2. We applied our vegetation composition and structure data to the ordination as a series of vectors in order to show correlations between vegetation, species, and site. We considered vectors explanatory if their p-value was ≤ 0.05 . We applied our treatments as polygons using the *ordiellipse* function in order to visualize any differences between communities across treatments. We then used the *ordiareatest* function to determine if the treatment ellipses were smaller than a randomized ellipse using our data would be.

Species' Densities

We calculated density estimates for butterfly species with ≥ 60 detections using program Distance (7.1, release 1; Thomas et al. 2010). We calculated estimates using all three years of data in order to maximize the number of species available for analysis. When calculating estimates, we compared combinations of key functions and series expansions. The two key functions were half-normal and hazard rate, and the three series expansions were cosine, simple polynomial, and hermite polynomial (Kral et al. 2018). We evaluated models based on ΔAIC values, visual assessment of detection curves, and X^2 tests (Kral et al. 2018). We then used the Multiple Covariates Distance Sampling engine to compare models with detection covariates including temperature, cloud cover, wind speed, year, Julian date, and time of day (Isaac et al. 2011). We did not assess observer differences as BK conducted all butterfly surveys. After choosing the final model from those with and without covariates, we post-stratified to create a density estimate for each treatment. When a species' detection total was ≥ 30 for ≥ 2 treatments, we performed an ANOVA to determine any differences between treatments.

Results

We detected a total of 14,325 individual butterflies from 40 species during the growing seasons of 2017-2019. Across all treatments, butterfly species richness ranged from 11.12 to 16.97 species per transect and abundance ranged from 86.93 to 128.97 individuals per transect each year. We found that the two treatments with interacting fire and grazing had significantly greater butterfly species richness ($p < 0.001$) and abundances ($p < 0.001$) than the treatments containing grazing only (Fig. 1.2). Floral species richness ranged from 17.65 to 26.35 species per transect and floral abundance ranged from 285.29 to 738.33 stems per transect each year. Floral richness and abundance were significantly different between all treatments except for season-long grazing and modified twice-over rest-rotation grazing, which were similar ($p < 0.02$ for all except for SLG and MTORG where $p = 0.98$ for richness and $p = 0.84$ for abundance).

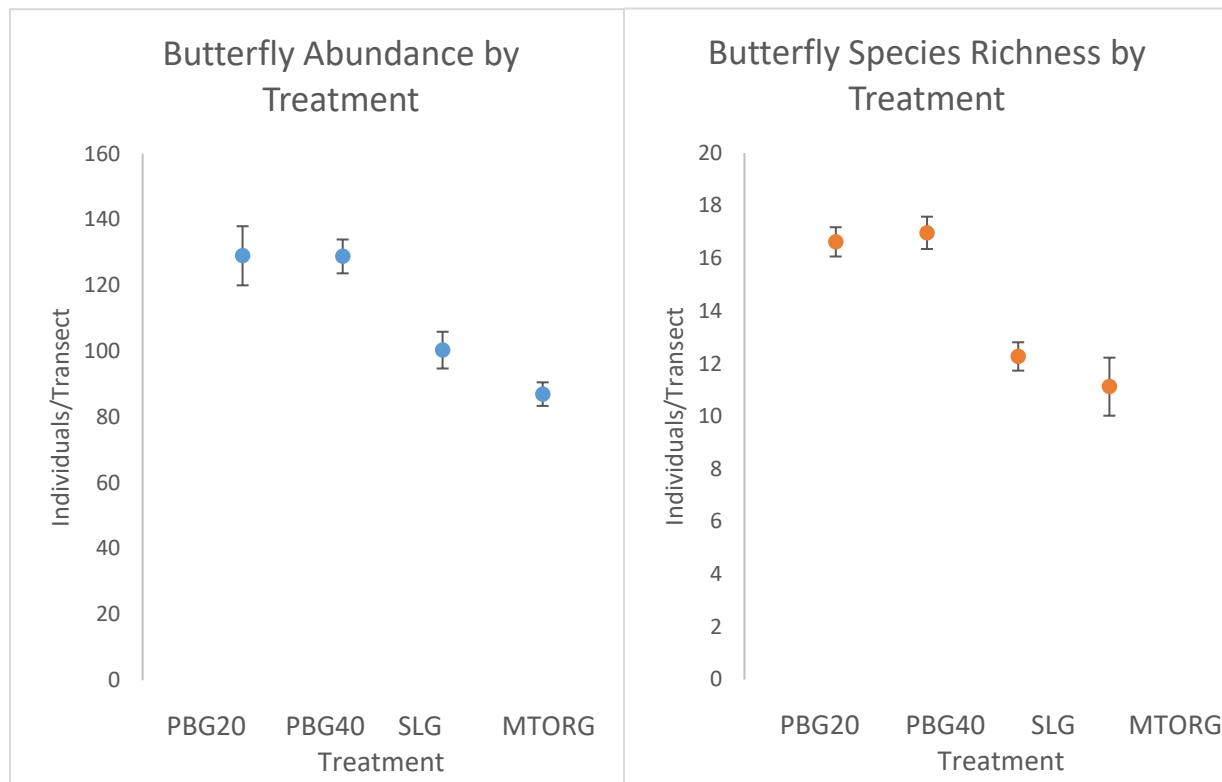


Figure 1.2. Butterfly total abundance and species richness compared across treatments. Abundance and richness values are based on the mean per transect summed across the season (i.e., three surveys summed). Bars indicate standard error. Letters denote results of post-hoc test ($p < 0.001$). PBG20 is patch-burn grazing with two seasons of fire; PBG40 is patch-burn grazing with one season of fire; SLG is season-long grazing; MTORG is modified twice-over rest-rotation grazing.

Community

Our multivariate analysis of the butterfly community revealed that the two treatments containing fire had different composition than the two grazing treatments without fire. The less common species were more associated with the treatments including fire, and the common species were more associated with treatments without fire (Fig 1.3). The two fire treatments were not statistically different from each other, nor were the two grazing treatments that lacked fire (Fig 1.3). We found that the MTORG treatment was the most homogenous butterfly community of the four grazing treatments, as its ellipse was smallest (Fig. 1.3). This was supported by the ANOVA of species richness per treatment, where MTORG and SLG had lower richness than

both of the PBG treatments (Fig. 1.2b). Additionally, we found with the *ordiareatest* permutation test that the MTORG ellipse was smaller than a randomized ellipse would be ($p = 0.001$), which means that it is less diverse than a random subset of our data would suggest. This was also true of the PBG40 treatment ($p = 0.02$), but because of the ANOVA result showing greater species richness than MTORG, we believe that this was caused by a lower rate of species turnover in this treatment. Eight vegetation variables had a significant explanatory influence on the butterfly community (Fig. 1.3). Native and introduced forb cover, native and introduced legume cover, and native c3 grass cover (cool-season grasses) were all explanatory variables.

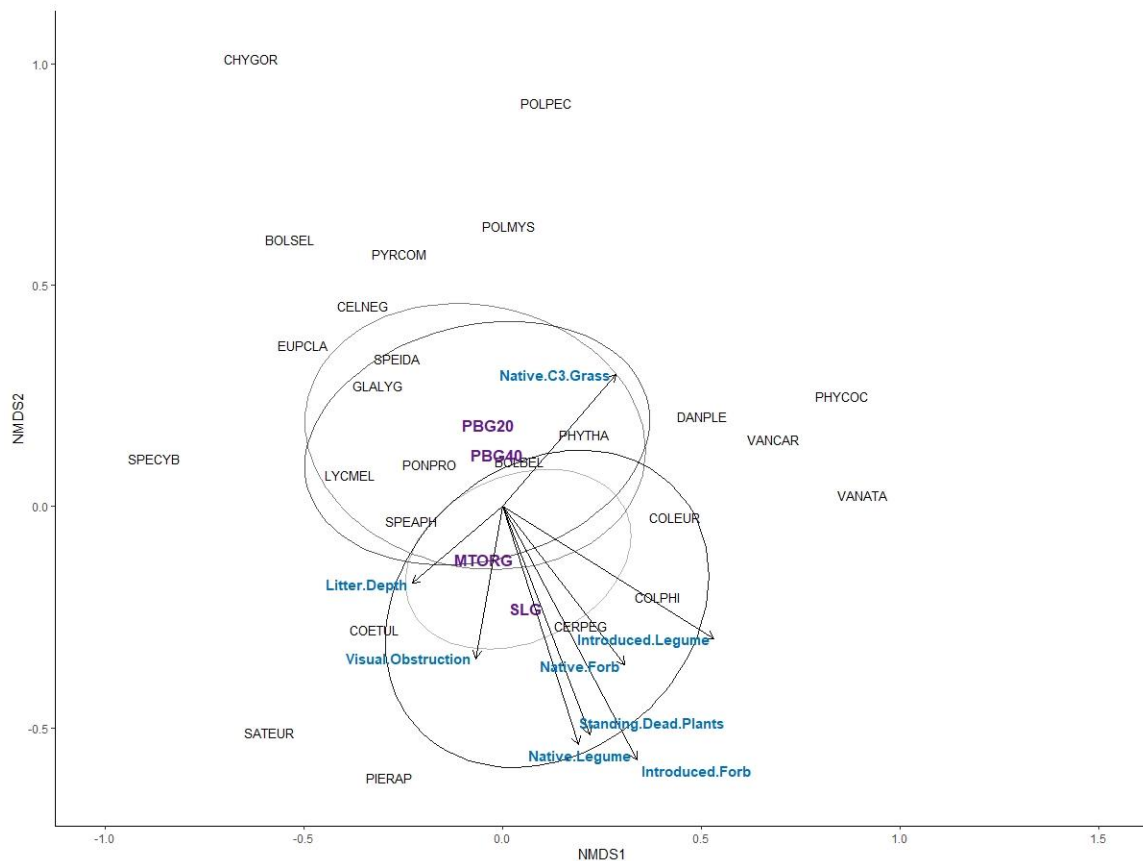


Figure 1.3. NMDS ordination of butterfly abundance data from 2017-2019. Using four dimensions and with a stress of 0.16. Treatments are represented with ellipses; PBG20 and PBG40 labels overlap almost completely. PBG20 is patch-burn grazing with two seasons of fire; PBG40 is patch-burn grazing with one season of fire; SLG is season-long grazing; MTORG is modified twice-over rest-rotation grazing. Butterfly species codes and vegetation vector codes can be found in Table 1.

Species' Densities

We calculated density estimates for 17 species with ≥ 60 detections. We used the hazard rate key function for most species (n=16), and used the half-normal key function for one. Final models most frequently included the cosine series expansion (n=12), followed by hermite polynomial (n=5). Most species' models were not improved by covariates (n=12), with the exception of year (n=1), wind (n=1), and temperature (n=3). Species' densities ranged from 0.02 to 62.05 individuals per hectare. The densities for the two species of conservation concern at our study sites ranged from 1.07 - 4.86 and 0.72 – 3.16 individuals/ha for the monarch and regal fritillary, respectively. Neither species had statistically significant differences between treatments, but both appear to show a trend towards higher densities in treatments including fire (Fig. 1.5). Six species showed differences in density across the treatments. Three had higher densities in one or both of the patch-burn grazing treatments than the grazing-only treatments, and three had higher densities in the grazing-only treatments than the patch-burn grazing treatments (Fig. 1.4). The remaining 11 species did not show significant differences in density between treatments (Fig. 1.5).

