THE EFFECTS OF ECOLOGICAL MANAGEMENT ON

TALLGRASS PRAIRIE BUTTERFLIES AND THEIR

NECTAR SOURCES

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CHAPTER I

DISTANCE SAMPLING REVEALS DIFFERENCES IN BUTTERFLY

DETECTABILITY

Distance sampling reveals differences in butterfly detectability

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ABSTRACT

The Pollard walk line transect is the most frequently used technique for assessing the

relative abundance of butterflies, but the abundance estimates it provides are vulnerable

to biases due to interspecific and interbehavioral differences in butterfly detectability.

Distance sampling has reduced detectability biases for a variety of taxa, including birds,

marine mammals, and plants, but has rarely been utilized for studies of butterfly

communities. We performed distance sampling along line transects to assess

detectability of grassland butterflies. Analyses of distance data using Program Distance

revealed substantial variation in butterfly detectability among species and among

different behaviors. Surprisingly, there were no effects of habitat structure on butterfly

detectability in areas that varied in their fire and grazing regime. Substantial variation in

butterfly detectability may be a factor in many butterfly research and monitoring projects worldwide. Program Distance generates abundance estimates that account for differences in detectability. Therefore, we recommend that biologists consider supplementing line transect sampling with distance sampling for butterfly monitoring and research.

 1. Introduction

Accurate estimation of abundance is a goal of many ecological studies of populations and natural communities. A major challenge to accurate estimation of abundance is bias due to differences in detectability among species, habitats, and observers (Burnham and Anderson 1984, Buckland et al. 2001, Dennis et al. 2006). Variation in detectability can lead to spurious conclusions about spatial and/or temporal trends in abundance. Various forms of distance sampling have proven useful for accounting and correcting for these biases, thus enhancing accuracy of abundance estimates.   Line transect distance sampling, developed primarily by vertebrate ecologists (Gates et al. 1968, Burnham and Anderson 1984, Buckland et al. 2001), involves recording the distance of each study organism from the transect line at the moment the organism is first seen. These distances are used to model the declining probability of detecting an organism as its distance from the transect line increases. The resulting mathematical model, known as a detection function, can then be used to develop robust estimates of population density and absolute abundance.

Distance sampling has been used widely in studies of abundance of birds (Marsden 1999, Diefenbach et al. 2003, Norvell et al. 2003), mammals (Corn and Conroy

1998, Zerbini et al. 2007), herpetofauna (Swann et al. 2002, Mazerolle et al. 2007), plants (Buckland et al. 2007), and darkling beetles (Parmenter et al. 1989, Crist and Wiens 1995), but has seldom been used to assess abundance of butterfly populations (but see Pocewicz et al. 2009). For the last two decades, the Pollard walk line transect (Pollard and Yates 1993) has been the most commonly used technique for assessing relative abundance of butterflies in ecological research (Collier et al. 2006, Rudolph et al. 2006) as well as monitoring (Brown and Boyce 1998, 2001, Powell et al. 2007). This sampling technique consists of recording the numbers of each butterfly species seen within a set distance on either side while slowly walking a pre-determined transect route (Pollard and Yates 1993). Sampling via the Pollard walk line transect is rapidly learned, requires no special equipment, and provides data that can be used to generate an index of relative abundance for each species at each site.

However, abundance estimates generated from Pollard walk line transect data are vulnerable to bias due to differences in detectability among species (Dennis et al. 2006). An analysis of 19 years of data from the British Butterfly Monitoring Scheme revealed significant correlations between indices of abundance derived from Pollard walk line transects and various species traits such as wingspan, visual apparency, and typical adult behavior (Dennis et al. 2006). Those findings strongly imply detectability bias due to those species traits. Studies that use Pollard walk line transect data to compare the abundance of a single species across space or time are also be subject to detectability bias (Brown and Boyce 1998, Dennis et al. 2006, Kery and Plattner 2007). For instance, sparse cover of 0.05-m tall plants in heavily grazed grasslands is unlikely to obscure butterflies from observers, whereas dense cover of grasses 2-m tall might reduce butterfly

detectability substantially, thus lowering the number of butterflies observed. Unfortunately, if such variation in detectability occurs, the researcher obtaining data via the Pollard walk line transect is unable to correct for this bias. Therefore, alternative sampling methods for butterflies that account and correct for detectability bias are needed (Dennis et al. 2006, Kery and Plattner 2007).

One partial solution to variable detectability is to record only butterflies seen within a short distance (often 2.5 m) of the observer, under the assumption that all butterflies so close to the observer will be detected, regardless of species traits or habitat structure. The use of a narrow strip, while likely reducing detectability bias, may not eliminate them completely. For example, some small, dull-colored species may be difficult to detect at distances as short as 2 meters. Restricting sampling to such narrow strips also might greatly reduce the number of butterflies detected relative to unlimited strip widths (Brown and Boyce 1998). This would be especially problematic with studies that seek to assess the abundance of rare species.

Some have advocated the use of line transect distance sampling for estimating butterfly abundance, due to the potential for distance sampling to account for detectability bias, and its use of an operationally unrestricted strip width, which might increase the number of butterflies observed per unit effort when compared to the Pollard walk line transect (Brown and Boyce 1998, Powell et al. 2007). However, no literature has demonstrated the ability of line transect distance sampling to account for detection bias among butterfly species. Although studies of *Lycaeides melissa samuelis* (Brown and Boyce 1998) and *Speyeria idalia* (Powell et al. 2007) used line transect distance sampling to generate estimates of population density, neither study tested for effects of

individual behavior on detectability, nor did they demonstrate a significant effect of habitat structure on detectability. Therefore, a compelling case for using distance sampling for studies of butterfly communities in heterogeneous environments has yet to be made.

In this paper, we examine variation in butterfly detectability and the corresponding role of distance sampling in generating abundance estimates that account for variable detectability. Our specific objectives were: (1) to determine if butterfly species differ significantly in their detectability; (2) to assess the relationship between butterfly size and detectability; (3) to examine the effect of butterfly behavior on detectability; and (4) to determine the influence of grassland vegetation structure on butterfly detectability. By achieving these objectives, we hope to provide scientists with a better understanding of the utility of distance sampling for butterfly research and monitoring projects. We predicted that butterfly species would differ in their detectability, and that these differences would be biologically meaningful. Furthermore, we predicted that individual butterfly behavior would affect detectability. Lastly, we predicted that high structured grassland vegetation would reduce butterfly detectability relative to low structured vegetation.

2. Methods

2.1. *Study design and treatments*

In 2006 and 2007, we collected distance data on all butterfly species observed at four tallgrass prairie sites managed by the Missouri Department of Conservation in southwestern Missouri, U.S.A. (Figure 1). Each site was divided into two pastures, with one managed with rotational fire and ungrazed by cattle, and one managed with rotational fire and cattle grazing (Fuhlendorf and Engle 2004). Prescribed burns were performed in March of 2006 and 2007. The result of this management was a variable grassland mosaic where habitat structure varies from recently burned or burned and grazed to undisturbed prairie (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006).

2.2. *Butterfly sampling*

We performed line transect distance sampling to assess the detectability and abundance of all butterfly species during five sampling periods in 2006 (May 22-26, June 5-9, June 27-30, July 17-20, and September 6-9) and four sampling periods in 2007 (June 5-11, June 25-27, July 23-26, and September 20-22). During each period, we sampled at least one transect route in each prairie management unit (mean transect length = 662 m, standard deviation = 289 m). The management units ranged from 14 to 37 ha. Transect routes were straight, and were placed systematically at the center of each unit. All portions of each transect route were at least 50 m from unit boundaries (to avoid edge effects) and 50 m from the nearest transect route (to minimize repeat sightings).

Butterfly sampling was performed during weather conditions appropriate for butterfly flight (temperature > 20 ℃, cloud cover < 70%, wind < 20 km/hr). During sampling, an observer walked the transect at 2 km/hr and recorded butterflies seen within

the 180º field-of-view spanning from the observer's left to the observer's right. Each

butterfly was identified to the species level if possible and its behavior (e.g. flying,

nectaring, perching, etc.) when first detected was recorded. If we deemed that a butterfly

was less than 5 m from the transect line, we visually estimated the perpendicular distance

between the butterfly's location and the transect line. For butterflies ≥5 m from the

transect, we used Bushnell Yardage Pro© laser rangefinders to measure the perpendicular

distance between the butterfly's location and the transect line. These rangefinders can

estimate distances from 5 to 200 m, and are accurate to +/- 1.0 m (Bushnell Performance

Optics ® 2004). Butterfly nomenclature follows that in Opler et al. (2010).

2.3. *Assessing vegetation structure*

To test our predictions about the effects of vegetation structure on butterfly

detectability, we compared butterfly detectability between two vegetation structures: (1)

low structured grassland (due to recent fire and intense grazing), and (2) high structured

grassland (due to little or no recent fire or grazing). Vegetation structure was quantified

in June of 2006 and 2007 at approximately 100 sampling points per prairie management

unit by biologists from the Missouri Department of Conservation (MDC). At each

sampling point, MDC biologists placed upright a 0.10 m wide x 2.0 m tall cover board,

and from 4 m away they assessed the percent visual obstruction in twenty 0.1-m vertical

strata. Values from the sampling stations were averaged to obtain the mean percent

visual obstruction for each prairie management unit (Harrell and Fuhlendorf 2002).

Intensely grazed prairie management units had mean percent visual obstruction of 12.6%,

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whereas ungrazed prairie units had mean percent visual obstruction of 23.5%. Analyses of variance support these differences at p < 0.001, indicating that these grassland types differed in habitat structure.

2.4. *Analyzing distance data*

In this study, we examined the effects of species, behavior, and habitat structure on butterfly detectability. We used distance sampling to generate estimates of effective strip width, a summary measure of detectability that can be compared among species, behaviors, habitats, and other factors (Brown and Boyce 1998, Forcada and Hammond 1998, Focardi et al. 2002). Effective strip width is defined as the distance x at which the number of individuals detected beyond x is equal to the number that one failed to detect within distance x (Buckland et al. 2001, p.53). Increasing effective strip width indicates increasing detectability of a set of objects, *i.e.* a species that is frequently detected at great distances from the transect line has a greater effective strip width than a species seldom detected at such distances.

To estimate effective strip width, we modeled detection functions using the Conventional Distance Sampling analysis engine of Program Distance 5.0, release 2 (Thomas et al. 2006). For each butterfly species, we pooled observations of the same behavior from multiple sites that shared the same habitat structure, and used the pooled observations to estimate the detection function and corresponding effective strip width for that dataset. Development of robust and accurate detection functions becomes more likely with a sample size of at least 60 observations (Buckland et al. 2001), therefore we

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limited our detection function modeling to datasets that met this sample size requirement, except in the case of *Cercyonis pegala*, with 57 and 56 observations in low structured and high structured grassland respectively.

For each dataset, we modeled detection functions from 12 general model types, which consisted of each of the possible combinations of four key functions (half normal, uniform, hazard rate, and negative exponential) and three adjustment types (cosine, simple polynomial, and hermite polynomial). For each of the 12 general model types, Program Distance reported the specific model with the lowest Akaike Information Criterion (AIC) value (Burnham and Anderson 2002). Of those 12 specific models, we selected the final model based on AIC values and Chi-square goodness of fit tests, as well as verifying that the detection function model closely matched the distribution of distance data when both were plotted together on a frequency histogram (Buckland et al. 2001). After selecting a detection function for each dataset, we recorded the effective strip width, plus its standard error and 95% confidence interval.

Sixty percent of butterflies observed in our study were flying when first detected, whereas only 25% were nectaring and 12% were perching. When including observations from all grassland management units, regardless of their vegetation structure, we observed at least 60 flying individuals of the following species: *C. pegala, Colias eurytheme, Cupido comyntas, Danaus plexippus, Euptoieta claudia, Papilio polyxenes*, *Phyciodes tharos*, *Precis coenia*, and *S. idalia*. For most species, the rarity of behaviors observed other than flying made it impossible for us to model the detection functions of those behaviors effectively. However, we were able to compare effective strip widths

among multiple behaviors for four species: *C. comyntas*, *P. tharos*, *P. coenia*, and *S. idalia*.

For our analysis of the effects of habitat structure on detectability, we made 60 or more observations of flying butterflies in each of the two habitat structure categories for the following species: *S. idalia*, *C. pegala*; *P. tharos*, and *C. comyntas*. To be able to meet the 60 observation criterion for *Colias philodice*, *C. eurytheme*, and *Pontia protodice*, we pooled distance observations from these species, which we suspect are similar in their detectability because of their similar size, shape, behavior, and brightness of color. Such pooling of similar species is an accepted practice for the analysis of distance sampling data (Marsden 1999, Alldredge et al. 2007).