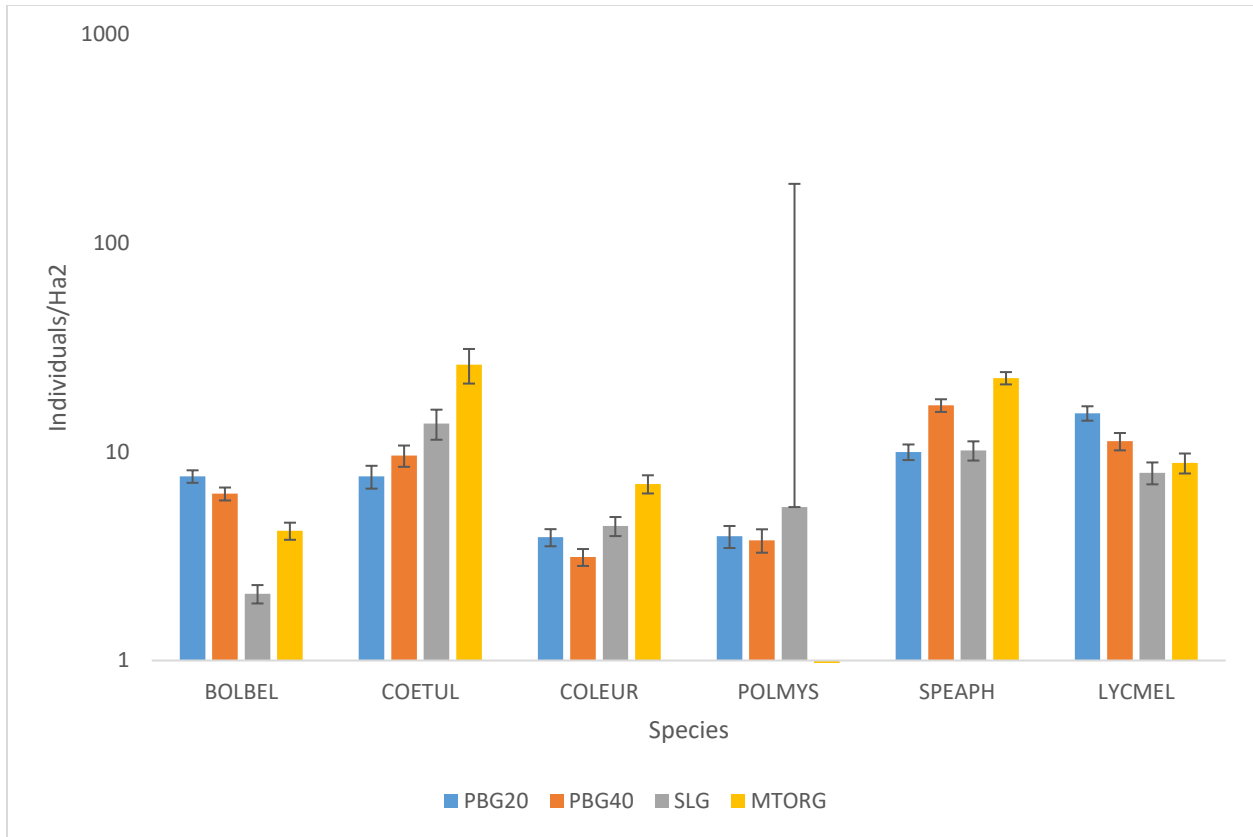


Figure 1.4. Density estimates for six species meeting a minimum threshold of ≥ 60 detections and displaying differences between treatments. These species all showed differences between treatments. Bars indicate standard error. PBG20 is patch-burn grazing with two seasons of fire; PBG40 is patch-burn grazing with one season of fire; SLG is season-long grazing; MTORG is modified twice-over rest-rotation grazing. Densities and standard error values can be found in Table 2, and species codes can be found in Table 1.

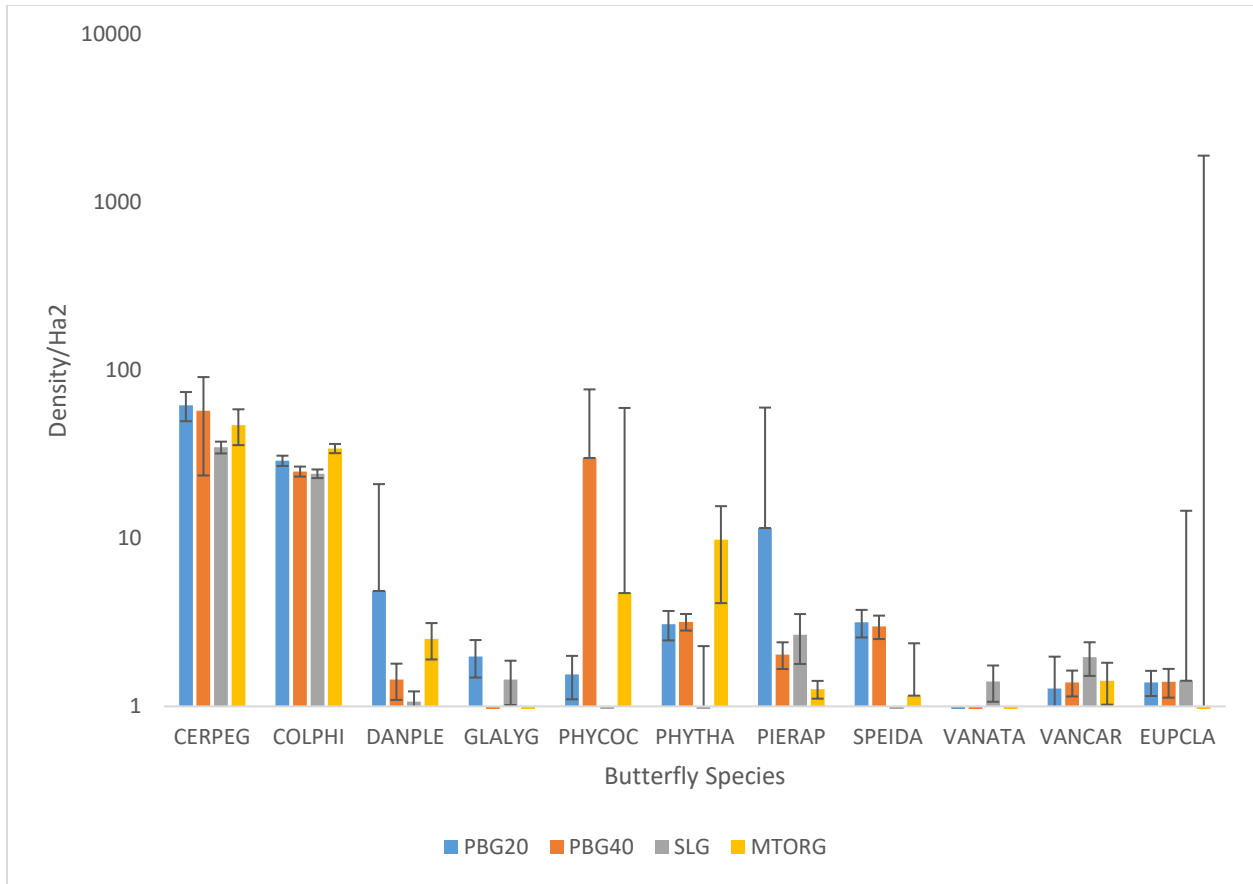


Figure 1.5. Density estimates for 11 species meeting a minimum threshold of ≥ 60 detections and displaying no differences between treatments. Bars indicate standard error, and the y-axis has been edited for clarity. PBG20 is patch-burn grazing with two seasons of fire; PBG40 is patch-burn grazing with one season of fire; SLG is season-long grazing; MTORG is modified twice-over rest-rotation grazing. Densities and standard error values can be found in Table 2, and species codes can be found in Table 1.

Table 1.1. List of all butterfly species codes. Includes both common and scientific names.

Species Code	Common Name	Scientific Name
BOLBEL	Meadow Fritillary	<i>Boloria bellona</i>
BOLSEL	Silver-Bordered Fritillary	<i>Boloria</i>
CELNEG	Summer Azure	<i>Celestrina neglecta</i>
CERPEG	Common Wood Nymph	<i>Cercyonis pegala</i>
CHYGOR	Gorgone Checkerspot	<i>Chlosyne gorgone</i>
COETUL	Common Ringlet	<i>Coenonympha tullia</i>

Table 1.1. List of all butterfly species codes (continued). Includes both common and scientific names.

Species Code	Common Name	Scientific Name
COLEUR	Orange Sulphur	<i>Colias eurytheme</i>
COLPHI	Clouded Sulphur	<i>Colias philodice</i>
DANPLE	Monarch	<i>Danaus pleixippus</i>
ENOANT	Northern Pearly-Eye	<i>Enodia anhedon</i>
EPACLA	Silver-Spotted Skipper	<i>Epargyreus clarus</i>
EUPCLA	Variegated Fritillary	<i>Euptoieta claudia</i>
GLALYG	Silvery Blue	<i>Glaucopsyche lygdamus</i>
LIMARC	Viceroy	<i>Limenitis archippus</i>
LIMART	Red-Spotted Purple	<i>Limenitis arthemis</i>
LYCDIO	Gray Copper	<i>Lycaena dione</i>
LYCHEL	Purplish Copper	<i>Lycaena helloides</i>
LYCHYL	Bronze Copper	<i>Lycaena hyllus</i>
LYCMEL	Melissa Blue	<i>Lycaeides melissa</i>
LYCPHL	American Copper	<i>Lycaena phlaeas</i>
NYMANT	Mourning Cloak	<i>Nymphalis antiopa</i>
PAPGLA	Eastern Tiger Swallowtail	<i>Papilio glaucus</i>
PAPPOL	Black Swallowtail	<i>Papilio polyxenes</i>
PHYBAT	Tawny Crescent	<i>Phyciodes batesii</i>
PHYCOC	Northern Crescent	<i>Phyciodes cocyta</i>
PHYTHA	Pearl Crescent	<i>Phyciodes tharos</i>
PIERAP	Cabbage White	<i>Pieris rapae</i>
POLMYS	Long-Dash Skipper	<i>Polites mystic</i>

Table 1.1. List of all butterfly species codes (continued). Includes both common and scientific names.

Species Code	Common Name	Scientific Name
POLPEC	Peck's Skipper	<i>Polites peckius</i>
POLTHE	Tawny-Edged Skipper	<i>Polites themistocles</i>
PONPRO	Checkered White	<i>Pontia protodice</i>
PYRCOM	Common Checkered Skipper	<i>Pyrgus communis</i>
SATEUR	Eyed Brown	<i>Satyroides eurydice</i>
SATTIT	Coral Hairstreak	<i>Satyrium titus</i>
SPEAPH	Aphrodite Fritillary	<i>Speyeria aphrodite</i>
SPECYB	Great Spangled Fritillary	<i>Speyeria cybele</i>
SPEIDA	Regal Fritillary	<i>Speyeria idalia</i>
STRMEL	Gray Hairstreak	<i>Strymon melinus</i>
VANATA	Red Admiral	<i>Vanessa atalanta</i>
VANCAR	Painted Lady	<i>Vanessa cardui</i>

Table 1.2. Further detail on species' density models and results. All values are rounded to the 3rd decimal place. All densities and standard errors are also represented in Figures 4 & 5. Species codes can be found in Table 1.1.