2.5. *Statistical analyses*

We compared effective strip widths among species, among behaviors and between habitat structures for each species, using Z tests with $\alpha = 0.05$ (Buckland et al. 2001). We performed linear regression using SPSS 15.0 (SPSS 2006) to examine the effects of wingspan on 1) detectability of flying butterflies and 2) interhabitat variation in detectability (calculated as the percent difference in ESW for a taxon among low and high structured grassland).

3. Results

3.1. *Interspecific variation in detectability*

In low structured and high structured grasslands, *C. comyntas* and *P. tharos* did not differ significantly in effective strip width; therefore, they did not differ in detectability. However, these species were much more difficult to detect than *C. pegala*, *S. idalia*, and the three pierids (Table 1). *C. pegala* was more difficult to detect than the three pierids and *S. idalia* in low structured grassland. In high structured grasslands, *C. pegala* was more difficult to detect than *S. idalia* but not the three pierids. Lastly, the three pierids were more difficult to detect than *S. idalia* in low structured grassland, but not in high structured grassland (Table 1).

When we expanded our analysis to include species with at least 60 observations regardless of grassland vegetation structure, we once again found that many species differed from one another in their detectability (Table 2). The magnitude of the differences was often large. For instance, the effective strip width of *Danaus plexippus* was more than 8 times greater than that of *C. comyntas* or *P. tharos*.

3.2. Relationships between butterfly wingspan and detectability

In low structured grassland (Figure 2a), there was a linear relationship between butterfly wingspan and detectability ($r^2 = 0.828$, n = 5 taxa, p = 0.020), with effective strip width increasing as wingspan increased, as indicated by the equation

$$\text{effective strip width (m)} = -4.674 + 0.238*\text{wingspan (mm)}. \qquad (1.1)$$

In high structured grassland (Figure 2b), there was a similar significant relationship, ($r^2 =$ 0.821, n = 5 taxa, p = 0.022), represented by the equation

$$\text{effective strip width (m)} = -3.275 + 0.188*\text{wingspan (mm)}. \tag{1.2}$$

When considering observations from the full range of variation in grassland structure (Figure 2c), wingspan again was a useful predictor of butterfly detectability ($r^2 = 0.887$, n = 9 species, p < 0.001), as represented by the equation

$$\text{effective strip width (m)} = -3.537 + 0.183*\text{wingspan (mm)} . \tag{1.3}$$

3.3. *Effects of behavior on butterfly detectability*

Individual behavior affected the detectability of four of the five taxa examined (Table 3). Flying individuals of *C. comyntas* were detected at significantly greater distances than perching individuals. Flying individuals of the three pierids and *S. idalia* and were more easily detected than nectaring individuals. For *P. tharos*, all three behaviors differed significantly in effective strip width, with nectaring individuals the easiest to detect and flying individuals the most difficult (Table 3). We failed to find evidence of an effect of behavior on the detectability of *Precis coenia*.

3.4. *Variation in butterfly detectability between different vegetation structures*

Grassland structure did not affect detectability for any of the five taxa examined (Table 1). However, we found a positive relationship between butterfly wingspan and the degree of interhabitat variation in detectability exhibited by each taxon at $p = 0.10$ ($r^2 = 0.532$, $n = 5$).

4. Discussion

4.1. *Overview*

Our study demonstrates that butterfly detectability in grassland is strongly dependent on butterfly size, moderately dependent on behavior of individual butterflies, but independent of or at most weakly dependent on variation in grassland vegetation structure. In most cases, the number of individuals observed were well above the guideline of 60 observations recommended by the developers of Program Distance (Buckland et al. 2001), providing evidence that the differences in detectability we found are robust. Given our results together with many examples demonstrating the importance of using distance sampling for other taxa (Buckland et al. 2001, Norvell et al. 2003), we find it surprising that no one has examined its utility to the study of butterfly communities.

4.2. *Interspecific variation in detectability*

As we had predicted, there was substantial interspecific variation in detectability, and there was a strong positive relationship between wingspan and detectability. For example, *S. idalia*, which has a median wingspan of 92 mm (Opler 1998), was detectable at distances approximately seven times greater than *C. comyntas*, which has a median wingspan of only 25 mm (Opler 1998). That the effective strip widths of these species differed so much is biologically significant as well as statistically significant, because it is evidence that sampling methods that do not correct for differential detectability may produce highly biased estimates of butterfly abundance. Our data support previous research (Brown and Boyce 1998, Dennis et al. 2006) that found Pollard walk line transects are prone to produce biased estimates of the relative abundance of each species; biased estimates are particularly problematic for studies of butterfly community composition (Dennis et al. 2006).

In contrast, distance sampling enables one to estimate differences in detectability and to adjust population estimates accordingly, because of the inverse relationship between effective strip width and population density, as seen in the equation:

$$D = n \,/\, (L{\cdot}2{\cdot}esw) \tag{1.4}$$

where D = the estimate of population density,

n = the number of individuals observed while walking a transect,

L = the length of the transect,

and *esw* = the effective strip width on each side of the transect line (Burnham and Anderson 1984, Buckland et al. 2001).

Butterfly wingspan is not the only factor that leads to interspecific variation in detectability. Morphological characteristics such as color and brightness of color can influence detectability, as can behavioral characteristics such as the amount of time spent flying, the speed of the flight, and the height of the flight (Gaston et al. 1995, Dennis et al. 2006). In our study, three pierids (*P. protodice*, *C. philodice*, and *C. eurytheme*) were detected at greater distances than those predicted by our regression model. Their bright colors (white, yellow, and yellow/orange respectively) contrasted well with the green prairie vegetation, and may have been an important reason that these species were more detectable than larger but more dull-colored species, *C. pegala* and *Euptoieta claudia*. More research using distance sampling is needed to further elucidate the influences of butterfly morphology on detectability.

Distance sampling is likely to be within the budget of most butterfly researchers, as it adds little cost beyond that incurred by sampling via the Pollard walk line transect. Laser rangefinders suitable for distance sampling are available for $140. Program Distance, the software required for analyzing distance data is available free on the Internet, as are some excellent manuals for learning how to use the software. Recording distances in the field requires little additional time. Learning how to use the software can consume much time; enrolling in a Program Distance training session to expedite learning might be worth the fee.

4.3. *Interbehavioral variation in detectability*

For four taxa, individual butterfly behavior had moderate effects on the distance at which an individual was detected. It is difficult for us to generalize about the effects of certain behaviors on detectability, as their effects were species-dependent. For instance, though nectaring individuals of two taxa (*S. idalia* and the Family Pieridae) were more difficult to detect than flying individuals, the reverse was true for *P. tharos*. We speculate that small, low-flying species such as *P. tharos* that are difficult to detect when in flight may become easier to detect when nectaring on bright colored flowers because the flowers draw the attention of the observer. We propose that this hypothesis be tested in the field.

In their analysis of data from the United Kingdom's Butterfly Monitoring Scheme, which uses the Pollard walk line transect, Dennis et al. (2006) demonstrated that behavioral traits of species were correlated with abundance estimates for those species. From this, they inferred Pollard walk line transect data are subject to detectability biases. Our findings suggest that Pollard walk line transect data are also subject to bias not only due to species traits, but also due to variation in the behavior of individuals within a species. Because the relative frequencies of butterfly behaviors vary spatiotemporally (Scott 1986, Kemp and Rutowski 2001, Devries et al. 2008), failure to account for behaviorally-mediated detectability variation can bias interspecific and intraspecific comparisons of abundance. For instance, one can imagine two sites in southwestern Missouri with equal population density of *S. idalia*, but at one site most individuals are nectaring, whereas at the other most butterflies are flying in search of sparse nectar sources and/or mates. Given that scenario, our findings lead us to predict that the number

of butterflies observed at the former site via the Pollard walk line transect will be biased downward due to the lower detectability of nectaring butterflies relative to flying ones.

To our knowledge, this study is the first to use distance sampling to test for and demonstrate the effects of individual behavior on butterfly detectability. As our research was conducted using only a few species in one vegetation type, much additional research is necessary to discern whether or not this phenomenon is widespread geographically and taxonomically.

4.4. *Why did habitat structure fail to affect detectability?*

Habitat structure is often an important source of detectability bias in ecological studies (Buckland et al. 2001, Focardi et al. 2002, Somershoe et al. 2006). However, we failed to find an effect of habitat structure on detectability of five butterfly taxa, even though the structural differences involved are known to have major effects on other ecological factors, such as bird community composition (Fuhlendorf et al. 2006). In our case, it appears that the taller grasses and forbs of high structured grassland failed to obstruct our view of butterflies in flight. Therefore, we tentatively conclude that for the taxa we studied, habitat structure of Missouri tallgrass prairies with minimal woody plant cover has little effect on butterfly detectability, and is not an important source of bias for Pollard walk data collected there. We are aware of only one study that has used distance sampling to examine the effects of habitat structure on butterfly detectability. In a study of the *L. melissa samuelis* in oak savannahs of Wisconsin, USA, there was no effect of percent shrub cover on butterfly detectability (Brown and Boyce 1998).

In finding a positive relationship between butterfly wingspan and the degree of interhabitat variation in detectability, we provided some evidence suggesting that such variation is greater for very large species than for small species. If this is verified by further research, choosing a methodology that detects and corrects for detectability bias due to habitat structure will be more important for a large species like *S. idalia* (with a wingspan of 92 mm) than smaller species.

We suspect that interhabitat variation in butterfly detectability is likely to be more pronounced when comparing observations among plant communities that differ more starkly than the two different grassland structures described in our study; for instance, when comparing butterfly abundances between grasslands and shrublands, or among grasslands, shrublands, and forests, as in recent studies (Hogsden and Hutchinson 2004, Waltz and Covington 2004, Poyry et al. 2005). For such studies in the future, we suggest that investigators consider using distance sampling to recognize and correct for differences in detectability that might exist.

4.5. *Conclusions*

In our study, distance sampling revealed variation in butterfly detectability due to species differences and individual behavior. Our findings support those of Dennis et al. (2006) and Kery and Plattner (2007), lending further evidence that Pollard walk line transects are subject to detectability biases. Given the high degree of interspecific variation in detectability we found, we conclude sampling methods that fail to account for

this bias that will be especially problematic for butterfly community studies that seek to compare abundances among species.

Fortunately, the algorithms built into Program Distance allow one to generate abundance estimates that have been adjusted to account for detectability biases. We recommend research to compare butterfly abundance estimates obtained via distance sampling with estimates derived from capture-mark-recapture (Watt et al. 1977) and mixed approaches such as those that combine Pollard walk line transects with capture-mark-recapture (Gross et al. 2007). However, given the variation in butterfly detectability that has been demonstrated, and the known robustness of estimates generated by distance sampling (Burnham et al. 1979, Buckland 2006), we recommend that biologists who estimate butterfly abundance consider using distance sampling to reduce sampling bias caused by variation in detectability.

Acknowledgments

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Table 1. Effective strip width (ESW) for distance data from butterflies in flight, compared among species and between two levels of grassland structure. There are no significant within-row differences. Species are listed in order of their wingspan, from smallest to largest.

Scientific Name	Low structured grassland					High structured grassland				
			95% C.I.[3]		N			95% C.I.		N
	ESW[1] (m)	S.E.[2]	Lower	Upper		ESW (m)	S.E.	Lower	Upper	
Cupido comyntas	2.2[a]	0.3	1.9	2.9	116	2.0[a]	0.3	1.4	2.7	104
Phyciodes tharos	2.3[a]	0.3	1.9	2.9	142	2.0[a]	0.2	1.7	2.4	194
Cercyonis pegala	7.1[b]	0.9	5.6	9.2	57	6.4[b]	1.1	4.6	8.9	56
three pierid species[4]	11.8[c]	1.9	8.6	16.1	65	10.1[bc]	2.2	6.5	15.7	60
Speyeria idalia	17.6[d]	1.6	14.6	21.1	64	14.0[c]	1.7	11.1	17.7	220

[1] Effective strip widths in the same column that do not share any letters are different at the p < 0.05 level as determined by Z tests.

[2] S.E. = standard error of effective strip width (m)

[3] C.I. = 95% confidence interval of effective strip width (m)

[4] *Colias eurytheme*, *Colias philodice*, and *Pontia protodice*

Table 2. Effective strip width (ESW) of butterfly species observed flying in a structurally diverse set of grasslands. Species are listed in order of their wingspan, from smallest to largest.

Scientific Name	Median Wingspan (mm)	ESW[5]	S.E.[6]	95% C.I.[7]		N
				Lower	Upper	
Cupido comyntas	25	**2.0ᵃ**	0.2	1.8	2.4	289
Phyciodes tharos	36	**1.9ᵃ**	0.1	1.7	2.1	547
Precis coenia	54	**5.7ᵇ**	0.6	4.6	7.1	162
Colias eurytheme	58	**10.5ᶜ**	2.0	7.2	15.2	108
Cercyonis pegala	62	**7.0ᵇ**	1.0	5.3	9.2	112
Euptoieta claudia	62	**6.0ᵇ**	0.8	4.5	8.0	65
Speyeria idalia	92	**13.9ᶜᵈ**	1.2	11.7	16.5	402
Papilio polyxenes	95	**12.5ᶜᵈ**	1.7	9.5	16.4	74
Danaus plexippus	106	**16.7ᵈ**	1.5	14.0	20.0	71

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[5] Effective strip widths that do not share any letters are different at the $p < 0.05$ level as determined by Z tests.