Species	Model	Truncation	Covariates	PBG20	SE	PBG40	SE	SLG	SE	MTORG	SE
BOLBEL	Half-normal cosine	5%	Year	7.626	0.527	6.293	0.447	2.087	0.211	4.181	0.393
CERPEG	Hazard rate hermite polynomial	11M	N/A	62.047	12.259	57.431	33.759	34.836	2.812	47.264	11.391
COETUL	Hazard rate hermite polynomial	16M	N/A	7.613	0.954	9.593	1.121	13.669	2.246	26.155	4.932
COLEUR	Hazard rate cosine	2.50%	N/A	3.893	0.366	3.129	0.291	4.407	0.462	7.015	0.701
COLPHI	Hazard rate hermite polynomial	2.50%	N/A	29.022	2.033	25.031	1.715	24.275	1.438	34.305	2.160
DANPLE	Hazard rate cosine	2.50%	N/A	4.863	16.170	1.444	0.351	1.068	0.160	2.517	0.615
GLALYG	Hazard rate cosine	8M	Wind	1.983	0.498	0.321	0.089	1.445	0.425	2.17E-02	0.0155
LYCMEL	Hazard rate cosine	2.50%	N/A	15.306	1.215	11.233	1.072	7.938	0.954	8.842	0.971

Table 1.2. Further detail on species' density models and results (continued). All values are rounded to the 3rd decimal place. All densities and standard errors are also represented in Figures 4 & 5. Species codes can be found in Table 1.1.

Species	Model	Truncation	Covariates	PBG20	SE	PBG40	SE	SLG	SE	MTORG	SE
PHYCOC	Hazard rate cosine	2.50%	Temp	1.55	0.448	30.078	46.983	0.115	0.025	4.725	55.015
PHYTHA	Hazard rate cosine	5%	Temp	3.083	0.6137	3.186	0.3599	0.849	1.434	9.833	5.716
PIERAP	Hazard rate cosine	2.50%	N/A	11.52	48.523	2.037	0.368	2.666	0.877	1.264	0.153
SPEAPH	Hazard rate hermite polynomial	5%	Temp	9.984	0.856	16.686	1.165	10.149	1.072	22.559	1.531
SPEIDA	Hazard rate cosine	5%	N/A	3.163	0.591	2.992	0.476	0.716	0.224	1.158	1.216
VANATA	Hazard rate cosine	N/A	N/A	0.361	0.223	0.526	0.208	1.408	0.342	0.412	0.071
VANCAR	Hazard rate hermite polynomial	5%	N/A	1.277	0.699	1.389	0.2440	1.963	0.444	1.421	0.397
EUPCLA	Hazard rate cosine	N/A	N/A	1.39	0.237	1.399	0.272	1.420	13.178	0.838	1895.859
POLMYS	Hazard rate cosine	2.50%	N/A	3.935	0.476	3.769	0.484	5.433	186.703	0.261	0.099

Discussion

Grasslands worldwide are disturbance-dependent ecosystems (Anderson 2006), but cultural aversions to fire have often resulted in the decoupling of fire and grazing processes that structured and maintained these systems (Fuhlendorf et al. 2009). In our broad-scale and well-replicated study of grassland management practices, we focused on comparing the influence of disturbance regimes with fire and grazing to disturbance regimes with grazing alone. We found significant differences in the butterfly community between management practices that included fire and those that did not. While communities differed between treatments with and without fire, they were similar between the two fire treatments and the two non-fire treatments, indicating that fire may play a critical role in shaping grassland butterfly communities. Moreover, the treatments that included both fire and grazing had more individuals of more species than did the treatments without fire, contradicting previous studies which discussed how fire can negatively impact butterfly abundance (Swengel 2001; Kral et al. 2017). However, most previous studies have assessed the influence of fire applied homogenously to management units as opposed to spatially and temporally varying fire in the presence of grazing (e.g., Benson et al. 2007). While it is likely that many species did experience some direct mortality during fires, because the fires were relatively small and were always directly adjacent to unburned areas, there were still large refuges available for butterflies in vulnerable life stages (Vogel et al. 2007).

Fire influenced all of the community metrics that we measured. The treatments that included fire had greater species richness and abundance and community composition within these treatments was significantly different from treatments that did not include fire. These results are likely due to increased floral abundance and diversity in treatments containing fire. The variables that best explained the butterfly community in our ordination included native and

introduced forb cover, and native and introduced legume cover. Butterflies rely on forbs and legumes both as larval host plants and as adult nectar sources, so a diverse community of flowering forbs and legumes is necessary to support a diverse butterfly community (Myers et al. 2012). Other explanatory variables included litter depth, dead plant cover, native cool-season grass cover, bare ground, and visual obstruction. These resources support other life history events or behaviors, such as litter for overwintering or bare ground for thermoregulation through basking (Clench 1966; Warchola et al. 2017), and these resources can be provided in spatio-temporally discrete areas by patch-burn grazing (McGranahan et al. 2016). Deep litter and dead plant material are typically abundant in the longest time since fire areas, bare ground is most abundant in the most recently burned areas, and floral resources are often abundant in one year since fire areas (Hovick et al. 2015). Some of these resources, such as litter and standing dead plant cover, were also abundant in our unburned treatments.

We found differences in six species' densities across treatments. Three species had higher densities in the patch-burn grazing treatments compared to the grazing without fire. Two of these species (meadow fritillary and long-dash skipper) are grassland obligates (Glassberg 2001; Royer 2003), and the third is facultative (Melissa blue; Glassberg 2001). We use the term "grassland obligate" to indicate species which are dependent solely upon grasslands for their entire life cycle, and "facultative" to indicate species that can use multiple ecosystem types. Three species (common ringlet, Aphrodite fritillary, and orange sulphur) had the highest density in the modified twice-over rest-rotation grazing treatment. However, all three of these species were extremely common throughout our entire site, and only common ringlets are grassland obligate species (Glassberg 2001; Royer 2003). Although the remaining two grassland obligate species (regal fritillary and wood nymph) at our site did not show statistically significant

densities between our treatments (Glassberg 2001; Royer 2003), there is a trend towards higher densities in the patch-burn grazing treatments. This mixed response of individual species to individual treatments mirrors previous work examining grazing management in the northern Great Plains (e.g. Bendel et al. 2018).

Although we did observe differences between butterfly communities among our treatments, it is important to note that our treatments are still developing. This study represents three years of data for the two patch-burn grazing treatments, which are on a four-year fire return interval, three years of data for the season-long grazing treatment, and two years of data for the modified twice-over rest-rotation grazing treatment, which is on a four-year grazing rotation. We also experienced some difficulty in applying our treatments, primarily with the late summer/early fall prescribed burns. In 2017, we were able to conduct all four burns, but we did so later in the season than intended due to dry weather. In 2018, we were able to conduct two of the four burns because of an unusually wet summer and fall. Previous studies have determined that land use legacies are as important as -- if not more important than -- current management (Debinski et al. 2011). Although we found significant results from our treatments, it is likely that results would be different had the study taken place on land where these treatments were the legacy, or if our study continued over a greater period of time. Some of our species showed trends in their densities that were not significant, and this result might be clarified by repetition of this study several years later, when our treatments have become established.

We compared the butterfly community and individual species' densities across four treatments, including season-long grazing, modified twice-over rest-rotation grazing, patch-burn grazing with one season of fire, and patch-burn grazing with two seasons of fire. It is of particular importance to focus on butterfly conservation at present as many butterflies are

experiencing precipitous decline worldwide (i.e. Van Dyck et al. 2009; Flockhart et al. 2015; Potts et al. 2010). Overall, our findings support the idea that patch-burn grazing is beneficial to butterflies. By leaving large areas of grassland unburned each year, we left refugia for sensitive species and still provided the resources that interacting fire and grazing can create (Vogel et al. 2010). In the northern Great Plains, we suggest that managers focus on spring burns; as we noted above, it can be exceedingly difficult to successfully conduct prescribed burns in the late summer. We recommend that carefully planned patch-burn grazing, with small patch sizes, should be used to support butterfly conservation plans in North American grasslands. Previous studies have found that this management type is also beneficial to other wildlife (Hovick et al. 2015; Doxon et al. 2011), and patch-burn grazing also supports cattle production, which is an economically-important activity in the region.

References

- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Cane, J., Cox, P. A., Dalton, V., Feinsinger, P., Ingram, M., Jones, C. E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-morales, S., Nabhan, G. P., Pavlik, B., Tepedino, V., & Torchio, P. (1998). The Potential Consequences of Pollinator Declines on the Conservation of Biodiversity and Stability of Food Crop Yields. *Conservation Biology*, 12(1), 8–17.
- Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength: Of fire-grazing interaction. *Ecology and Evolution*, 1(2), 132–144. <https://doi.org/10.1002/ece3.12>
- Anderson, R. C. (2006). Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *The Journal of the Torrey Botanical Society*, 133(4), 626–647.

- Benson, T. J., Dinsmore, J. J., & Hohman, W. L. (2007). Responses of Plants and Arthropods to Burning and Disking of Riparian Habitats. *Journal of Wildlife Management*, 71(6), 1949–1957. <https://doi.org/10.2193/2006-412>
- Black, S. H., Shepherd, M., & Vaughan, M. (2011). Rangeland management for pollinators. *Rangelands*, 33(3), 9–13. <https://doi.org/10.2111/1551-501X-33.3.9>
- Bloom, S. A. (1981). Similarity Indices in Community Studies: Potential Pitfalls. *Marine Ecology Progress Series*, 5, 125–128. <https://doi.org/10.3354/meps005125>
- Cid, M. S., Ferri, C. M., Brizuela, M. A., & Sala, O. (2008). Structural heterogeneity and productivity of a tall fescue pasture grazed rotationally by cattle at four stocking densities. *Grassland Science*, 54(1), 9–16. <https://doi.org/10.1111/j.1744-697x.2008.00099.x>
- Clench, H. K. . (1966). Behavioral Thermoregulation in Butterflies. *Ecology*, 47(6), 1021–1034.
- Davis, J. D., Debinski, D. M., & Danielson, B. J. (2007). Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. *Landscape Ecology*, 22(9), 1341–1354. <https://doi.org/10.1007/s10980-007-9111-9>
- Dixon, P. (2003). VEGAN, a package of {R} functions for community ecology. *Journal of Vegetation Science*, 14(6), 927–930.
- Doxon, E. D., Davis, C. A., Fuhlendorf, S. D., & Winter, S. L. (2011). Aboveground macroinvertebrate diversity and abundance in sand sagebrush prairie managed with the use of pyric herbivory. *Rangeland Ecology and Management*, 64(4), 394–403. <https://doi.org/10.2111/REM-D-10-00169.1>
- Engle, D. M., Fuhlendorf, S. D., Roper, A., & Leslie, D. M. (2008). Invertebrate Community Response to a Shifting Mosaic of Habitat. *Rangeland Ecology & Management*, 61(1), 55–62.