[6] S.E. = standard error of effective strip width (m)

[7] C.I. = 95% confidence interval of the effective strip width (m)

Table 3. Effective strip width (ESW) of butterfly species engaging in different behaviors observed in a structurally diverse set of grasslands. Species are listed in order of their wingspan, from smallest to largest.

Scientific Name	FLYING			NECTARING			PERCHING		
	ESW[8] (m)	S.E.[9]	N	ESW (m)	S.E.	N	ESW (m)	S.E.	N
Cupido comyntas	2.0[a]	0.2	289				1.5[b]	0.1	128
Phyciodes tharos	1.9[b]	0.1	547	2.9[a]	0.3	166	2.3[a]	0.1	153
Precis coenia	5.7[a]	0.6	147	4.3[a]	0.5	49			
Family Pieridae (three pierid species[10])	12.6[a]	1.8	189	7.9[b]	1.4	55			
Speyeria idalia	13.9[a]	1.2	402	9.7[b]	0.8	118			

[8] Effective strip widths in the same row that do not share any letters are different at the $p < 0.05$ level as determined by Z tests.

[9] S.E. = standard error of effective strip width (m)

[10] *Colias eurytheme*, *Colias philodice*, and *Pontia protodice*

a)

b)
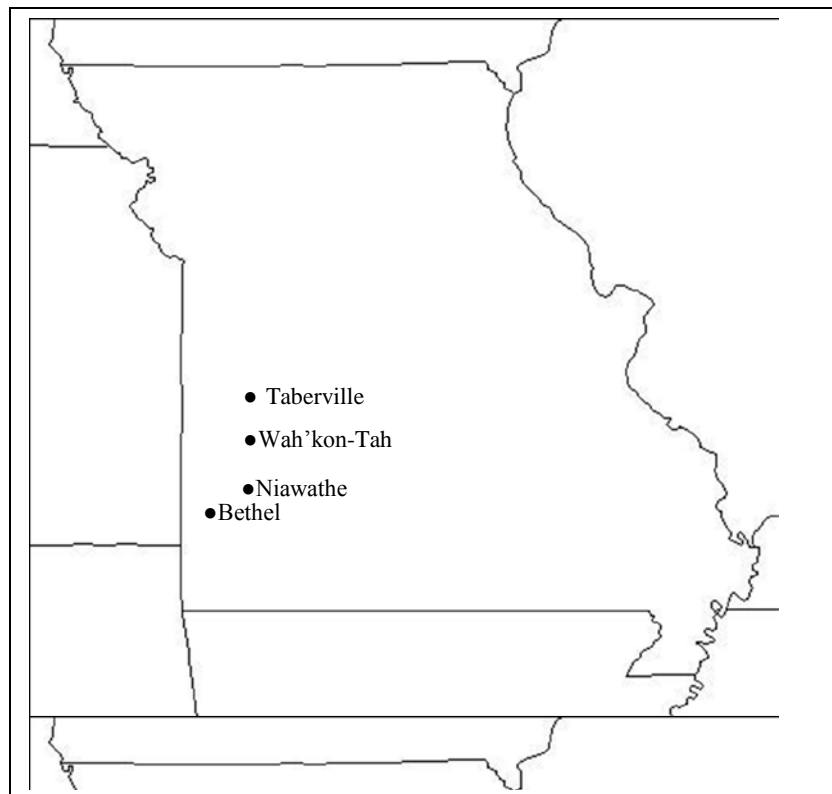
● Taberville

●Wah'kon-Tah

●Niawathe
●Bethel

Figure 1. Maps showing (a) the location of Missouri within the U.S.A., and (b) the locations of study sites in southwestern Missouri.
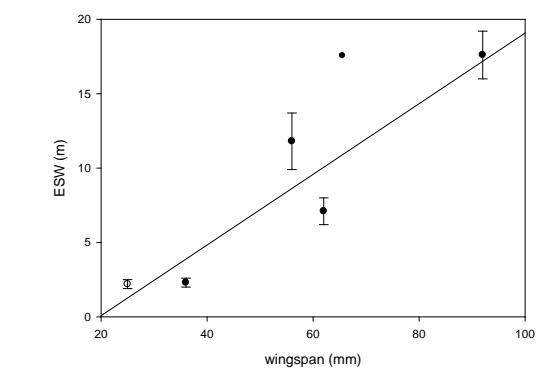
a)
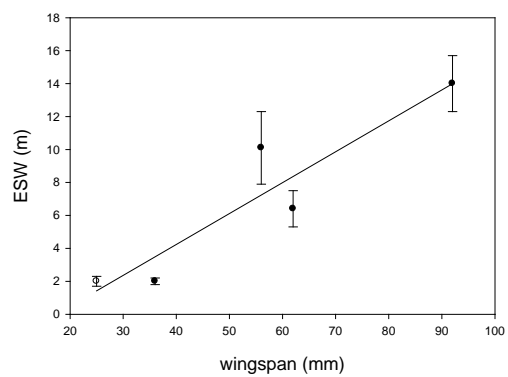
b)
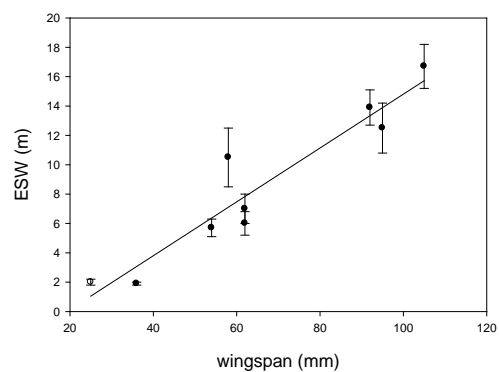
c)

Figure 2. Effective strip width (ESW) regressed over butterfly wingspan for observations from a) low structured grassland vegetation, b) high structured vegetation, and c) all grassland vegetation structures. Vertical bars represent standard errors of effective strip width.

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CHAPTER II

A STUDY OF NECTAR USE SPECIALIZATION:

SUBDOMINANT FORBS ARE PREFERRED NECTAR SOURCES

OF TALLGRASS PRAIRIE BUTTERFLIES

A study of nectar use specialization:

subdominant forbs are preferred nectar sources of tallgrass prairie butterflies

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ABSTRACT

Although the larvae of many butterflies are known to be host plant specialists, much less

is known about the dietary preferences of adult butterflies. We tested predictions that

tallgrass prairie butterfly species would vary in their nectar use, and that prairie

specialists would use nectar sources selectively whereas habitat generalists would not.

We performed our study in four tallgrass prairies in southwestern Missouri, USA, in 2006

and 2007. During each sampling period, butterflies differed significantly in their choice

of nectar sources. All butterfly species were selective. *Speyeria idalia*, a prairie specialist

of conservation concern, showed strong selectivity for three different nectar sources over the course of each summer. Multiple butterfly taxa, including two imperiled species (*S. idalia* and *Atrytone arogos*), were highly selective in early June for *Echinacea pallida*. In late July, most butterfly taxa were selective for *Liatris pycnostachya*. Our findings demonstrate the important role that a few subdominant forbs play in conservation of tallgrass prairie butterfly communities. We urge grassland managers and restoration ecologists to consider applying practices that promote subdominant forbs to ensure the presence of nectar sources that are vital to prairie specialist butterflies.

1. Introduction

The primary focus of native grassland management research has been upon studying the factors that impact biomass production of the dominant forage grasses used by livestock (Fuhlendorf and Engle 2001, Holechek et al. 2001). This is problematic, because grassland forbs, legumes, and flowering woody plants provide many ecosystem functions, including serving as food sources for myriad insect species, including grassland butterflies (Daily 1997, Kearns et al. 1998). In contrast to the focus on graminoids in native grassland management research, butterfly ecologists have focused attention on subdominant flowering plants for decades. Many studies have examined the food preferences of butterfly larvae, and there are numerous examples of larval specialization for plants from a single family, genus, or species (Ehrlich and Raven 1965, Gilbert and Singer 1975). The diets of adult butterflies have received much less attention, however (New 1997, Baz 2002). Most butterflies are known to feed on nectar

(Boggs 1987), but there is disagreement as to whether most butterflies are nectar source generalists (Sharp et al. 1974, Scott 1986, Shreeve 1992) or nectar source specialists (Wiklund and Ahrberg 1978, Loertscher et al. 1995, Tiple et al. 2009). This remains contentious due to the dearth of butterfly natural history information; complete lists of nectar sources exist for only a few butterfly species, and the relative importance of nectar sources is known for even fewer (Baz 2002, Stefanescu and Traveset 2009). Solving this problem has important implications to butterfly ecology. If nectar source generalization is the norm, adult nutritional needs of most species might easily be met by habitats with a copious supply of nectar-producing forbs, legumes, and woody plants, regardless of the species composition of those nectar sources. However, if instead most butterflies are nectar source specialists, then nectar source species composition at a given site is likely to be an important factor in determining butterfly species composition and abundance (Tiple et al. 2009).

A second important question is whether or not rare butterflies have more specialized dietary preferences than common species, as some have proposed (Loertscher et al. 1995, Baz 2002, Hardy et al. 2007). If nectar source specialization is characteristic of rare butterflies but not common butterflies, nectar source availability would be implicated as an important determinant of butterfly rarity (Tudor et al. 2004). Additionally, because nectar source availability can impact butterfly longevity (Hill 1992), fecundity (Jervis and Boggs 2005), dispersal ability (Brower et al. 2006), and abundance (Schultz and Dlugosch 1999), efforts to conserve butterfly populations will be improved by greater understanding of nectar source use, availability, and specialization.

Tallgrass prairie, one of the most endangered ecosystems in North America (Ricketts 1999), is home to 80 butterfly species (Opler and Krizek 1984). The majority of these butterfly species are habitat generalists that occur in numerous ecosystems. However, a few are largely or entirely restricted to prairie; most of these prairie specialists are imperiled (Schlicht and Orwig 1998, Heitzman and Heitzman 2006, Schlicht et al. 2007). The elimination of 98% of pre-Columbian tallgrass prairie is the primary cause of historic declines of prairie-specialist butterfly populations (Opler 1991, Swengel 1996). However, prairie specialists are often absent from remaining prairies with apparently suitable habitat. Insufficient supplies of nectar limited grassland butterfly populations in Oregon (Schultz and Dlugosch 1999) and in Sweden (Bergman et al. 2008), and might also limit tallgrass prairie butterfly populations (Ross 2001, Shepherd and Debinski 2005). Unfortunately, little is known regarding the relative importance of nectar sources used by tallgrass prairie butterflies, and even less is known regarding the effects of nectar supply on the dynamics of these butterfly species. Therefore, it is critical that we develop a greater understanding of the role of prairie forbs and legumes in providing nectar for imperiled species, as well as the importance of these plants in supporting pollinator communities.

A paradox exists in grassland ecology. Grasslands evolved with fire and grazing pressure (Axelrod 1985, Anderson 2006), yet the few existing studies on prairie butterflies suggest that these species are sensitive to fire and grazing (Swengel 1996, 1998; Vogel et al. 2007). Our resolution of this paradox is limited by our incomplete understanding of prairie butterfly nectar source preferences and the importance of rare plants in the conservation of these species. Our conservation-oriented goal for this paper

is to help resolve this knowledge gap by studying nectar source use of prairie butterflies. Our specific objectives are to: 1) assess the relative availability of nectar sources; 2) test the prediction that tallgrass prairie butterfly species differ in their use of nectar sources; 3) test the prediction that tallgrass prairie butterfly species are nectar source specialists; and (4) test the prediction that prairie-specialist butterfly species use nectar sources selectively, whereas habitat-generalist butterfly species do not.

2. Methods

2.1. Study design and treatments

We performed our field research at four conservation areas managed by the Missouri Department of Conservation (MDC) in southwestern Missouri: Taberville Prairie, Wah'Kon-Tah Prairie, Niawathe Prairie, and Bethel Prairie (BPCA) (Figure 1). The first three are native tallgrass prairie remnants, whereas BPCA was reseeded with native tallgrass prairie grasses and forbs in the late 1990s after decades of heavy grazing and invasion of non-native forage species (David Darrow, personal communication). Each conservation area was split into two management units (for a total of four paired replications), with one unit managed with grazing and patch fires (one third of the area burned each year with free roaming livestock among all patches known as patch burning) (Fuhlendorf and Engle 2004), and one unit with the patch fires but not grazing. While the treatments represent a disturbance gradient, our focus for this study is not on evaluating the treatments but instead focusing on the relationship between nectar sources and

butterflies. An earlier descriptive study at Wah'Kon-Tah Prairie reported that *Asclepias tuberosa* and *A. syriaca* were important nectar sources for *S. idalia* (Ross 2001), but we know of no other publications on butterfly/nectar source relations in the central tallgrass prairie region.