- Flockhart, D. T., Pichancourt, J. B., Norris, D. R., & Martin, T. G. (2015). Unravelling the annual cycle in a migratory animal: Breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology*, *84*(1), 155–165.
<https://doi.org/10.1111/1365-2656.12253>
- Fuhlendorf, S. D., & Engle, D. M. (2004). Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, *41*(4), 604–614.
<https://doi.org/10.1111/j.0021-8901.2004.00937.x>
- Hovick, T. J., Carroll, J. M., Elmore, R. D., Davis, C. A., & Fuhlendorf, S. D. (2017). Restoring fire to grasslands is critical for migrating shorebird populations. *Ecological Applications*, *27*(6), 1805–1814. <https://doi.org/10.1002/eap.1567>
- Hovick, T. J., Elmore, R. D., Fuhlendorf, S. D., Engle, D. M., & Hamilton, R. G. (2015). Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications*, *25*(3), 662–672. [papers3://publication/uuid/E1562BC7-6897-4B5C-ACFB-59B367431705](https://doi.org/10.1890/1051-0761-1337)
- Isaac, N. J. B., Cruickshanks, K. L., Weddle, A. M., Marcus Rowcliffe, J., Brereton, T. M., Dennis, R. L. H., Shuker, D. M., & Thomas, C. D. (2011). Distance sampling and the challenge of monitoring butterfly populations. *Methods in Ecology and Evolution*, *2*(6), 585–594. <https://doi.org/10.1111/j.2041-210X.2011.00109.x>
- Kral, K. C., Harmon, J., Limb, R., & Hovick, T. J. (2018). Improving our science: the evolution of butterfly sampling and surveying methods over time. *Journal of Insect Conservation*, *22*(1), 1–14. <https://doi.org/10.1007/s10841-018-0046-z>

- Kral, K. C., Hovick, T. J., Limb, R. F., & Harmon, J. P. (2018). Multi-scale considerations for grassland butterfly conservation in agroecosystems. *Biological Conservation*, 226(July), 196–204. <https://doi.org/10.1016/j.biocon.2018.08.002>
- Limb, R. F., Hovick, T. J., Norland, J. E., & Volk, J. M. (2018). Grassland plant community spatial patterns driven by herbivory intensity. *Agriculture, Ecosystems and Environment*, 257(November 2017), 113–119. <https://doi.org/10.1016/j.agee.2018.01.030>
- Long, O. M., Warren, R., Price, J., Brereton, T. M., Botham, M. S., & Franco, A. M. A. (2017). Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology*, 86(1), 108–116. <https://doi.org/10.1111/1365-2656.12594>
- Losey, J. E., & Vaughan, M. (2006). *The Economic Value of Ecological Services Provided by Insects*. 56(4), 311–323.
- McGranahan, D. A., Hovick, T. J., Elmore, R. D., Engle, D. M., Fuhlendorf, S. D., Winter, S. L., Miller, J. R., & Debinski, D. M. (2016). Temporal variability in aboveground plant biomass decreases as spatial variability increases. *Ecology*, 97(3), 555–560. <https://doi.org/10.1890/15-0906.1>
- Moranz, R. A., Debinski, D. M., McGranahan, D. A., Engle, D. M., & Miller, J. R. (2012). Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodiversity and Conservation*, 21(11), 2719–2746. <https://doi.org/10.1007/s10531-012-0330-2>
- Moranz, R. A., Fuhlendorf, S. D., & Engle, D. M. (2014). Making sense of a prairie butterfly paradox: The effects of grazing, time since fire, and sampling period on regal fritillary abundance. *Biological Conservation*, 173, 32–41. <https://doi.org/10.1016/j.biocon.2014.03.003>

- Myers, M. C., Hoksich, B. J., & Mason, J. T. (2012). Butterfly response to floral resources during early establishment at a heterogeneous prairie biomass production site in Iowa, USA. *Journal of Insect Conservation*, *16*(3), 457–472. <https://doi.org/10.1007/s10841-011-9433-4>
- Ohwaki, A. (2019). Entire - area spring burning versus abandonment in grasslands : butterfly responses associated with hibernating traits. *Journal of Insect Conservation*, *0123456789*. <https://doi.org/10.1007/s10841-019-00181-7>
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution*, *25*(6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Robel, R. J., Briggs, J. N., Dayton, A. D., & Hulbert, L. C. (1970). Relationships between Visual Obstruction Measurements and Weight of Grassland Vegetation. *Journal of Range Management*, *23*(4), 295–297.
- Sala, O. E., Chapin Iii, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., Wall, D. H., ... Wall16, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Source: Science, New Series*, *287*(5459), 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Samways, M. J. (2007). Insect Conservation: A Synthetic Management Approach. *Annual Review of Entomology*, *52*(1), 465–487. <https://doi.org/10.1146/annurev.ento.52.110405.091317>
- Swengel, A. B. (2001). A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation*, *10*(7), 1141–1169. <https://doi.org/10.1023/A:1016683807033>

- Swengel, A. B., & R., S. S. (2009). Spatiotemporal Variation of Violet-Feeding Large Fritillaries (Euptoieta, Speyeria) (Lepidoptera: Nymphalidae) in Central and Northern Wisconsin. *The Great Lakes Entomologist*, 42(3 & 4), 121–138.
- Szigeti, V., Korosi, A., Harnos, A., Nagy, J., & Kis, J. (2016). Measuring floral resource availability for insect pollinators in temperate grasslands - A review. *Ecological Entomology*, 41(3), 231–240. <https://doi.org/10.1111/een.12298>
- Thom, M. D., Daniels, J. C., Kobziar, L. N., & Colburn, J. R. (2015). Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida. *PLoS ONE*, 10(5), 1–22. <https://doi.org/10.1371/journal.pone.0126755>
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., & Burnham, K. P. (2010). *Distance software: design and analysis of distance sampling surveys for estimating population size*. 47, 5–14. <https://doi.org/10.1111/j.1365-2664.2009.01737.x>
- Toledo, D., Sanderson, M., Spaeth, K., Hendrickson, J., & Printz, J. (2014). Extent of Kentucky Bluegrass and Its Effect on Native Plant Species Diversity and Ecosystem Services in the Northern Great Plains of the United States. *Invasive Plant Science and Management*, 7(04), 543–552. <https://doi.org/10.1614/IPSM-D-14-00029.1>
- Van Dyck, H., Van Strien, A. J., Maes, D., & Van Swaay, C. A. M. (2009). Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology*, 23(4), 957–965. <https://doi.org/10.1111/j.1523-1739.2009.01175.x>
- Vogel, J. A., Debinski, D. M., Koford, R. R., & Miller, J. R. (2007). Butterfly responses to prairie restoration through fire and grazing. *Biological Conservation*, 140, 78–90. <https://doi.org/10.1016/j.biocon.2007.07.027>

Warchola, N., Crone, E. E., & Schultz, C. B. (2017). Balancing ecological costs and benefits of fire for population viability of disturbance-dependent butterflies. *Journal of Applied Ecology*, *January*, 1–10. <https://doi.org/10.1111/1365-2664.12983>

CHAPTER 2: BEHAVIORAL TIME BUDGETS OF REGAL FRITILLARIES (*SPEYERIA IDALIA*) AND MONARCHS (*DANAUS PLEXIPPUS*)

Abstract

Organism behavior is an important factor in assessing the efficacy of land management as conservation, but typically population or community analyses alone dictate management decisions. Behavioral studies can provide managers with more information about individual species, which can help inform management decisions for diverse species with a variety of resource needs. We investigated regal fritillary (*Speyeria idalia*) and monarch (*Danaus plexippus*) behaviors across treatments with varying spatial and temporal application of fire and grazing to improve and inform management. We collected behavioral data with 10-minute time-budget surveys. We recorded all behaviors as they occurred, including basking, chasing, fleeing, mating, nectaring, patrolling, ovipositing, and resting. We surveyed 64 monarchs and 32 regal fritillaries in the summers of 2018-19. We compared time budgets for each species by time since fire (year of fire, one year since fire, or unburned) using a MANOVA. We found no differences for either species, possibly due to sample size. We also assessed the influence of vegetation characteristics on individual behaviors. Monarch nectaring was positively correlated with native forb cover, and regal fritillary patrolling was negatively correlated with smooth brome (*Bromus inermis*) cover. We suggest that managers implement strategies to support a robust floral community and mitigate smooth brome in order to support these species. Further, we suggest that future behavioral studies focus more narrowly on life history behaviors, such as mating and ovipositing, in order to better understand these species' landscape resource needs and inform management.

Introduction

Butterflies provide important ecosystem services in most terrestrial systems (Allen-Wardell et al. 1998; Brereton et al. 2010; Samways 2007), and their contribution to agricultural and natural pollination worldwide is economically valuable (Losey and Vaughn 2006). Additionally, many butterfly species can be indicators of management effectiveness or ecosystem condition because of their short generations and varied habitat requirements (Brereton et al. 2010; New 1997; Thomas 2005). In spite of this, many butterfly populations continue to decline globally and are in need of informed conservation actions to prevent future species losses. Behavioral studies can help fill this need.

Emerging threats to butterfly populations in grasslands include habitat fragmentation (Davis et al. 2007), extreme weather events caused by climate change (Long et al. 2017), and poor management of remaining lands (Bonari et al. 2017). Habitat degradation in grasslands often takes the form of altered disturbance regimes, which can promote woody encroachment and reduce available floral resources for pollinators such as butterflies (Fuhlendorf and Engle 2004; Baum and Sharber 2012). These pressures can act in synergy to negatively impact butterflies and drive the current need to expand conservation efforts for these imperiled species.

Grassland butterflies in North America may benefit from restoring natural disturbance regimes such as fire and grazing (Fuhlendorf et al. 2009, Fuhlendorf et al. 2012). Prior to European settlement, the Great Plains were subject to frequent disturbances through the interaction of large mammal grazing and fire (Anderson 2006). In contrast, current management focuses on moderate, evenly applied disturbance from domestic cattle, typically excluding fire (Fuhlendorf and Engle 2001). The resulting uniformity in vegetation structure favors generalist species, and can limit grassland obligate species, which rely on the structural heterogeneity

created by dynamic and interacting fire and grazing that once occurred in grasslands throughout North America (e.g. Britten and Glasford 2002; Hammond and McCorkle 1983). While the fire and grazing interaction can cause direct mortality to immobile life stages, it can also improve resource availability for many species (Brown et al. 2017). One way to mitigate this paradox is through the use of patch-burn grazing, wherein only one small portion of a pasture is burned each year (Moranz et al. 2014; Fuhlendorf and Engle 2004). For instance, regal fritillaries (*Speyeria idalia*) require a variety of vegetation throughout their lives including senesced vegetation for oviposition and overwintering as larvae, violets (*Viola* spp.) as larval host plants in the spring, and flowering forbs for adult food sources in the summer (Kopper et al. 2001), all of which may be provided in different patches in a patch-burn grazing framework (McGranahan et al. 2016). Working towards an understanding of how – and if – a species’ needs are met by management actions is necessary for informed and effective conservation.

Previous research on butterfly response to fire and grazing has shown mixed responses. Some studies found no differences in communities between different disturbance regimes, and have stated that land use legacies are more explanatory than current management practices (Debinski et al. 2011). Other butterfly community studies showed that fire and grazing, and each separately, all support distinct communities, although the fire and grazing interaction had the greatest abundance (Vogel et al. 2007). Studies on a single species’ population response have found that time since fire is an important factor, with regal fritillaries showing a preference for recently burned patches at the end of the summer, but not immediately following burns (Moranz et al. 2014). All these research questions are important to answer, and behavioral studies can build on these lessons. Behavioral studies can provide more information about how sensitive species use resources, and whether that use differs between land management types.

Butterflies' behavioral time budgets can provide greater detail on species responses, which is especially important for species of conservation concern. Understanding how a species uses different areas of a landscape can help us create better conservation plans. For instance, if a species is only ever observed flying over a recently burned patch, and never mating, ovipositing, or performing other life history behaviors, we may want to advocate for smaller burn patch sizes in order to make these little-used areas easily traversable. By using a time budget framework, researchers are able to document every behavior an individual performs in the field, as it occurs, without focusing on one component as many behavioral studies do (e.g., Kaiser et al. 2018). In heterogeneous landscapes such as grasslands managed with fire and grazing, it may be beneficial to understand how an individual alters its behavior across different patch types (Knowlton and Graham 2010).

In this study, we monitored behavior of two species of conservation concern, the regal fritillary (*Speyeria idalia*) and the monarch (*Danaus plexippus*). Monarch butterfly populations are in precipitous decline in parts of their range (Schultz et al. 2017), as are regal fritillaries (Powell et al. 2007). Both species have been proposed for listing under the Endangered Species Act in the United States (USFWS 2018; USFWS 2015). Monarch migration is considered an “endangered phenomenon” (Brower et al. 2012), and because they are migratory, monarchs face a variety of threats across their different habitats, including host plant loss (Zaya et al. 2017), parasites (Leong et al. 1997), and drought (Couture et al. 2015). Regal fritillaries, which are a grassland obligate species, are threatened mainly by habitat fragmentation and degradation (Keyghobadi et al. 2006; Swartz et al. 2015). Both species face additional pressures from climate change (Fourcade and Öckinger 2016), agriculture (Grant et al. 2018), and invasive species (Keeler et al. 2006).

To understand how management influences behaviors of two butterflies of conservation concern, we surveyed regal fritillaries and monarchs across grasslands that were managed either with grazing alone, or grazing and fire together. Our primary objectives were to 1) quantify monarch and regal fritillary behavioral time budgets in grasslands managed with fire and grazing, and 2) evaluate the influence of vegetation characteristics on the behaviors of these two species.

Methods

Site Description

Our study took place at the Central Grasslands Research Extension Center (CGREC), located near Streeter, North Dakota. The North Dakota Agricultural Experiment Station managed CGREC for the single mission of conducting scientific research and extending this research into the surrounding community. CGREC is located in the Missouri Coteau ecoregion, and receives an average of 39.9 cm of rain each year, with a high temperature in August reaching 18.6° C, and a low temperature in January reaching -15.3° C (NDAWN 2017). Common native grasses include western wheatgrass (*Pascopyrum smithii*) and green needlegrass (*Nasella viridula*), and common non-native, invasive grasses include Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) (Limb et al. 2017). Forbs include several species of milkweed (*Asclepias* spp.), goldenrod (*Solidago* spp.), thistle (*Cirsium* spp.), and blazingstar (*Liatris* spp.). The dominant shrub is western snowberry (*Symphoricarpos occidentalis*).

Data Collection

Behavioral Observations

We conducted 10 minute time-budget surveys on the behavior of regal fritillaries and monarchs (Pickens and Root 2009; Wang and Messing 2003). We located individuals of the target species opportunistically while conducting other butterfly-focused surveys. At the onset of each observation period, we recorded the location and management type, date, time of day, and weather. We determined sex visually by dimorphic characteristics. To record behaviors, we built an ethogram table including all possible behaviors and recorded them as they occurred (Table 1), without pooling into set intervals. We also recorded the species of any plant a butterfly used during an observation period.

Table 2.1. Behavioral ethogram. The behaviors we observed in monarch and regal fritillary time budgets. With the exception of mating, which we only observed in monarchs, we recorded all behaviors in both species at least once.

Behavior	Description	Citation
Resting	Sitting on vegetation or substrate; wings closed	Clench 1966
Basking	Sitting on vegetation or substrate; wings open	Clench 1966
Foraging flight/nectaring	Flight above vegetation canopy, occasionally stopping to sit on open flower with proboscis extended	Curtis et al. 2015
Mating	Two butterflies, typically in flight, connected at the abdomen	Rutowski 1982
Ovipositing: monarchs	Female on <i>Asclepias</i> spp., occasionally pausing to flex her abdomen and deposit an egg	Ladner and Altizer 2005

Table 2.1. Behavioral ethogram (continued). The behaviors we observed in monarch and regal fritillary time budgets. With the exception of mating, which we only observed in monarchs, we recorded all behaviors in both species at least once.

Behavior	Description	Citation
Ovipositing: regal fritillaries	Female in low flight, occasionally dipping below the vegetation canopy, walking through senesced vegetation occasionally flexing her abdomen to deposit an egg	Kopper et al. 2000
Chasing	Flighted pursuit of any organism; will be separated into conspecific, misc. Lepidoptera, other insect, or vertebrate	Kemp 2000
Fleeing	Flight closely followed by any organism; will be separated into conspecific, misc. Lepidoptera, other insect, or vertebrate	Kemp 2000
Patrolling	Flight that appears to follow a pattern and cover a specific area; likely to be broken up by bouts of chasing	Peixoto and Benson 2009

Vegetation Surveys

We quantified vegetation characteristics by recording the canopy cover of bare ground, litter, and both native and non-native forbs, grasses, shrubs, and legumes. We visually estimated canopy cover using cover classes (0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, 96-100%; Daubenmire 1959). Observers recorded cover types within 10, 0.5 m² quadrats spaced evenly along a 150 m transect. We placed two of these transects in each 8 ha sub-patch, with a total of eight sub-patches per pasture, and 16 transects per pasture. We also recorded all flowering ramets along a 1 m wide, 150 m long, transect in each sub-patch, and identified these plants to the species level.

Statistical Analysis

Treatment Effects

We initially calculated duration, frequency, and proportion of time spent in each behavior for each individual, and then calculated the mean for each species. We used a multivariate analysis of variance (MANOVA) to test for differences in time budget by treatment. Since we implemented our treatments at a pasture scale, not a patch scale, we chose to continue with analysis at this level wherever possible. Due to sample size constraints (n=64 monarchs; n=32 regal fritillaries), we analyzed monarchs at the treatment level (pasture scale; grazing only or grazing and fire), but analyzed regal fritillaries only within the grazing and fire treatments by time since fire (patch scale; year of fire, one year since fire, unburned).

We examined the influence of vegetation characteristics on butterfly behaviors using an NMDS ordination with the binomial distance measure, which handles small sample sizes well (Bloom 1981). Before running ordinations, we tested for correlations among our vegetation variables using the package *corrplot* (Wei and Simko 2017). We found that visual obstruction

was correlated to smooth brome cover ($r=0.58$) and native woody plant cover ($r=0.63$). We chose to remove visual obstruction in order to keep the maximum number of variables to test, as it was also nearly correlated to two other variables (introduced forb cover, 0.52; bare ground, -0.48). Litter depth and standing dead plant cover were also correlated ($r=0.71$). We removed standing dead plant cover, as it had less overall variation than litter depth, and therefore may be less likely to show a relationship. After accounting for correlated pairs, 14 vegetation variables were included in multivariate analyses. We created a plot for each species separately using the binomial similarity index with package *vegan* in the R statistical environment (Oksanen 2015; R Core Team 2019). We used vegetation characteristics as vectors to visualize relationships between behaviors and vegetation, and only kept vectors with a p-value of ≤ 0.1 . We used two dimensions and our maximum allowable stress was 0.15.

We used the significant vectors from the ordination to indicate possible relationships between specific behaviors and vegetation characteristics. The vectors in the ordination indicated which vegetation characteristics influence the overall time budget, but did not tell us how strongly individual behaviors were affected. We performed linear regressions for any behaviors that appeared near the significant vectors using the package *lme4* (Table 2; Bates et al. 2015). We included treatment as a fixed effect, and sex as a random effect because it is likely to cause differences among individuals, but we are not interested in these differences. We then used the *car* package to extract p-values, and the *MuMIn* package to extract conditional r^2 values, which account for both random and fixed effects (Fox and Weisberg 2019; Barton 2018).

Results

We recorded behaviors of 64 monarchs and 32 regal fritillaries in the summers of 2018 and 2019 for a total of 80 hours of field observations. We observed 29 female and 35 male

monarchs, and 13 female and 19 male regal fritillaries. We calculated frequency as the percent of individuals whose observations included a given behavior. For monarchs, we most frequently recorded patrolling (60.9% of observations), with resting a close second (54.7% of observations). All other behaviors were recorded in $\leq 20\%$ of observations, with ovipositing the least frequently observed behavior (7.8% of observations). For regal fritillaries, we again most frequently recorded patrolling (65.6% of observations included patrolling), with nectaring the second most frequent (59.3% of observations). Besides mating, which we never observed in regal fritillaries, the least frequent behavior was ovipositing (12.5% of observations). We recorded all behaviors in both species, with the exception of mating, which we saw only in monarchs (Table 1).

We found no differences in either the overall time budget or individual behaviors between treatments for either species (Fig. 2.1 & 2.2), with the exception of basking for regal fritillaries, which was marginally significant ($p=0.06$). We most commonly observed basking in the one year since fire patches, and least commonly in unburned patches. Conspecific abundance ($p=0.04$) and native forb cover ($p=0.05$) significantly explained overall time budget variations for monarchs. Floral richness ($p=0.07$) and bare ground cover ($p=0.06$) were also marginally significant. Native forb cover was most closely aligned with nectaring and foraging behaviors, bare ground was closest to mating, and conspecific abundance was relatively close to ovipositing. Smooth brome cover ($p=0.009$) and introduced forb cover ($p=0.04$) were explanatory variables for regal fritillaries' time budget variations. Native woody cover ($p=0.06$) was marginally significant. Introduced forbs appeared to be related to ovipositing. Native woody cover was most closely aligned to nectaring and foraging behaviors. Smooth brome cover appeared to be negatively correlated with flight behaviors (chasing, fleeing, and patrolling), as they appear opposite to one another.

To further explore relationships between behaviors and vegetation characteristics, we followed the ordinations with regressions. Mating was explained by bare ground cover for monarchs ($p=0.0009$; adjusted $R^2=0.151$; Table 2.2). Smooth Brome cover explained patrolling for regal fritillaries ($p=0.0034$; adjusted $R^2=0.2203$; Table 2.2). We found no other significant models.