2.2. Surveys of nectar plant use by butterflies

In the context of butterfly nectaring, we define nectar source "use" as the proportion of visitations to a plant species out of all visitations (Baz 2002). "Selectivity", referred to as "electivity" by some ecologists (Jacobs 1974, Singer and Stireman 2005), is use of nectar sources that is disproportionate to the relative availability of those nectar sources (Ezzeddine and Matter 2008). Selectivity for a nectar source implies that it is particularly desirable to butterflies due to the volume and/or nutrient contents of the nectar (Ezzeddine and Matter 2008); along with nectar source use, selectivity serves as a measure of nectar source specialization.

We studied nectar plant use during three periods in 2006 (June 5-9, June 27-30, and July 17-20) and 2007 (June 5-11, June 25-27, and July 23-26) while simultaneously assessing butterfly abundance at each site using line transect distance sampling (Chapter 1 of this document). We chose these periods because they are important phases in the flight season of *S. idalia*, our focal butterfly species, with early June the period of initial emergence of males, late June the period of peak abundance (due to presence of numerous males and females), and late July a period with numerous females but very few males (Kopper et al. 2001). Transect routes were straight, were placed systematically at

the center of each burn unit, and their lengths were proportional to the size of each burn

unit. Each transect route was at least 50 m from unit boundaries and 50 m from the

nearest transect route to minimize repeat sightings of the same individuals.

We assessed nectar source use between 8:00 and 18:30 CST, during weather

conditions appropriate for butterfly activity (temperature > 20 ºC, cloud cover < 70%,

wind < 20 km/hr) (Pollard and Yates 1993). When we observed nectaring, we recorded

the butterfly species and the species of the nectar source. Butterfly nomenclature follows

that in Opler et al. (2010). Each butterfly species was designated as a habitat generalist

or prairie specialist based on habitat characterizations from the literature (Opler and

Krizek, 1984; Scott, 1986; Ries et al., 2001; Shepherd and Debinski 2005, Vogel et al.

2007).

2.3. Surveys of floral resource availability

During early June and late June sampling periods of 2006, we assessed floral

resource availability by counting the flowering stems of each nectar-producing species

within 0.5-m x 2.0-m quadrats spaced every 20 m for the length of each butterfly transect

route. In late July 2006 and all three sampling periods of 2007, we counted flowering

stems within strip transects in order to sample a larger proportion of each site. Each strip

transect was 4 m wide, equal in length to the corresponding butterfly transect (mean

transect length = 662 m, standard deviation = 289 m), and was centered on each butterfly

transect route. Floral resource surveys were performed within a few hours of butterfly

sampling. We consulted Hilty (2009, 2010) to ascertain which plant species produce

nectar. Later, we calculated the relative availability of each nectar source by dividing the

number of flowering stems of that species by the number of flowering stems of all nectar

sources. Plant nomenclature is from the USDA PLANTS database (USDA, NRCS.

2010).

2.4. Statistical analyses

We tested for interspecific differences in nectar source use using chi-square tests

(Ezzeddine and Matter 2008). To obtain sufficient expected frequencies in chi square

contingency tables, data from both years of the study were pooled for each sampling

period. We tested for selectivity of butterfly taxa that we observed nectaring at least 10

times during a sampling period (Duffy and Jackson 1986). When we failed to meet this

sample size criterion for hesperiid species, we pooled data from all hesperiids. We also

pooled data from the remaining butterfly species that failed to meet the 10 observation

criterion (referred to henceforth as "other butterflies"). Under the null hypothesis of no

selectivity, a nectar source's true proportion of use (p_o) will be equal to its true proportion

of availability (p_a). To compare proportion of use to proportion of availability, we

calculated Bonferroni-adjusted confidence intervals for each proportion using the

formulae

$$P_o - Z_{\alpha/2k} \sqrt{(P_o (1 - P_o)/n_o)} \leq p_o \leq P_o + Z_{\alpha/2k} \sqrt{(P_o (1 - P_o)/ n_o)} \qquad (1.5)$$

and

$$P_a - Z_{\alpha/2k} \sqrt{(P_a (1- P_a)/ n_a)} \leq p_a \leq P_a + Z_{\alpha/2k} \sqrt{(P_a (1- P_a)/ n_a)} \qquad (1.6)$$

where P_o = the observed proportion of use, P_a = the observed proportion of availability, $Z_{\alpha/2k}$ is the upper standard normal table value with a probability of $\alpha/2k$, $\alpha = 0.05$, k = the number of nectar-producing plant species tested, n_o = number of butterflies observed nectaring on any nectar source, and n_a = number of stems observed of all nectar-producing species (Byers et al. 1984). When confidence intervals for true proportion of use and true proportion of availability did not overlap, these proportions were significantly different, indicating selectivity. When proportion of use was greater than proportion of availability, the butterfly taxon in question exhibited selectivity for that nectar source; when proportion of use was less than proportion of availability, that butterfly taxon exhibited selectivity against that nectar source.

3. Results

3.1. *Availability of nectar sources*

Though seldom used by butterflies in our study, *Erigeron strigosus* was the most abundant nectar source in early June of 2006 and 2007, with 47% and 39% of all flowering stems respectively (Table 1). The second and third most abundant nectar sources were *Rudbeckia hirta* and *Tephrosia virginiana* in 2006, and *Mimosa quadrivalvis* and *Orbexilum pedunculatum* in 2007. Some nectar sources used by butterflies were far less abundant, including five species used multiple times by *S. idalia*: *Echinacea pallida* (with 4% and 7% of all flowering stems in 2006 and 2007

respectively), *Verbesina helianthoides* (with 1% each year), and three species never

recorded within our nectar source transects (*Asclepias purpurascens*, *A. syriaca*, and *A.*

tuberosa).   None of these five nectar sources were observed at BPCA during our 2 year

study. In late June, *Pycnanthemum tenuifolium* and *R. hirta* were the most abundant

nectar sources. Together, these species produced 78% and 48% of all flowering stems in

2006 and 2007 respectively. *Monarda fistulosa*, often used by *S. idalia* in late June,

produced only 5% and 1% of all flowering stems in 2006 and 2007, and some other

nectar sources used by *S. idalia* were even less abundant. In late July, *P. tenuifolium* and

R. hirta were once again the most abundant nectar sources. *Liatris pycnostachya*, a

frequently used nectar source, was far less abundant (producing only 8% of all flowering

stems) (Table 1).

3.2.   *Nectar source use and selectivity*

3.2.1. *General observations*

In two years, we observed 1220 individuals of 40 butterfly species nectaring on

47 plant species. *Speyeria idalia*, with 261 observations, and *Phyciodes tharos*, with 204

observations, were viewed nectaring more than any other species. In contrast, 36

butterfly species were observed nectaring fewer than 50 times.

3.2.2. *Early June*

In early June across the two sampling years, we observed 689 individuals of 32

butterfly species nectaring on 25 plant species. We observed 25 butterfly species

nectaring on *E. pallida*, eight nectaring on *V. helianthoides*, and all other nectar sources used by zero to four butterfly species.

We found significant variation in nectar use among butterfly taxa in early June (chi square = 168.6, df = 9, p < 0.0001), with *P. tharos* (the most abundant habitat generalist of the region) using a more diverse set of nectar plants than *S. idalia*, hesperiids, and other butterflies. We observed more individuals (134) of *S. idalia* nectaring than any other species, with 83% of them nectaring on *E. pallida*, and the remainder nectaring on seven other plant species (Table 2). We observed 106 *P. tharos* nectaring on 14 plant species. *Echinacea pallida* was the nectar source most frequently visited by *P. tharos* in early June 2006, and ranked third in early June 2007. Hesperiids nectared almost exclusively on *E. pallida,* with 98% (179 of 183) using this plant in 2006 and 84% (138 of 164) using it in 2007. Two hesperiid species, *Atrytone arogos* (a prairie specialist) and *Polites themistocles* (a habitat generalist), were seen frequently enough in early June to permit analysis. In the two years combined, 83% (45 of 54) of *A. arogos* and 90% (35 of 39) of *P. themistocles* used *E. pallida*. When we pooled observations from other butterflies, we found they also used *E. pallida* more than any other nectar source.

At BPCA, nectaring was rarely observed in early June of either year, with only 32 individuals of six butterfly species nectaring on nine plant species. We saw no *S. idalia* nectaring at BPCA, even though we saw 52 individuals engaged in other behaviors there. We observed one hesperiid nectaring, as opposed to the 346 hesperiids we saw nectaring at the other three sites, and observed no *A. arogos* whatsoever at BPCA. All 13 observations of *P. tharos* nectaring on *E. strigosus* were made at BPCA, even though *P.*

tharos and *E. strigosus* were abundant at the other three sites. We failed to observe any butterflies nectaring on *E. pallida* or *V. helianthoides*, even though at the other three sites, we observed 522 and 50 butterflies nectaring on these species respectively.

Phyciodes tharos, *S. idalia*, the hesperiids, and other butterflies showed significant selectivity toward one or more nectar sources (Table 3). In 2006, these butterfly taxa were selective for *E. pallida*. In 2007, *P. tharos* was selective for *V. helianthoides*, but the other butterfly taxa listed above were selective for *E. pallida*, as were *A. arogos* and *P. themistocles*. *Speyeria idalia* was also selective for *A. syriaca*, a plant which was so uncommon at our sites that it was never detected during our nectar plant availability surveys. In both years, all butterfly taxa exhibited selectivity against *E. strigosus*, the most abundant nectar source. Most butterfly taxa also selected against *R. hirta*, *M. quadrivalvis*, *A. millefolium*, *C. grandiflora*, *O. pedunculatum*, and *T. virginiana*, even though these plant species were six of the 10 most abundant nectar sources of early June.

3.2.3. Late June

We observed fewer butterflies nectaring in late June of 2006 and 2007, with only 191 individuals of 23 butterfly species nectaring on 14 nectar sources (Table 4). More species (11) nectared on *P. tenuifolium* than any other, whereas 9 species nectared on *E. pallida* and *R. hirta*. We found significant variation in nectar use among *P. tharos*, *S. idalia*, and other butterflies (chi square = 128.7, df = 6, p < 0.0001). *Phyciodes tharos* exhibited selectivity for *R. hirta* in 2007. *Speyeria idalia* exhibited selectivity for *M. fistulosa*, but exhibited selectivity against three abundant species in 2007: *E. strigosus*, *P.*

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tenuifolium, and *R. hirta* (Table 5). Hesperiids were rarely seen nectaring in late June, with only 11 individuals of five species. Five hesperiids used *E. pallida*, though approximately 95% of *E. pallida* inflorescences had already senesced and stopped producing nectar. As in early June, few butterflies (21) were observed nectaring at BPCA, but eight of these were *S. idalia*.

3.2.4. Late July

In late July of 2006 and 2007, we observed 343 individuals of 25 species nectaring on 16 plant species. More butterfly species (23) nectared on *L. pycnostachya* than on any other nectar source. *P. tenuifolium*, *Cephalanthus occidentalis*, and *Vernonia baldwinii* were used by 16, 8, and 8 species respectively; all other nectar sources were used by five species or fewer. As in early June, nectar use by *P. tharos* differed significantly from that of *S. idalia*, hesperiids, and other butterflies (p < 0.0001 for all three comparisons). *Phyciodes tharos* used *P. tenuifolium* and *R. hirta* most often (Table 6), exhibiting selectivity for *P. tenuifolium* in 2007 (Table 7). Few *S. idalia* nectared on those plants; instead 78% used *L. pycnostachya*. However, in contrast to early June, *S. idalia* and hesperiids also differed in nectar source use (chi-square = 19.5, df = 4, p < 0.0007). "Other butterflies" used many of the same nectar sources as the hesperiids, and in similar proportions. In both years, *S. idalia*, the hesperiids, and other butterflies exhibited selectivity for *L. pycnostachya* (Table 7). The hesperiids and other butterflies exhibited selectivity for *C. occidentalis* in 2006. Multiple butterfly species exhibited selectivity against *R. hirta* and *Sabatia campestris.* In contrast to the June sampling

periods, BPCA had more nectaring butterflies (100) than any of the other three sites, including 8 hesperiid species.

4.   Discussion

If most butterflies are nectar source generalists, as some ecologists have suggested (Sharp et al. 1974, Shreeve 1992), then they will use nectar sources in proportion to availability, and co-occurring butterfly species will seldom differ in nectar source use and selectivity. In tallgrass prairies of southwestern Missouri we found the opposite trends. All butterfly taxa, including habitat generalists and prairie specialists, used nectar sources disproportionate to availability, and co-occurring taxa frequently differed in nectar source use and selectivity. In sum, all of these taxa exhibited nectar source specialization. Given the phylogenetic diversity of the butterfly taxa we studied, with 6 families represented (Nymphalidae, Hesperiidae, Pieridae, Papilionidae, Lycaenidae, and Satyridae), we suspect that nectar source specialization is characteristic of many tallgrass prairie butterfly species. Our findings, when considered along with studies of nectar use in other regions (Loertscher et al. 1995, Baz 2002, Tudor et al. 2004, Erhardt and Mevi-Schutz 2009), support the premise that nectar source specialization is a common feature of butterfly communities.

Our study provided mixed results regarding the hypothesis that habitat specialist butterflies exhibit nectar source specialization to a greater degree than do habitat generalist butterflies (Hardy et al. 2007). *Phyciodes tharos*, a habitat generalist, used at least five nectar sources during each sampling period when 40 or more observations were

made. It was the only butterfly to frequently use two of the most abundant nectar sources: *Erigeron strigosus* and *R. hirta*. These nectar sources occur in a variety of habitats across most of the continental United States (USDA, NRCS. 2010); the ability of *P. tharos* to obtain sustenance from such common, wide-ranging species might play a large role in allowing *P. tharos* to occupy a variety of ecosystems from the Rocky Mountains to the Atlantic Coast (Opler and Krizek 1984). As predicted, two prairie-specialist butterflies (*S. idalia* and *Atrytone arogos*) exhibited much stronger levels of nectar source specialization. During each sampling period (early June, late June, late July), *S. idalia* strongly favored a single, rare nectar source, but used a few others as well. The preferred nectar source changed through time, from *E. pallida* in early June, to *Monarda fistulosa* in late June, and to *Liatris pycnostachya* in late July. *Atrytone arogos* also exhibited strong nectar source specialization; it nectared almost exclusively on *E. pallida* and *V. helianthoides* during its June flight period, even though these forbs were much less abundant than other nectar sources. However, contrary to what theory had led us to predict, a habitat generalist (*Polites themistocles*) was as selective as *A. arogos* for preferred nectar sources. Others (Royer 1988, Iftner et al. 1992, Bouseman et al. 2006) have observed *P. themistocles* using a wide variety of nectar sources, as one might predict based on its broad distribution and its occupation of a variety of habitats.

A potential consequence of nectar source specialization is increased likelihood that a butterfly species will be limited in abundance and distribution by availability of preferred nectar sources (Tudor et al. 2004). Though we found *S. idalia* at all four sites, population densities were lowest at Bethel Prairie Conservation Area (BPCA) (Chapter 3 of this document), the site where we failed to observe nectar sources *E. pallida* and *V.*

helianthoides. Additionally, the abundance of *S. idalia* was positively correlated with that of *E. pallida* (Chapter 3 of this document). We found *A. arogos* at all three sites that had flowering stems of *E. pallida* and *V. helianthoides*, but not at BPCA. We suspect that the absence of those preferred nectar sources might have played an important causal role in the apparent absence of *A. arogos* at BPCA. The inter-site variation in distribution of *A. arogos* cannot be explained by distribution of the larval host plants, as *A. arogos* larvae feed on *Andropogon gerardii* and *Schizachyrium scoparium* (Dole et al. 2004), dominant grasses at all four study sites and most tallgrass prairies range-wide (Sims 1999).

Other studies offer evidence as to the importance of the genus *Echinacea* as a nectar source to *A. arogos*. In the northern prairie states of Iowa, Minnesota, and North Dakota, 32 of 43 nectaring individuals of *A. arogos* used *E. angustifolia*, whereas the next most-visited nectar source was the exotic thistle *Carduus nutans* (Swengel and Swengel 1999). In our 3 year study of grazed prairies in the Flint Hills of Kansas, where flowering stems of *Echinacea* spp. occur in very low density (much lower than at our three southwestern Missouri that had *E. pallida*), 5 of 9 *A. arogos* nectared on *Echinacea* spp. (Moranz et al., unpublished manuscript). During butterfly inventories of 27 tallgrass prairies in eastern Kansas, seven *A. arogos* were observed nectaring at four sites; all seven were on *E. pallida* (R. Moranz, unpublished data). Lastly, the peak abundance of *A. arogos* in southwestern Missouri is synchronous with the peak abundance of *E. pallida* (Ross 2001). Due to the high frequency with which prairie populations of *A. arogos* use *Echinacea* spp. as nectar sources, we speculate the distribution of *A. arogos* within the

central grasslands of North America is strongly correlated with the distribution of *Echinacea* spp., and we consider this an important topic for further research.

Every publication we found that presented data or anecdotal accounts of nectar use by imperiled hesperiids in tallgrass prairie provided evidence that *Echinacea* spp. are frequently used nectar sources, though none of these publications assessed selectivity. *Problema byssus* is said to prefer *Echinacea* and *Asclepias* species in Missouri (Heitzman and Heitzman 2006). In one central Missouri study, *P. byssus* was recorded using only *E. pallida* and *E. purpurea* (Clinebell 2003). In the northern plains, 12 of 13 nectaring observations of *Hesperia ottoe* and 190 of 354 observations of *H. dacotae* (a candidate for listing under the federal Endangered Species Act) were on *Echinacea angustifolia* (Swengel and Swengel 1999). In southwestern Minnesota, *E. angustifolia* was the primary nectar source used by *H. dacotae* and other butterfly species with similar flights (Selby 2006). Given the high degree of selectivity for *E. pallida* shown by hesperiids in our study, and the numerous studies that have reported *Echinacea* spp. as the nectar source most frequently used by hesperiids, we propose that *Echinacea* spp. serve as keystone species (Power et al. 1996) in the central grasslands of North America.

Grassland vegetation research has often focused on the dominant grasses, with little attention given to subdominant forbs. For instance, some studies of the effects of fire and/or grazing on grasslands have collected data on plant functional groups rather than species (Coppedge et al.1998, Harrell et al. 2001, Cummings et al. 2007). Such data are easier to collect than species composition data, and have been particularly useful for understanding the habitat relations of grassland birds, which appear to respond to functional groups and vegetation structure more than species composition (Winter et al.

2005, Fuhlendorf et al. 2006). However, when considered on their own merit, data on

plant functional groups are not enough to advance our understanding of butterfly/habitat

relations, because they include little information on the nectar resources used by

butterflies.   Similarly, Whittaker plot sampling (Shmida 1984, Stohlgren et al. 1995) and

other standard methods of sampling plant community composition can provide useful

information for butterfly ecologists, but are insufficient on their own. Plant community

sampling methods typically indicate presence and/or percent cover of each species, yet in

our experience, the cover of nectar sources such as *E. pallida* and *L. pycnostachya* is

often so low that differences in abundance among sites are not detected with these

methods. Given the importance of subdominant forbs to grassland butterflies, we

recommend that grassland vegetation researchers devote more effort to studying their

ecology.

Some attempts to restore grasslands have focused on establishing dominant

grasses, and have devoted little money and effort into establishing subdominant forbs

(but see Helzer and Steuter 2005). We suspect that those restoration attempts are unlikely

to be valuable for butterfly conservation if key nectar sources are absent. One might

predict restorations that seek to maximize plant species richness increase the likelihood of

species-rich butterfly communities. In some regions, butterfly species richness has been

shown to be positively correlated with plant species richness (Thomas and Mallorie 1985,

Hawkins and Porter 2003). However, in one study that encompassed all of California,

path analysis revealed that plant species richness at a moderate spatial scale had only

weak causal effects on butterfly species richness (Hawkins and Porter 2003). We suspect

that providing ample quantities of preferred nectar sources (as well as larval host plants)

is more important for the conservation of prairie-specialist butterflies than is maximizing plant species richness, though more research is needed.

We, like others before us (Dennis et al. 2006), recommend that land managers seeking to conserve imperiled prairie butterflies should consider maintaining or enhancing the abundance of preferred, native nectar sources throughout the flight season of each focal butterfly species. For butterflies having a short flight season of 2 to 3 weeks, such as northern populations of *A. arogos*, this could be done with a single nectar source, such as *E. pallida*. In contrast, longer-lived butterflies such as *S. idalia* need a seasonal succession of nectar sources (Ross 2001; this study). However, maintaining populations of these plants is not enough to ensure their utility to butterflies: conditions need to be appropriate for them to flower and produce nectar. Land managers should seek information on the effects of management practices on flowering, as some practices are not conducive. For example, mowing tallgrass prairie hayfields in southwestern Missouri in early July delays the flowering of *Liatris pycnostachya* until after the annual brood of *S. idalia* adults have died (Raymond Moranz, pers. obs.). Cattle grazing, the primary land use in tallgrass prairie (Fuhlendorf and Engle 2004), decreases the abundance of *E. pallida* and *L. pycnostachya* when the stocking rate of cattle is high (Drew 1947; Chapter 3 of this document).

In conclusion, tallgrass prairie butterflies often exhibited significant selectivity for nectar sources, supporting the hypothesis that prairie butterflies are nectar source specialists rather than nectar source generalists. Our findings also highlight the conservation importance of providing preferred nectar sources to prairie butterflies. *E. pallida* stands out as a keystone resource for butterflies in tallgrass prairies of

southwestern Missouri, as all butterfly taxa selected for it during our study. This nectar source appears to be particularly important to imperiled, prairie-specialist butterfly species such as *A. arogos* and *S. idalia*. Long-lived butterflies, such as *S. idalia*, should be provided with a succession of preferred nectar sources throughout their flight season.

Acknowledgments

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Table 1. Relative availability of nectar sources during six time periods. Values shown are percentages of total of all flowering stems during each period.

Plant Scientific Name	EARLY JUNE 2006	EARLY JUNE 2007	LATE JUNE 2006	LATE JUNE 2007	LATE JULY 2006	LATE JULY 2007
Achillea millefolium	3.2	6.5	0.5	0.6		
Amorpha canescens	4.3	1.8		4.1		
Baptisia alba			0.5	0.3	0.6	
Castilleja coccinea	0.9					
Ceanothus americanus	2.2	0.1		3.4		
Cephalanthus occidentalis					0.4	
Coreopsis grandiflora	0.5	6.7		1.8		
Coreopsis palmata	0.1					
Dalea candida			0.3	1.0		
Dalea purpurea			0.3	1.2		
Diodea teres					1.9	2.1
Echinacea pallida	3.9	6.7	0.5	4.2		
Erigeron strigosus	47.0	38.9	2.0	10.2	0.5	0.6
Eryngium yuccifolium			0.6		2.8	1.9
Eupatorium perfoliatum						0.8
Eupatorium serotinum					0.1	
Euphorbia corollata			0.2	0.8	3.3	2.5
Helenium flexuosum			0.5	1.1	0.5	0.2
Helianthus mollis					0.7	0.7
Hypericum perforatum			0.8		0.2	
Leucanthemum vulgare		0.7				
Liatris pycnostachya					7.4	7.8
Linum sulcatum			0.7		8.9	1.0
Medicago lupulina				0.8		
Mimosa quadrivalvis	4.5	17.1		0.8		
Monarda fistulosa	0.2		4.8	1.0		
Orbexilum pedunculatum	4.3	10.2				
Parthenium integrifolium	3.2	1.9		2.1		
Penstemon tubaeflorus	0.4	1.0				
Physostegia virginiana			0.1	1.2		
Polygala sanquinea				8.6		7.7
Ptilimnium nuttallii			5.7	2.8	1.7	6.2
Pycnanthemum tenuifolium		0.4	52.2	23.2	45.6	20.9
Ratibida pinnata			0.4			0.3
Rudbeckia hirta	12.3	1.5	25.9	25.2	20.1	23.7
Ruellia humilis	0.5		0.9	1.1	2.2	
Sabatia campestris						8.9
Salvia azurea						0.2
Silphium integrifolium						1.4
Solidago missouriensis						1.4
Stylosanthes biflora		0.1		0.7	0.5	3.3
Tephrosia virginiana	11.7	2.7		0.2		

Plant Scientific Name	EARLY JUNE		LATE JUNE		LATE JULY	
	2006	2007	2006	2007	2006	2007
Teucrium canadense			0.3	0.3		
Tradescantia ohiensis		1.4		0.1		
Verbesina helianthoides	1.0	1.0	2.0	1.9		0.4
Vernonia baldwinii					1.2	6.3

Table 2. The number of butterflies observed using each nectar source in early June of 2006 and 2007.