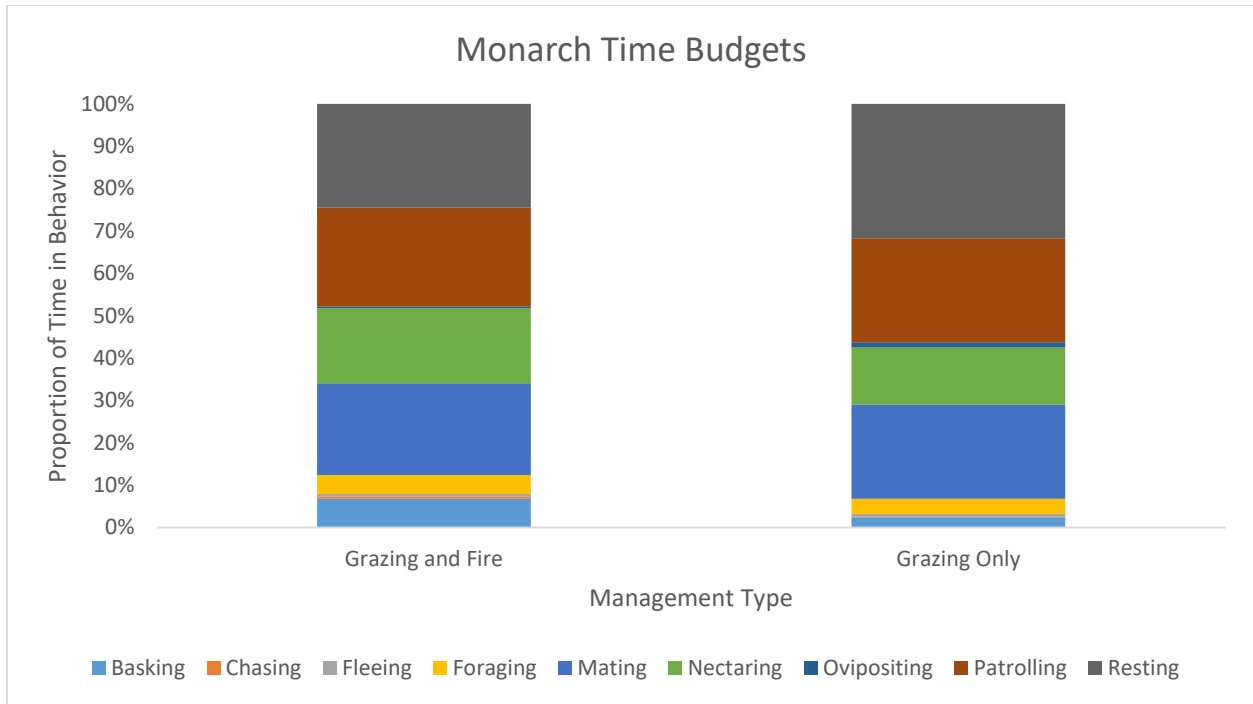


Figure 2.1. Mean percent time in each behavior for all monarch butterflies. Chasing was marginally significant ($p=0.105$), with slightly more chasing occurring in the grazing and fire pastures than in the grazing only pastures. No other behaviors differed between treatments (all $p \geq 0.254$). ($n=37$ for grazing and fire; $n=26$ for grazing only).

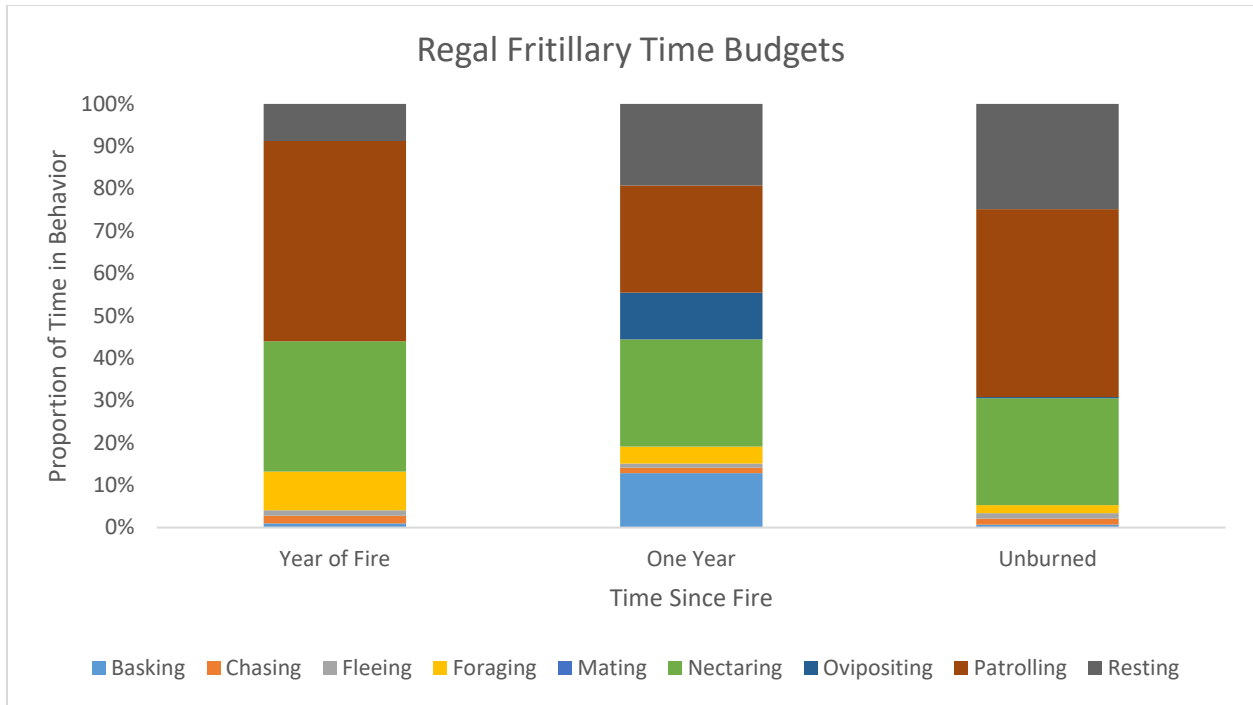


Figure 2.2. Mean percent time in each behavior for regal fritillaries. We found that basking was marginally different between patch types ($p=0.06$), with the most basking occurring in the one year since fire patches, and the least in the unburned patches. No other behaviors differed between patch types (all $p \geq 0.17$). ($n=5$ for year of fire; $n=10$ for one year since fire; $n=17$ for unburned).

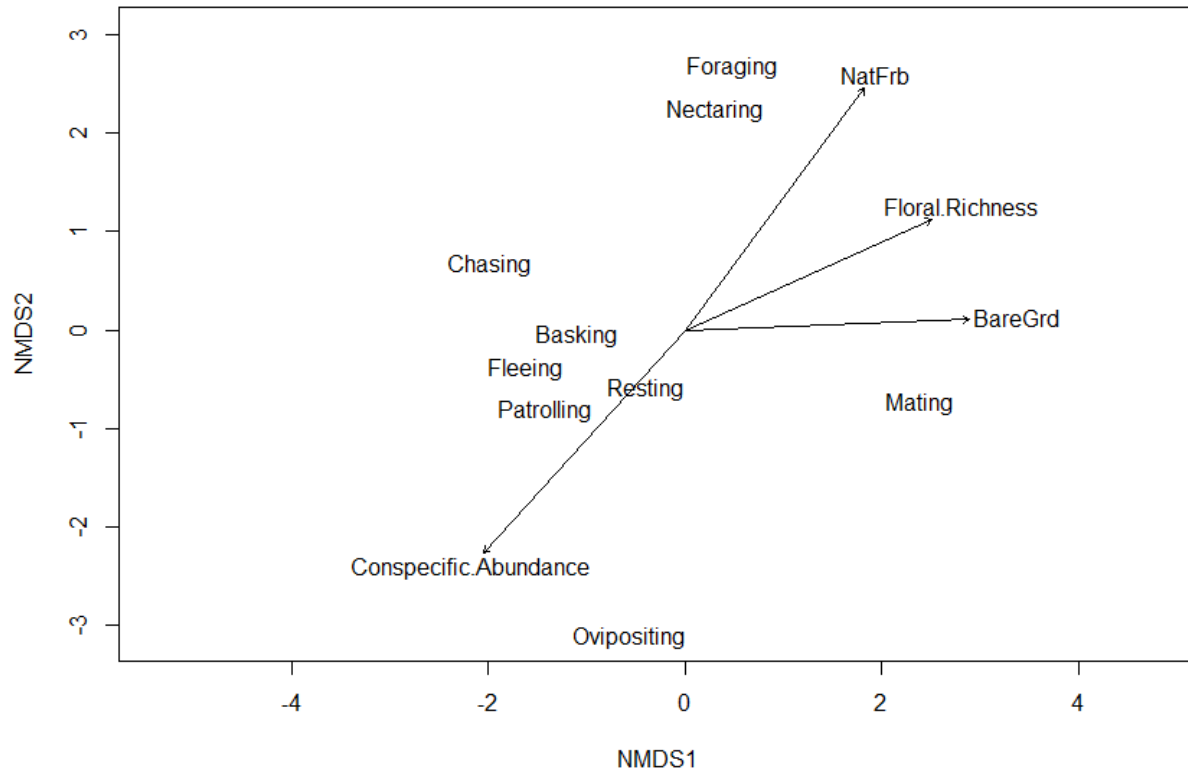


Figure 2.3. Ordination plot displaying monarch behaviors and explanatory vegetation variables ($p \leq 0.1$). We used two dimensions and a maximum stress of 0.15. We used total duration of time in each behavior for all 64 monarch observations. (Codes are: NatFrb = Native Forb Cover, BareGrn = Bare Ground Cover).

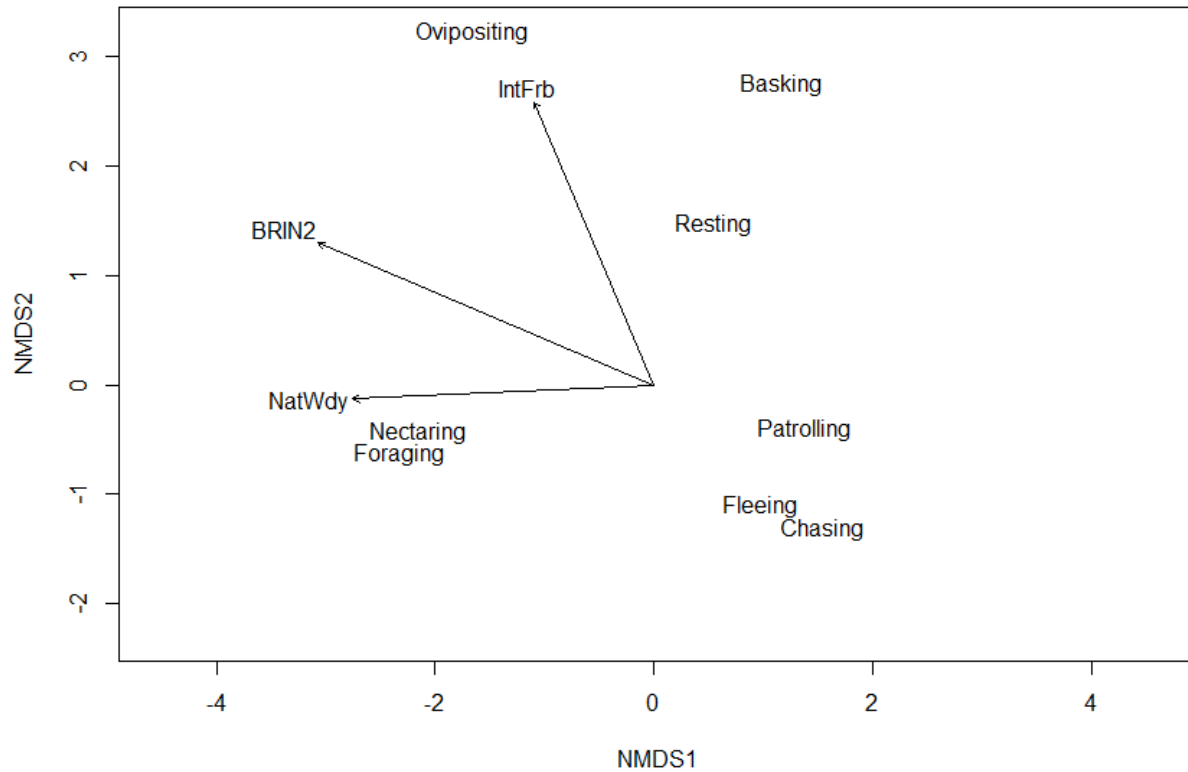


Figure 2.4. Ordination plot displaying regal fritillary behaviors and explanatory vegetation variables ($p \leq 0.1$). We used two dimensions and a maximum stress of 0.15. We used total duration of time in each behavior for all 32 regal fritillary observations. (Codes are: IntFrb = Introduced Forb Cover, BRIN2 = Smooth Brome (*Bromus inermis*) Cover, NatWdy = Native Woody Plant Cover).

Table 2.2. All the combinations of behaviors and vegetation composition variables that were indicated as significant in the two ordinations (Figures 4 & 5). Marginally significant models are marked with °, significant models are marked with *, and very significant models are marked with **. Conditional R² values are given where applicable. All models included treatment as a fixed effect and sex of individual butterfly as a random effect.

Species	Behavior	Vegetation Variable	P-Value	R ²
Monarch	Nectaring	Native Forb Cover	0.058*	0.058
Monarch	Nectaring	Floral Richness	0.577	--
Monarch	Ovipositing	Native Forb Cover	0.8306	--
Monarch	Nectaring	Conspecific Abundance	0.3839	--
Monarch	Ovipositing	Conspecific Abundance	0.5654	--
Monarch	Bare Ground	Mating	0.0009**	0.151
Regal Fritillary	Chasing	Introduced Forb Cover	0.278	--
Regal Fritillary	Chasing	Smooth Brome Cover	0.103°	--
Regal Fritillary	Fleeing	Introduced Forb Cover	0.472	--
Regal Fritillary	Fleeing	Smooth Brome Cover	0.326	--
Regal Fritillary	Patrolling	Introduced Forb Cover	0.150	--
Regal Fritillary	Patrolling	Smooth Brome Cover	0.005**	0.25
Regal Fritillary	Ovipositing	Introduced Forb Cover	0.264	--
Regal Fritillary	Ovipositing	Smooth Brome Cover	0.178	--

Discussion

Our study focused on the time budgets of monarchs and regal fritillaries in grasslands with different disturbance regimes, and in particular, we assessed behavioral time budgets between different patch types. Most previous research on these species in grasslands as focused on population-level dynamics (e.g., Kral et al. 2018; Moranz et al. 2014). We quantified monarch and regal fritillary behavioral time budgets in grasslands managed with varying spatiotemporal disturbances, and did not find differences in time budgets based on management type. We also assessed the influence of vegetation characteristics on the behaviors of these species, and we did find that some individual behaviors are altered by certain vegetation characteristics. Ultimately, we suggest that further studies include more specific behavioral observations in order to further investigate these relationships.

We did not find differences in time budgets between patch types for either monarchs or regal fritillaries. However, we expect that a larger dataset would amplify trends. In particular, we expect differences in the likelihood of oviposition among patch types, due to the requirements of each species for this behavior. We would anticipate that regal fritillaries oviposit almost exclusively in areas with the longest time since fire, as they prefer to oviposit in dense litter, where their caterpillars then overwinter before feeding in the spring (Kopper et al. 2000). For monarchs, we anticipate that the one year since fire would prove most attractive, since this is where the most milkweed is in bloom and easily detectable (Baum and Sharber 2012; Garlick 2007).

Vegetation composition may help us explain some individual behaviors in greater detail. Smooth brome, which is an invasive, non-native grass, dominates much of our grazing-only pastures, but is less prevalent in our grazing and fire pastures. Smooth brome is known to alter

the physical structure of prairies where it invades heavily (Otfinowski and Kenkel 2010). In support of this idea, we found a correlation between smooth brome cover and visual obstruction. Such altered vegetation structure may impede male regal fritillaries from their preferred patrolling style, where they fly low over the vegetation canopy, occasionally dipping into the canopy (Kopper et al. 2001). Although regal fritillary mating habits have not been recorded, it is possible that this is part of how males seek females (Thurman et al. 2018; Estrada and Gilbert 2010), which could imply that smooth brome cover could hinder mating behavior as well as flight behaviors. We also found a trend between monarch mating behavior and bare ground. The trend between native forb cover and nectaring and foraging behaviors for monarchs is to be expected. Butterflies detect flowers both by vision and olfactory senses (Koshitaka et al. 2011; Balkenius et al. 2006; Kelber and Pfaff 1999), so it makes sense that the more flowering plants there are, the easier it will be for butterflies to find them. The potentially negative trend between native forb cover, which includes milkweed, and oviposition is likely due in part to the low number of observations of oviposition. Additionally, previous studies have found that monarchs prefer to oviposit in less dense milkweed patches (Pitman et al. 2018), which may explain the inverse trend we observed in the ordination.

Our study was challenging primarily because of sample sizes. After two summers of data collection, we had a total of 64 monarchs and 32 regal fritillaries. However, because of the conservation status of these two species (Schultz et al. 2018, Hammond and McCorkle 1983), we believe that further years of data collection may not yield greatly increased samples. We initially intended to compare time budgets for both species between treatment types, not patch types, but this proved impossible for regal fritillaries. We had only one successful observation of a regal fritillary in a grazing-only pasture. Almost all of our unsuccessful observations of regal

fritillaries failed while they were patrolling, in observations that consisted solely of patrolling. This leads us to believe that most regal fritillaries do not regularly occupy our grazing-only pastures, and only utilize them as a corridor to move to a more suitable landscape (Keyghobadi et al. 2006).

In this study, we sought to understand behaviors of monarchs and regal fritillaries across areas with different disturbance regimes. Although we did not find differences in the total time budgets of either species, we did find that some vegetation characteristics influence individual behaviors. Most notably, regal fritillaries are less likely to exhibit patrolling behavior in areas of high smooth brome cover. Smooth brome is a growing concern in the northern Great Plains (Otfinowski and Kenkel 2010), so we suggest that managers who aim to support regal fritillaries implement strategies to mitigate it. We also suggest that to support both species, managers implement strategies that encourage a diverse, continuous floral community throughout the entire butterfly flight season.

References

- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Cane, J., Cox, P. A., Dalton, V., Feinsinger, P., Ingram, M., Jones, C. E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-morales, S., Nabhan, G. P., Pavlik, B., Tepedino, V., & Torchio, P. (1998). The Potential Consequences of Pollinator Declines on the Conservation of Biodiversity and Stability of Food Crop Yields. *Conservation Biology*, 12(1), 8–17.
- Anderson, R. C. (2006). Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *The Journal of the Torrey Botanical Society*, 133(4), 626–647.

- Balkenius, A., Rosén, W., & Kelber, A. (2006). The relative importance of olfaction and vision in a diurnal and a nocturnal hawkmoth. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *192*(4), 431–437. <https://doi.org/10.1007/s00359-005-0081-6>
- Baum, K. A., & Sharber, W. V. (2012). Fire creates host plant patches for monarch butterflies. *Biology Letters*, *8*(6), 968–971. <https://doi.org/10.1098/rsbl.2012.0550>
- Bennett, V. J., Smith, W. P., & Betts, M. G. (2012). Evidence for Mate Guarding Behavior in the Taylor's Checkerspot Butterfly. *Journal of Insect Behavior*, *25*(2), 183–196. <https://doi.org/10.1007/s10905-011-9289-1>
- Brereton, T., Roy, D. B., Middlebrook, I., Botham, M., & Warren, M. (2010). The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation*, *15*, 139–151. <https://doi.org/10.1007/s10841-010-9333-z>
- Britten, H. B., & Glasford, J. W. (2002). Genetic population structure of the Dakota skipper (Lepidoptera: Hesperia dacotae): A North American native prairie obligate. *Conservation Genetics*, *3*(4), 363–374. <https://doi.org/10.1023/A:1020576732699>
- Brower, L. P., Taylor, O. R., Williams, E. H., Slayback, D. A., Zubieta, R. R., & Ramírez, M. I. (2012). Decline of monarch butterflies overwintering in Mexico: Is the migratory phenomenon at risk? *Insect Conservation and Diversity*, *5*(2), 95–100. <https://doi.org/10.1111/j.1752-4598.2011.00142.x>
- Brown, J., York, A., Christie, F., & McCarthy, M. (2017). Effects of fire on pollinators and pollination. *Journal of Applied Ecology*, *54*(1), 313–322. <https://doi.org/10.1111/1365-2664.12670>

- Carleton, A., & Schultz, C. B. (2013). Restoration action and species response: Oviposition habits of *Plebejus icarioides fenderi* (Lepidoptera: Lycaenidae) across a restoration chronosequence in the Willamette Valley, Oregon, USA. *Journal of Insect Conservation*, *17*(3), 511–520. <https://doi.org/10.1007/s10841-012-9535-7>
- Couture, J. J., Serbin, S. P., & Townsend, P. A. (2015). Elevated temperature and periodic water stress alter growth and quality of common milkweed (*Asclepias syriaca*) and monarch (*Danaus plexippus*) larval performance. *Arthropod-Plant Interactions*, *9*(2), 149–161. <https://doi.org/10.1007/s11829-015-9367-y>
- Debinski, D. M., Moranz, R. A., Delaney, J. T., Miller, J. R., Engle, D. M., Winkler, L. B., McGranahan, D. A., Barney, R. J., Trager, J. C., Stephenson, A. L., & Gillespie, M. K. (2011). A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere*, *2*(12), art131. <https://doi.org/10.1890/ES11-00226.1>
- Estrada, C., & Gilbert, L. E. (2010). Host plants and immatures as mate-searching cues in *Heliconius* butterflies. *Animal Behaviour*, *80*(2), 231–239. <https://doi.org/10.1016/j.anbehav.2010.04.023>
- Fish, U. S., & Service, W. (2016). *Species status assessment: Monarch butterfly*. <https://www.fws.gov/savethemonarch/pdfs/SSAFactSheet.pdf>
- Flockhart, D. T., Pichancourt, J. B., Norris, D. R., & Martin, T. G. (2015). Unravelling the annual cycle in a migratory animal: Breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology*, *84*(1), 155–165. <https://doi.org/10.1111/1365-2656.12253>