Nectar sources	Phyciodes tharos (habitat generalist)		Speyeria idalia (prairie specialist)		Atrytone arogos (prairie specialist)		Polites themistocles (habitat generalist)		other hesperiid spp.		other butterfly spp.	
	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007
Achillea millefolium		3										1
Amorpha canescens	9									1	4	
Asclepias purpurascens			3									
Asclepias syriaca				5								
Asclepias tuberosa			1	1								
Leucanthemum vulgare		1										
Coreopsis grandiflora	3	10		1								
Echinacea pallida	17	11	41	70	5	40	5	30	169	68	32	34
Erigeron strigosus	1	12						2		3		2
Mimosa quadrivalvis		2										
Monarda fistulosa			4	3								1
Orbexilum pedunculatum		1									2	4
Parthenium integrifolium												8
Rhus glabra		1										
Rudbeckia hirta	8	3	1				1		1		1	1
Stylosanthes biflora		1										
Tephrosia virginiana											2	
Teucrium canadense		1								1		
Tradescantia sp.	1											
Verbesina helianthoides	4	17		4	1	8		1	1	10	3	4
three other plant species											1	2
TOTAL	43	63	50	84	6	48	6	33	171	83	45	57

Table 3. Butterfly selectivity for nectar sources in early June of 2006 and 2007. "+" indicates butterflies selected nectar source more often than expected based on its availability. "-" indicates butterflies selected nectar source less often than expected based on its availability. "ns" indicates test failed to find significant evidence of selectivity for or against that nectar source. All tests conducted with α = 0.05.

Nectar sources	Phyciodes tharos (habitat generalist)		Speyeria idalia (prairie specialist)		Atrytone arogos (prairie specialist)		Polites themistocles (habitat generalist)		Other hesperiid spp.		other butterfly spp.	
	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007
Achillea millefolium		ns		-		ns		ns	-			ns
Amorpha canescens	ns								-			
Asclepias purpurascens			ns									
Asclepias syriaca				+								
Asclepias tuberosa			ns									
Coreopsis grandiflora	ns	ns		-		ns		ns	-			-
Echinacea pallida	+	ns	+	+		+		+	+	+	+	+
Erigeron strigosus	-	-	-	-		-		-	-	-	-	-
Mimosa quadrivalvis		-		-		-		-	-	-		-
Monarda fistulosa			ns	ns								
Orbexilum pedunculatum		-		-		ns		ns	-			ns
Parthenium integrifolium												+
Rudbeckia hirta	ns	ns	-						-		-	
Tephrosia virginiana			-						-		ns	
Verbesina helianthoides	ns	+				+		ns		+	ns	ns

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Table 4. The number of butterflies observed using each nectar source in late June of 2006 and 2007.

Nectar sources	*Phyciodes tharos* (habitat generalist)		*Speyeria idalia* (prairie specialist)		Hesperiids		other butterfly spp.	
	2006	2007	2006	2007	2006	2007	2006	2007
Amorpha canescens								7
Baptisia alba						1		
Buchnera americana						1		
Coreopsis grandiflora		3						
Coreopsis palmata		2						1
Echinacea pallida				2	2	3	2	6
Helenium amarum				1				
Liatris pycnostachya							1	
Monarda fistulosa			17	48		1	5	4
Polygala sanguinea								1
Pycnanthemum tenuifolium	6		9	4			16	11
Rudbeckia hirta	5	13				1	4	6
Stylosanthes biflora								1
Verbesina helianthoides		1				2		1
TOTAL	**11**	**19**	**26**	**55**	**2**	**9**	**28**	**38**

Table 5. Butterfly selectivity for nectar sources in late June of 2006 and 2007. "+" indicates butterflies selected nectar source more often than expected based on its availability. "-" indicates butterflies selected nectar source less often than expected based on its availability. "ns" indicates test failed to find significant evidence of selectivity for or against that nectar source. All tests conducted with α = 0.05.

Nectar sources	Phyciodes tharos (habitat generalist)		Speyeria idalia (prairie specialist)		other butterfly spp.	
	2006	2007	2006	2007	2006	2007
Erigeron strigosus		ns		-		-
Monarda fistulosa			+	+	ns	ns
Polygala sanguinea		ns				
Pycnanthemum tenuifolium	ns	ns	ns	-	ns	ns
Rudbeckia hirta	ns	+	ns	-	ns	ns

Table 6. The number of butterflies observed using each nectar source in late July of 2006 and 2007.

Nectar sources	*Phyciodes tharos* (habitat generalist) 2006	2007	*Speyeria idalia* (prairie specialist) 2006	2007	Hesperiids 2006	2007	other butterfly spp. 2006	2007
Baptisia alba						1		
Cephalanthus occidentalis			2		9	1	7	4
Diodea teres							1	
Eryngium yuccifolium		2			2	1	1	6
Eupatorium serotinum		1				4		1
Helianthus mollis							4	1
Liatris pycnostachya			24	12	25	21	24	34
Pycnanthemum tenuifolium	5	27	1	1	8	25	16	11
Rhus glabra								2
Rudbeckia hirta	7	18			2	1	1	2
Salvia azurea				1				
Silphium integrifolium						1		1
Solidago missouriensis	1	6						
Stylosanthes biflora		1						
Vernonia baldwinii			1	4		3	1	6
TOTAL	**13**	**55**	**28**	**18**	**46**	**58**	**55**	**69**

Table 7. Butterfly selectivity for nectar sources in late July of 2006 and 2007. "+" indicates butterflies selected nectar source more often than expected based on its availability. "-" indicates butterflies selected nectar source less often than expected based on its availability. "ns" indicates test failed to find significant evidence of selectivity for or against that nectar source. All tests conducted with α = 0.05.

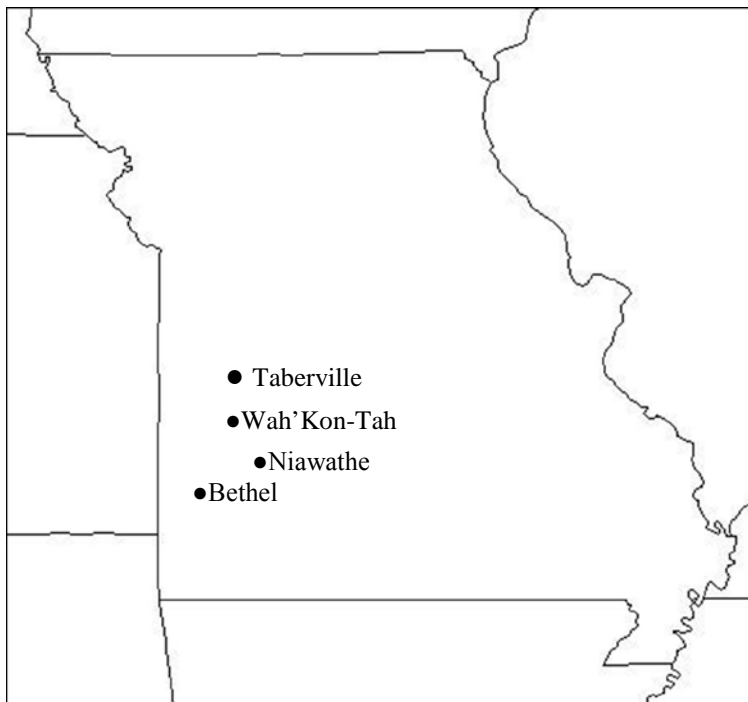| Nectar sources	*Phyciodes tharos* (habitat generalist)		*Speyeria idalia* (prairie specialist)		Hesperiids		other butterfly spp.	
	2006	2007	2006	2007	2006	2007	2006	2007
Cephalanthus occidentalis					+		+	
Eryngium yuccifolium								+
Liatris pycnostachya		ns	+	+	+	+	+	+
Polygala sanguinea								-
Pycnanthemum tenuifolium	ns	+	-	ns	-	+	-	ns
Rudbeckia hirta	ns	ns	-	ns	-	-	-	-
Sabatia campestris		-		ns	-			-

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a

b

Figure 1. Maps showing (a) the location of Missouri within the U.S.A., and (b) the locations of study sites in southwestern Missouri.

CHAPTER III

A PRAIRIE BUTTERFLY PARADOX:
THE EFFECTS OF FIRE, GRAZING AND SAMPLING PERIOD ON *SPEYERIA
IDALIA* ABUNDANCE

A prairie butterfly paradox: the effects of fire, grazing and sampling period on *Speyeria idalia* abundance

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ABSTRACT

        The tallgrass prairie region of North America hosts a number of grassland-

obligate butterfly species. Paradoxically, though tallgrass prairie requires periodic

disturbance to control woody plants, evidence suggests that some grassland-obligate

butterfly species respond negatively to disturbance agents such as fire and grazing. For

example, some prior studies of *Speyeria idalia* (regal fritillary) have shown strongly

negative effects of dormant-season prescribed burning on this species. We examined the

effects of time since fire, grazing and sampling period on the abundance of *S. idalia* at

four tallgrass prairie sites in southwestern Missouri, USA. Each prairie site consisted of two pastures: one rotationally burned in early spring (with one-third burned each year) and grazed by yearling cattle from late April to August (also known as patch-burn grazing, or pyric herbivory), and one rotationally burned but not stocked with cattle. Butterfly population density was assessed via line transect distance sampling in three sampling periods of 2006 and 2007: early June, late June, and late July. The availability of floral resources was measured simultaneous to butterfly sampling. Both years, *S. idalia* population density was dependent on time since fire. In 2006, time since fire and sampling period interacted to impact population density. In 2007, population density of *S. idalia* was a function of a three-way interaction of time since fire, grazing, and sampling period. Grazing had consistent negative effects on abundance of *S. idalia* and two of its preferred nectar sources, *Echinacea pallida* and *Liatris pycnostachya*. This was especially true in the most recently burned patches, which were grazed intensely, which is characteristic of pyric herbivory. In ungrazed pastures, recent fire appeared to enhance abundance of *S. idalia* and its preferred nectar sources, particularly in late July. There was a strong positive correlation between abundance of *S. idalia* and *E. pallida* in early June and between *S. idalia* and *L. pycnostachya* in late July. Rotational fire alone and pyric herbivory (rotational fire with grazing) can be compatible with *S. idalia* conservation, but *S. idalia* and its nectar sources appear to be sensitive to specific attributes of these disturbance regimes.

1. Introduction

North American prairies host multiple butterfly species which appear to be sensitive to disturbance, particularly fire (Swengel 1996). Some of these disturbance-sensitive species are restricted in their distribution to prairies, ecosystems dependent on disturbances such as fire and grazing (Anderson 2006). We refer to the sensitivity of these butterfly species to the disturbances that maintain their habitat as the "prairie butterfly paradox", and seek to better understand how these disturbance-sensitive species can persist in disturbance-dependent ecosystems. As these butterfly species have become imperiled in recent decades (Schlicht and Orwig 1998), gaining a better understanding of the effects of disturbance on prairie-specialist butterflies has become increasingly important for efforts to conserve them.

Because of its large size, bright coloration, and its dependence on high-quality grasslands, *Speyeria idalia* (regal fritillary) serves as a flagship species for the conservation of prairie-specialist butterflies (Williams 2002, Russell et al. 2004). Though habitat loss due to conversion to intensive agriculture and urban development is the primary cause for the imperiled status of *S. idalia* (Hammond 1995), a second factor often cited is grassland fire (Swengel 1996, Swengel 1998, Powell et al. 2007, Vogel et al. 2007). *S. idalia* is non-migratory, and occupies prairie during the entire year. It spends the dormant-season (fall-winter-early spring) in immature stages that are immobile (egg, pupa) or of limited mobility (larva) (Kopper et al. 2001). Dormant-season fire often kills immature stages of most prairie-specialist butterfly species, including *S. idalia* (Swengel 1996), and burning entire prairies has extirpated numerous

populations of *S. idalia* (Swengel 1996, Swengel and Swengel 2001a, Powell et al. 2007).

In some cases, rotational burning (burning a different portion of a prairie each year) has

also led to precipitous decreases in *S. idalia* abundance (Swengel and Swengel 2001a),

though this has primarily been observed in small prairies (less than 30 ha) without

controlled studies.

The negative responses to fire demonstrated by *S. idalia* and other prairie-

specialist invertebrates has led some to suggest that prairie fire was infrequent during the

evolutionary history of these species (Schlicht and Orwig 1998, Nekola 2002). Yet a vast

body of evidence indicates otherwise, and removal of fire has already caused great losses

of prairie to woody plant encroachment (Sauer 1950, Wright and Bailey 1982, Axelrod

1985, Collins and Steinauer 1998, Briggs et al. 2002, Anderson 2006). Since European-

Americans settled central North America, fire frequency has decreased (Steinauer and

Collins 1996, Samson et al 2004), resulting in woody plant encroachment that has

transformed millions of acres of prairie into woodlands and other ecosystems no longer

suitable for some prairie specialist fauna (Coppedge et al 2001, Walker and Hoback

2007). Prescribed burning halts and reverses woody plant encroachment (Hartnett and

Fay 1998), thus restores and maintains grassland habitat for prairie-specialists such as *S.

idalia*. In addition to maintaining grassland structure, fire can alter floral production of

forbs, legumes, and woody plants (Hartnett and Fay 1998). Rangewide, *S. idalia* adults

take nectar from a variety of forbs and legumes (Iftner et al. 1992), but within a given

area, they tend to specialize on a few preferred species (Heitzman and Heitzman 2006,

Chapter 2 of this document).   If fire impacts floral production of key nectar sources, the

distribution and abundance of *S. idalia* might be altered, given that nectar source

availability has been shown to affect distribution and abundance of other butterflies (Hill 1992, Schultz and Dlugosch 1999).

Like fire, grazing has been an important process in tallgrass prairie for thousands of years (Milchunas et al. 1988, Lauenroth et al. 1994, Knapp et al. 1999). Although cattle grazing is currently the dominant land use on tallgrass prairie (Fuhlendorf and Engle 2004), grazing effects on these prairie-specialist butterflies have seldom been studied (but see Swengel and Swengel 2001a, Vogel et al. 2007). Given that ungulates graze selectively on preferred plant species (Coppedge et al. 1998, Towne et al. 2005), they may preferentially consume nectar sources that would otherwise sustain adult butterflies through courtship, mating, and oviposition. Alternatively, ungulates may preferentially consume other plant species, thereby enhancing nectar source abundance through competitive release.

Pyric herbivory, defined as the ecological interaction of fire and grazing, is believed to have been a widespread and frequent disturbance in the grasslands of pre-Columbian America (Fuhlendorf et al. 2009). With pyric herbivory, fire drives the spatiotemporal distribution of grazing animals; in turn, grazing impacts the occurrence and spread of fire. Fire drives herbivory by stimulating many of the native prairie plant species to produce regrowth that is highly nutritious to large ungulates (Towne and Owensby 1984). These ungulates graze very intensively in the recently burned grassland, and graze very lightly the adjacent unburned grassland (Coppedge and Shaw 1998, Fuhlendorf and Engle 2004). This distribution of grazing increases heterogeneity of vegetation structure (Fuhlendorf and Engle 2004), which in turn enhances the diversity of

grassland bird communities (Fuhlendorf et al 2006). However, the effects of pyric herbivory on prairie specialist butterflies are currently unknown.

Given the growing body of evidence suggesting that fire, grazing, and pyric herbivory were common disturbances in tallgrass prairie during much of prehistory, prairie-specialist butterflies such as *S. idalia* likely evolved with these disturbances as major selective forces. The primary goal of our research was to examine how these disturbances impact *S. idalia* populations and flowering stem density of *S. idalia*'s nectar sources. In this study, we compared prairies managed with rotational fire to prairies managed with pyric herbivory (rotational fire and cattle grazing). Our specific objectives were to 1) examine the effects of time since fire, cattle grazing, and sampling period on the population densities of *S. idalia* and its nectar sources, and 2) assess the relationship between *S. idalia* and nectar source population densities. We predicted that recent fire would reduce *S. idalia* density, but increase density of nectar sources. We also predicted that *S. idalia* density would increase with time since fire.

2. Methods

2.1 Study design and treatments

We performed our field research at four sites managed by the Missouri Department of Conservation (MDC) in southwestern Missouri: Taberville Prairie Conservation Area, Wah'Kon-Tah Prairie, Niawathe Prairie Conservation Area, and Bethel Prairie Conservation Area (BPCA) (Figure 1). The first three sites are native

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tallgrass prairie remnants. In the 20th century, decades of heavy grazing and seeding of

non-native pasture grasses had converted BPCA from tallgrass prairie into non-native

pasture. In the 1990s, the MDC applied herbicides to kill herbaceous vegetation at

BPCA, and subsequently seeded BPCA with a mixture of tallgrass prairie grasses, forbs,

and legumes in order to restore it to tallgrass prairie (David Darrow, personal

communication). Between 2000 and 2004, the four sites experienced similar

management regimes of rotational burning, occasional haying, and in a few cases, light

grazing by cattle. In 2005, the MDC used fencing to divide each site into two pastures,

one managed with grazing and rotational burning (also known as patch-burn grazing),

and one managed with rotational burning only. Pastures ranged from 60 to 105 ha in

area. Subsequently, the MDC divided each pasture into three burn units approximately

equal in size; across the experiment, burn units were 20 to 34 ha in area (Figure 2). This

resulted in a split-plot experimental design, with grazing status (grazing or no grazing) as

the main plot treatment, and time since fire (in years) as the subplot treatment. Main plot

and subplot treatments were assigned randomly. Each year, the MDC added cattle to

each of the four patch-burn grazing pastures between April 12 and May 3, and removed

them between August 10 and August 17. Cattle were mixed-breed (except for Holsteins

only at the Taberville patch-burn grazing pasture in 2006) yearling steers and heifers,

stocked at a density of 2.2 ha/animal unit, which is a moderate stocking density for the

region (Brent Jamison, personal communication). Cattle weighted an average of 261 kg

when added to the pastures, and their average daily gain was 0.7 kg/head/day (Brent

Jamison, personal communication). Within each pasture, the MDC burned one unit in

March 2005, a second unit in March 2006, and a third unit in March 2007, so that by

summer 2006, each pasture had one unit burned that year, a second unit burned the previous year, and one burned 2 years earlier (time since burn values were 0, 1, and 2 years respectively). Units burned the same year assampling are hereafter referred to as recently burned.

2.2   *Butterfly surveys*

We sampled *S. idalia* populations during three periods in 2006 (June 5-9, June 27-30, and July 17-20) and 2007 (June 5-11, June 25-27, and July 23-26). These periods are important phases in the flight season of *S. idalia*, with early June the period of initial emergence of males, late June the time of peak abundance (due to males and females), and late July a period with numerous females but very few males (Kopper et al. 2001). During each sampling period, we estimated *S. idalia* population density in each burn unit using line transect distance sampling, as described in Chapter 1 of this dissertation. Sampling was conducted between 8:00 and 18:30 CST, during weather conditions appropriate for butterfly flight (temperature > 20 ºC, cloud cover < 70%, wind < 20 km/hr) (Pollard and Yates 1993). When *S. idalia* was seen nectaring, we recorded the species of the nectar source used by each individual. As described in Chapter 1 of this dissertation, we used Program DISTANCE, version 5.0, release 2 to convert the number of butterflies seen per unit distance walked to an estimate of population density for each burn unit (Thomas et al. 2010).

2.3   *Floral resource surveys*

During each butterfly sampling period of 2007, we assessed floral resources of experimental units by counting the number of flowering stems of each species of nectar-producing forb and legume found within strip transects that were centered on each butterfly transect route. Each strip transect was 4 m wide, and equal in length to the corresponding butterfly transect. Floral resource surveys were performed within a few hours of butterfly sampling.

2.4   *Statistical analysis*

Prior to statistical analyses, butterfly and nectar source densities were square root transformed in order to meet the assumption of homoscedasticity (Gotelli and Ellison 2004). For each year of the study (2006 and 2007), we used SAS 9.1.3 (SAS Institute Inc. 2007) to perform a separate analysis of variance for split-plot design with repeated measures (with sampling period as the repeated measure factor) in order to test the effects of grazing, time since fire, and sampling period on population density of *S. idalia*. We used SAS's SLICE function to test for simple effects (i.e., differences in levels of one factor when all other factors are held constant), and SAS's DIFF function as the multiple comparison procedure.

Because the array of nectar sources in bloom changes greatly from early June to late June to mid July, we performed separate split-plot analyses of variance to text for treatment effects on the most frequently visited nectar sources of each sampling period: (1) *Echinacea pallida* in early June, (2) *Monarda fistulosa* in late June, and (3) *Liatris*

pycnostachya in late July (Moranz et al. 2010, unpublished manuscript). For each time period of 2007, we also performed split-plot analysis of variance on the number of flowering ramets of all nectar sources combined. For each sampling period of 2007, we used SPSS 15.0 (SPSS 2006) to correlate abundance of *S. idalia* with the abundances of (1) the most frequently visited nectar source, and (2) all nectar sources.

3. Results

3.1. Butterfly population density

3.1.1. Main effects and interactions

We observed 1321 *S. idalia* during the two years, finding them at all pastures in both years of the study. Population densities of *S. idalia* increased from 2006 to 2007 in grazed and ungrazed pastures, by 12% and 130% respectively. All three factors (grazing, time since fire, and sampling period) significantly impacted *S. idalia* population density in each year of the study. In 2006, time since fire and sampling period interacted significantly to impact density ($F = 4.31$, d.f. $= 4, 38$, $P = 0.006$), with the impact of time since fire becoming more negative as the summer progressed. Time since fire and grazing had marginally interactive effects on population density ($F = 2.81$, d.f. $= 2, 21$, $P = 0.082$). More definitively, grazing as a main effect reduced population density by 42% relative to ungrazed prairie ($F = 7.24$, d.f. $= 1, 21$, $P = 0.014$).

In 2007, all three factors (grazing, time since fire, and sampling period) interacted significantly in their effects on *S. idalia* population density ($F = 5.74$, d.f. $= 4, 37$, $P <$

0.001). Time since fire had a positive effect on *S. idalia* density in grazed pastures, and a negative effect in ungrazed pastures. Conversely, the effect of grazing depended on time since fire; it had very negative effects on recently burned patches, but weakly negative effects on patches burned 2 years prior. The strength of the time since fire x grazing interaction depended on the sampling period, and was strongest in early June and late July. Grazing (as a main effect) reduced *S. idalia* population density, but to a greater degree than in 2006: density was reduced by 72% relative to ungrazed pastures. As in 2006, the importance of grazing as a main effect became greater as the summer progressed, with ungrazed pastures having higher densities than grazed pastures by factors of 1.6, 6.4, and 7.6 for early June, late June, and late July respectively.

3.1.2. *Simple effects*

Effect slicing and multiple comparison procedures revealed multiple simple effects in 2006 (Table 1A, B, C) and 2007 (Table 2A, B, C). In early June 2006 (Table 1A), time since fire increased *S. idalia* population density in grazed pastures, with patches burned 2 or more years prior having densities more than 5 times higher than recently burned patches. We failed to find evidence of an effect of time since fire on population densities in ungrazed pastures in early June 2006. In early June 2007, grazed pastures exhibited the same trend as in 2006, with patches burned 2 years prior having densities approximately 26 times higher than recently burned patches (Table 2A). In ungrazed pastures, the opposite pattern was apparent, as recently burned patches had higher densities than patches burned 1 and 2 years earlier. Grazing reduced densities in recently burned patches but not in patches burned in prior years.

In late June 2006 (Table 1B), we failed to find simple effects of grazing or time since fire on *S. idalia* density. However, in late June 2007 (Table 2B), time since fire increased density in the ungrazed pastures, with patches burned 1 and 2 years earlier having densities approximately two times higher than those found in recently burned patches. Grazed prairie had fewer *S. idalia* than ungrazed prairie at all three levels of time since fire (Table 2C).

The effects of grazing and time since fire on density in late July were consistent from 2006 to 2007 (Tables 1C and 2C respectively). Time since fire reduced density in ungrazed pastures, with recently burned patches having much higher densities than patches burned 1 or 2 years prior. Grazing strongly reduced density in recently burned patches, but not in patches burned in prior years. Densities were approximately 7 times higher and 45 times higher in ungrazed, recently burned prairie than grazed, recently burned prairie in 2006 and 2007 respectively.

3.2.   *Nectar source density*

In all three sampling periods of 2007, time since fire affected nectar source density (Table 3A, B, C). However, the direction of the impact (positive or negative) depended on sampling period, grazing, and the nectar source in question. One pattern was consistent in each of the three sampling periods: time since fire affected densities of all nectar sources in the grazed pastures, with the recently burned patches always having far lower densities than patches burned 1 year prior, and having densities lower than patches burned 2 years prior in two out of three sampling periods. Grazing either reduced

nectar source density or had no significant effect, depending on sampling period and time since fire.

In early June 2007, grazing and time since fire interacted to affect the flowering ramet density of all nectar sources (F = 5.08, d.f. = 2, 12, P = 0.025). In grazed pastures, flowering ramet density in patches burned that spring was approximately 75% lower than in patches burned 1 and 2 years earlier (Table 3A). In the ungrazed pastures, flowering ramet density was not affected by time since fire. Grazing reduced nectar source density relative to ungrazed pasture in recently burned patches, but not in patches burned 1 or 2 years earlier.

We found *Echinacea pallida* within nectar source strip transects at three sites, but not at the Bethel Conservation Area (where we failed to see any ramets of this species during the study). Grazing and time since fire had marginally interactive effects on flowering ramet density of *E. pallida* (F= 3.16, d.f. = 2, 12, P = 0.079). In ungrazed pastures, there was a significant effect of time since fire, with much higher densities of flowering ramets in recently burned patches than in patches burned 2 years earlier (Table 3A). Grazed pastures failed to exhibit an effect of time since fire. However, recently burned patches in grazed pastures had marginally lower densities of *E. pallida* flowering ramets than the analogous patches in ungrazed pastures.

In late June 2007, we failed to find evidence of an interaction between time since fire and grazing on density of all nectar sources. However, time since fire (as a main effect) increased density of all nectar sources (F = 4.87, d.f. = 2, 13.7, p = 0.025), especially in grazed prairie, where densities in recently burned prairie were only 18% and 24% as high as those in prairie burned 1 year and 2 years earlier respectively (Table 3B).