- Fourcade, Y., & Öckinger, E. (2016). Host plant density and patch isolation drive occupancy and abundance at a butterfly's northern range margin. *Ecology and Evolution*, 7(1), 331–345.
<https://doi.org/10.1002/ece3.2597>
- Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience*, 51(8), 625–632.
[https://doi.org/10.1641/0006-3568\(2001\)051\[0625:RHOREM\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2)
- Fuhlendorf, S. D., & Engle, D. M. (2004). Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, 41(4), 604–614.
<https://doi.org/10.1111/j.0021-8901.2004.00937.x>
- Fuhlendorf, S. D., Engle, D. M., Elmore, R. D., Limb, R. F., & Bidwell, T. G. (2012). Conservation of Pattern and Process: Developing an Alternative Paradigm of Rangeland Management. *Rangeland Ecology & Management*, 65(6), 579–589.
<https://doi.org/10.2111/REM-D-11-00109.1>
- Fuhlendorf, S. D., Engle, D. M., Kerby, J., & Hamilton, R. (2009). Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, 23(3), 588–598. <https://doi.org/10.1111/j.1523-1739.2008.01139.x>
- Garlick, K. M. (2007). Visual and olfactory sensory systems employed by monarch butterflies (*Danaus plexippus*). *American Midland Naturalist*, 158(2), 207–214.
- Grant, T. J., Parry, H. R., Zalucki, M. P., & Bradbury, S. P. (2018). Predicting monarch butterfly (*Danaus plexippus*) movement and egg-laying with a spatially-explicit agent-based model: The role of monarch perceptual range and spatial memory. *Ecological Modelling*, 374(September 2017), 37–50. <https://doi.org/10.1016/j.ecolmodel.2018.02.011>

- Hammond, P. C., & McCorkle, D. V. (1983). The Decline and Extinction of *Speyeria* Populations Resulting from Human Environmental Disturbances (Nymphalidae: *Arygininae*). In *The Journal of Research on the Lepidoptera* (Vol. 22, Issue 4, pp. 217–224).
- Järv, L., Kotta, J., Kotta, I., & Raid, T. (2011). Linking the Structure of Benthic Invertebrate Communities and the Diet of Native and Invasive Fish Species in a Brackish Water Ecosystem. *Annales Zoologici Fennici*, 48(3), 129–141.
<https://doi.org/10.5735/086.048.0301>
- Keeler, M. S., Chew, F. S., Goodale, B. C., & Reed, J. M. (2006). Modelling the impacts of two exotic invasive species on a native butterfly: Top-down vs. bottom-up effects. *Journal of Animal Ecology*, 75(3), 777–788. <https://doi.org/10.1111/j.1365-2656.2006.01098.x>
- Kelber, A., & Pfaff, M. (1999). True colour vision in the orchard butterfly, *Papilio aegaeus*. *Naturwissenschaften*, 86(5), 221–224. <https://doi.org/10.1007/s001140050601>
- Keyghobadi, N., Unger, K. P., Weintraub, J. D., & Fonseca, D. M. (2006). Remnant populations of the regal fritillary (*Speyeria idalia*) in Pennsylvania: Local genetic structure in a high gene flow species. *Conservation Genetics*, 7(2), 309–313. <https://doi.org/10.1007/s10592-006-9127-8>
- Kopper, B. J., Charlton, R. E., & Margolies, D. C. (2000). Oviposition site selection by the regal fritillary, *Speyeria idalia*, as affected by proximity of violet host plants. *Journal of Insect Behavior*, 13(5), 651–665. <https://doi.org/10.1023/A:1007887809621>
- Kopper, B. J., Margolies, D. C., & Charlton, R. E. (2001). Life History Notes on the Regal Fritillary, *Speyeria idalia* (Drury) (Lepidoptera: Nymphalidae), in Kansas Tallgrass Prairie. *Journal of the Kansas Entomological Society*, 74(3), 172–177.

- Kopper, B. J., Shu, S., Charlton, R. E., & Ramaswamy, S. B. (2001). Evidence for Reproductive Diapause in the Fritillary *Speyeria idalia* (Lepidoptera: Nymphalidae). *Annals of the Entomological Society of America*, 94(3), 427–432. [https://doi.org/10.1603/0013-8746\(2001\)094\[0427:EFRDIT\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2001)094[0427:EFRDIT]2.0.CO;2)
- Koshitaka, H., Arikawa, K., & Kinoshita, M. (2011). Intensity contrast as a crucial cue for butterfly landing. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 197(11), 1105–1112. <https://doi.org/10.1007/s00359-011-0671-4>
- Kral, K. C., Hovick, T. J., Limb, R. F., & Harmon, J. P. (2018). Multi-scale considerations for grassland butterfly conservation in agroecosystems. *Biological Conservation*, 226(July), 196–204. <https://doi.org/10.1016/j.biocon.2018.08.002>
- Landis, D. A., Fiedler, A. K., Hamm, C. A., Cuthrell, D. L., Schools, E. H., Pearsall, D. R., Herbert, M. E., & Doran, P. J. (2012). Insect conservation in Michigan prairie fen: Addressing the challenge of global change. *Journal of Insect Conservation*, 16(1), 131–142. <https://doi.org/10.1007/s10841-011-9398-3>
- Leong, K. . L., Yoshimura, M. A., Kaya, H. K., & Williams, H. (1997). Instar susceptibility of the monarch butterfly (*Danaus plexippus*) to the neogregarine parasite, *Ophryocystis elektroscirrha*. *Journal of Invertebrate Pathology*, 69(1), 79–83. <https://doi.org/10.1006/jipa.1996.4634>
- Long, O. M., Warren, R., Price, J., Brereton, T. M., Botham, M. S., & Franco, A. M. A. (2017). Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology*, 86(1), 108–116. <https://doi.org/10.1111/1365-2656.12594>

- Losey, J. E., & Vaughan, M. (2006). *The Economic Value of Ecological Services Provided by Insects*. *56*(4), 311–323.
- Mair, L., Thomas, C. D., Franco, A. M. A., & Hill, J. K. (2015). Quantifying the activity levels and behavioural responses of butterfly species to habitat boundaries. *Ecological Entomology*, *40*(6), 823–828. <https://doi.org/10.1111/een.12248>
- McGranahan, D. A., Engle, D. M., Fuhlendorf, S. D., Winter, S. L., Miller, J. R., & Debinski, D. M. (2013). Inconsistent outcomes of heterogeneity-based management underscore importance of matching evaluation to conservation objectives. *Environmental Science and Policy*, *31*, 53–60. <https://doi.org/10.1016/j.envsci.2013.03.005>
- McGranahan, D. A., Hovick, T. J., Elmore, R. D., Engle, D. M., Fuhlendorf, S. D., Winter, S. L., Miller, J. R., & Debinski, D. M. (2016). Temporal variability in aboveground plant biomass decreases as spatial variability increases. *Ecology*, *97*(3), 555–560. <https://doi.org/10.1890/15-0906.1>
- Moranz, R. A., Debinski, D. M., McGranahan, D. A., Engle, D. M., & Miller, J. R. (2012). Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodiversity and Conservation*, *21*(11), 2719–2746. <https://doi.org/10.1007/s10531-012-0330-2>
- Moranz, R. A., Fuhlendorf, S. D., & Engle, D. M. (2014). Making sense of a prairie butterfly paradox: The effects of grazing, time since fire, and sampling period on regal fritillary abundance. *Biological Conservation*, *173*, 32–41. <https://doi.org/10.1016/j.biocon.2014.03.003>

- Myers, M. C., Hoksich, B. J., & Mason, J. T. (2012). Butterfly response to floral resources during early establishment at a heterogeneous prairie biomass production site in Iowa, USA. *Journal of Insect Conservation*, *16*(3), 457–472. <https://doi.org/10.1007/s10841-011-9433-4>
- New, T. R. (1997). Are Lepidoptera an effective ‘umbrella group’ for biodiversity conservation? *Journal of Insect Conservation*, 5–12.
- Oksanen, J. (2015). *Multivariate Analysis of Ecological Communities in R: vegan tutorial*. [https://doi.org/10.1016/0169-5347\(88\)90124-3](https://doi.org/10.1016/0169-5347(88)90124-3)
- Otfinowski, R., & Kenkel, N. C. (2010). Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies. *Biological Invasions*, *12*(5), 1349–1361. <https://doi.org/10.1007/s10530-009-9551-z>
- Parham, G. (2015). U.S. Fish and Wildlife Service Will Study the Status of Four Midwest Wildlife Species. In *News Release*. <https://doi.org/10.1145/3132847.3132886>
- Pickens, B. A., & Root, K. V. (2009). Behavior as a tool for assessing a managed landscape: a case study of the Karner blue butterfly. *Landscape Ecology*, *24*, 243–251. <https://doi.org/10.1007/s10980-008-9302-z>
- Pitman, G. M., Flockhart, D. T. T., & Norris, D. R. (2018). Patterns and causes of oviposition in monarch butterflies: Implications for milkweed restoration. *Biological Conservation*, *217*(October 2017), 54–65. <https://doi.org/10.1016/j.biocon.2017.10.019>
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution*, *25*(6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>

- Rudolph, D. C., Ely, C. A., Schaefer, R. R., Williamson, J. H., & Thill, R. E. (2006). Monarch (*Danaus plexippus* L. Nymphalidae) migration, nectar resources and fire regimes in the Ouachita Mountains of Arkansas. *Journal of the Lepidopterists' Society*, 60(3), 165–170.
- Sala, O. E., Chapin Iii, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., Wall, D. H., ... Wall16, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Source: Science, New Series*, 287(5459), 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Samways, M. J. (2007). Insect Conservation: A Synthetic Management Approach. *Annual Review of Entomology*, 52(1), 465–487. <https://doi.org/10.1146/annurev.ento.52.110405.091317>
- Swartz, M. T., Ferster, B., Vulinec, K., & Paulson, G. (2015a). Measuring Regal Fritillary Butterfly (*Speyeria idalia*) Habitat Requirements in South-Central Pennsylvania: Implications for the Conservation of an Imperiled Butterfly. *Northeastern Naturalist*, 22(4), 812–829. <https://doi.org/10.1656/045.022.0414>
- Swartz, M. T., Ferster, B., Vulinec, K., & Paulson, G. (2015b). Measuring Regal Fritillary Butterfly (*Speyeria idalia*) Habitat Requirements in South-Central Pennsylvania: Implications for the Conservation of an Imperiled Butterfly. *Northeastern Naturalist*, 22(4), 812–829. <https://doi.org/10.1656/045.022.0414>
- Thomas, J. A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1454), 339–357. <https://doi.org/10.1098/rstb.2004.1585>

- Thurman, T. J., Brodie, E., Evans, E., & McMillan, W. O. (2018). Facultative pupal mating in *Heliconius erato*: Implications for mate choice, female preference, and speciation. *Ecology and Evolution*, 8(3), 1882–1889. <https://doi.org/10.1002/ece3.3624>
- Tiley, G. E. D. (2010). Biological Flora of the British Isles: *Cirsium arvense* (L.) Scop. *Journal of Ecology*, 98(4), 938–983. <https://doi.org/10.1111/j.1365-2745.2010.01678.x>
- Wang, X. G., & Messing, R. H. D. A. (2003). Foraging behavior and patch time allocation by *Fopius arisanus* (Hymenoptera: Braconidae), an egg larval parasitoid of tephritid fruit flies. *Journal of Insect Behavior*, 16(5), 593–612 ST-Foraging behavior and patch time all.
- Wilson, R. G., & McCarty, M. K. (1984). Germination, and Seedling and Rosette Development of Flodman Thistle (*Cirsium flodmanii*). *Weed Science*, 32(6), 768–773.