We found no differences in overall nectar source abundance between grazed and ungrazed pastures, and found no treatment effects on *Monarda fistulosa* abundance. Only 4 of 24 prairie patches had flowering ramets of *M. fistulosa* within our strip transects.

In late July 2007, we failed to find significant main effects or interactive effects on density of all nectar sources. Time since fire as a simple effect increased density of all nectar sources in the grazed pasture, with recently burned and grazed prairie having densities only 37% of prairie burned 1 year earlier (Table 3C). Time since fire and grazing interacted significantly (F = 7.09, d.f. = 2, 12, P = 0.009) to affect the density of flowering ramets of *Liatris pycnostachya*. In ungrazed pastures, recently burned patches had much higher densities of this species than patches burned 1 or 2 years earlier (Table 3C). Grazing reduced the abundance of *L. pycnostachya*, but only in recently burned patches.

3.3.   *Relationships between butterfly and nectar source population densities*

In early June 2007, the population density of *S. idalia* was positively correlated with the flowering stem density of all nectar sources (Pearson's r = 0.36, P = 0.041), but was correlated more strongly with the density of *E. pallida* (Pearson's r = 0.47, P = 0.006). In late June 2007, *S. idalia* population density was correlated neither with density of all nectar sources nor with *M. fistulosa* density. In late July 2007, once again there was no relationship between *S. idalia* population density and abundance of all nectar

source, but there was a strong positive correlation between densities of *S. idalia* and *L. pycnostachya* (Pearson's r = 0.66, p < 0.001).

4.   Discussion

Our interest in the "prairie butterfly paradox" challenged me to learn more about the responses of *S. idalia* to the disturbances that are common in tallgrass prairie. Prior studies have demonstrated that fire kills *S. idalia* immatures (Swengel 1996, Swengel 1998), therefore we predicted that *S. idalia* population density would be locally reduced by fire. We also predicted density of this species would increase with time since fire. However, we did not detect a reduction in *S. idalia* density attributable solely to recent fire. Rather, we found complex population responses that were mediated by the interaction of time since fire with sampling period. Either fire did not kill many *S. idalia* larvae, or recolonization of recently burned areas occurred much faster than anticipated. Given the high fuel loads in the tallgrass prairie experimental units after 2 years without major disturbance, early spring prescribed fires were uniform, leaving few unburned microsites within these units. Because *S. idalia* immatures spend the winter and spring aboveground (Powell et al. 2007), we suspect that all or nearly all immatures within burn units were destroyed. Yet, within a few months of burning experimental units, those units were recolonized by *S. idalia* adults, which presumably had emerged in adjacent units that had not been burned that spring. During some sampling periods, particularly in late July of both years, population densities were highest in the recently burned units of the ungrazed pastures, implying that *S. idalia* found recently burned units more suitable than the grassland from which they had emerged. The validity of our finding that the

time since fire and sampling period have interactive effects on *S. idalia* density is bolstered by obtaining very similar results in 2006 and 2007, even though (1) fires were rotated to different experimental units, and (2) precipitation differed greatly between 2006 and 2007 (with 2006 a drought year, and 2007 an unusually wet year). The large change in density among sampling periods demonstrates that sampling during a single time period can lead to inaccurate conclusions regarding treatment effects on butterfly density.

Whereas previous studies (Swengel 1996, Swengel 1998, Powell et al. 2006, Vogel et al. 2007) had demonstrated negative effects of recent fire on *S. idalia* density, our study is the first to demonstrate a positive response of *S. idalia* density to recent fire. Why did *S. idalia* increase in response to recent fire in ungrazed pastures? Our data suggest that the adult butterflies tracked the availability of nectar sources and were able to recolonize these areas as long as unburned areas were in close proximity. Time since fire clearly affected nectar source density during multiple periods of *S. idalia*'s flight season. Recent fire stimulated the blooming of *Echinacea pallida* and *Liatris pycnostachya*, the most frequently utilized nectar sources in early June and late July, respectively. Due to the strong correlations between *S. idalia* density and density of these nectar sources, the enhanced blooming of these key floral resources appears to be the likely cause for high *S. idalia* density in recently burned patches during early June of 2007 and late July of both years. In contrast, Swengel (1996) sampled *S. idalia* early in its flight period (between June 14th and 19[th)], which might not have provided *S. idalia* adults with enough time to recolonize burned sites. Sampling early in the flight season also precluded the Swengel (1996) study from observing the positive response of *L.*

pycnostachya flowering to fire (and the positive response of *S. idalia* populations to *L. pycnostachya* flowering). This difference between our findings strengthens our argument that the timing of sampling can have important effects on the conclusions one makes concerning effects of fire on butterfly density.

Our findings also differ from studies that found negative effects of rotational fire on *S. idalia* density. We propose experimental scale as the primary explanation for differences between our findings and those of Swengel and Swengel (2001). Whereas our experimental prairies were 60 to 105 ha, the majority of prairies studied in their study were smaller than 30 ha. They speculated that *S. idalia* populations in small prairies would be more vulnerable to extirpation via rotational fire, due to the higher chance that an entire cohort of immatures would be aggregated in the portion that gets burned. We concur with that speculation, given the research on other taxa that has shown populations occupying small patches of habitat are more vulnerable to environmental stochasticity (Haddad 2009). We speculate that the larger size of the prairies we studied permitted them to host larger, more widely dispersed populations of *S. idalia,* with more adults available to recolonize recently burned areas. In another study in which burning reduced *S. idalia* abundance, 66% of the grassland landscape was burned in the year preceding the study, and 47% was burned in the first year of the study (Vogel et al. 2007). In contrast, only 33% of each pasture was burned each year in our study. We suspect that the relatively smaller burns and larger experimental units in our study reduced mortality enough to permit the population to better recolonize recently burned areas.

The design of our study does not enable me to conclude whether or not *S. idalia* populations were benefited or harmed at the pasture scale by rotational fire. We

acknowledge *S. idalia* might have been even more abundant if these sites had not been

burned at all between 2005 and 2007, due to the absence of fire-caused mortality of

roughly 33% of the immatures each spring. However, we observed an increase in

population density from 2006 to 2007, which contradicts the expectation that rotational

fire reduces *S. idalia* density. Given the demonstrated importance of nectar availability

to other butterflies (Schultz and Dlugosch 1999, Brower et al. 2006), and the strong

positive correlations we found between density of *S. idalia* and two important nectar

sources, fire-enhanced blooming of those nectar sources might increase survivorship and

fecundity of *S. idalia* females enough to offset mortality of immatures caused by fire.

Our study is the first to examine the response of butterfly density to pyric

herbivory, the fire-grazing interaction. Relative to rotational fire without grazing, pyric

herbivory reduced *S. idalia* density, in part by reducing density of important nectar

sources in recently burned prairie (particularly *E. pallida* and *L. pycnostachya*). Recently

burned patches were grazed much more intensely than patches burned in previous years

(Fuhlendorf and Engle 2004), thus had much less plant biomass, fewer flowering ramets

of preferred nectar sources, and fewer *S. idalia.* Treatment effects on *S. idalia* density

were similar in 2006 and 2007, even though different herds of cattle were placed in the

pastures each year and fire was rotated from one patch to another. Though some nectar

sources were trampled by cattle, we hypothesize the primary cause of reduced nectar

source density in these patches was consumption by cattle. Corroboration of this came

from finding hundreds of ramets of *E. pallida* with their peduncles clipped off within the

grazed pastures. Even though white-tailed deer (*Odocoileus virginianus*) were observed

at all of our sites, we have no evidence that they consumed *E. pallida*; of thousands of

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flowering ramets observed in ungrazed pastures, we saw none with their peduncles clipped off. It has long been recognized that cattle sometimes consume *Echinacea* spp. (Weaver and Fitzpatrick 1934, Beebe and Hoffman 1968, Eddy 1990); our study is the first to document a decline in butterfly density caused by grazing of this preferred nectar source.

We think that our findings would have been similar if pastures had been stocked with bison rather than cattle. Although bison in large landscapes have been shown to be more selective for grass (Peden et al. 1974, Plumb and Dodd 1993) (and thus less likely to consume forb nectar sources), when grazing management variables are kept the same, bison and cattle have very similar effects on plant community composition (Towne et al. 2005). Pyric herbivory reduces differences in foraging behavior between bison and cattle, as both species select the recently burned patch and spend less time searching the entire pasture for preferred forage species (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009

Given the close linkage we demonstrated between population density of *S. idalia* and some of its nectar sources, we suspect that the effects of fire and pyric herbivory on *S. idalia* populations elsewhere would also be mediated by effects on nectar sources. Any study of fire and/or grazing treatment effects on *S. idalia* should simultaneously examine treatment effects on nectar sources. We recommend against extrapolating our findings on *S. idalia* to the rare prairie skippers, some of which are slow to recolonize sites from which they've been extirpated (Panzer 2002). The effects of fire, grazing, and pyric herbivory on other prairie specialist butterfly species deserve empirical study.

In our study, burning one third of a grassland each year was compatible with short-term conservation of *S. idalia*, even in two grasslands that were isolated from other unburned grassland by at least 1 kilometer (Niawathe and Bethel). However, the scale of burning is important to consider. Prescribed burns in our study were 20 to 34 ha, and *S. idalia* recolonized the recently burned patches soon after emergence. We suspect that *S. idalia* may completely recolonize large burn units (burn units over 400 ha) much more slowly, due to the long-distance dispersal that would be required to reach the patch interior. This would be problematic if the fire return interval is shorter than the time it takes for *S. idalia* to fully recover to its pre-fire distribution and abundance. At the other extreme, Swengel and Swengel (2001) have demonstrated that rotational burning of small prairies can quickly lead to extirpation of *S. idalia*.

Is cattle grazing compatible with the conservation of *S. idalia*? It depends on one's goal for *S. idalia* population size and the specific parameters of grazing management. We found that adding cattle to rotationally burned grassland reduced habitat quality for *S. idalia* adults, particularly in patches burned earlier the same year. However, *S. idalia* remained in all grazed pastures at the end of the study. Adjusting any of the variables of grazing management (such as grazing species, breed, age, season, duration, and stocking density) is likely to alter the effects of pyric herbivory on *S. idalia,* given the influence those variables have on grazing intensity and selectivity (Milchunas et al. 1998, Holechek et al. 2001). Stocking density is a particularly important factor to consider (Kruess and Tscharntke 2002, WallisDeVries et al. 2007). In rotationally burned prairies of southwestern Missouri and areas with similar levels of primary productivity, heavier stocking density than those our study used could result in significant

reduction of nectar source availability in all patches, not just the most recently burned patch. Using substantially lower stocking density would reduce grazing intensity within the recent burn patch, which in turn might increase abundance of *E. pallida*, *L. pycnostachya*, and perhaps other nectar sources in that patch. However, with reduced grazing intensity also comes reduced biomass removal, increasing the likelihood that the forage there becomes decadent. This in turn would cause grazing animals to spend more time foraging in other patches, where they might selectively forage for preferred nectar sources. In addition to the uncertain impact it would have upon *S. idalia* density, reducing grazing density would diminish the among-patch structural heterogeneity that is an important objective of returning pyric herbivory to grasslands (Fuhlendorf and Engle 2001, Archibald et al. 2005).

Because environmental heterogeneity is an important source of biodiversity (Christensen 1997, Wiens 1997), we concur with those (Fuhlendorf and Engle 2001, Swengel and Swengel 2001b, Brudvig et al 2007) who have recommended that grasslands be managed for heterogeneity. We believe that managing sites with a variety of practices is particularly important for a habitat-specialist butterfly like *S. idalia*, which is so sensitive to disturbance. Though rotational burning and pyric herbivory are effective tools for maintaining components of prairie ecosystems, they do not benefit all components (Brudvig et al 2007). Given the extreme sensitivity of some invertebrate taxa to fire (Nekola 2002, Schlicht et al. 2009), maintaining small but permanent non-fire refugia (Swengel and Swengel 2007) in prairie landscapes should be strongly considered by prairie managers as long as practical alternatives to fire are available for limiting woody plant encroachment.

Acknowledgments

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Table 1. Effects of time since fire and grazing on *Speyeria idalia* population densities (individuals/ha) in 2006. Different letters within a row indicate $P < 0.05$ for pairwise comparisons.

Period and Treatment	Time since fire (years)			P (row)
	0	1	2	
(A) Early June				
Ungrazed	4.8	6.5	8.3	*0.771*
Grazed	2.4a	5.3ab	13.0b	*0.066*
P (column)	*0.400*	*0.433*	*0.474*	
(B) Late June				
Ungrazed	3.2	11.8	7.0	*0.250*
Grazed	0.1	3.2	4.9	*0.232*
P (column)	*0.175*	*0.080*	*0.526*	
(C) Late July				
Ungrazed	14.2a	0.8b	1.1b	*0.001*
Grazed	2.1	0.7	1.6	*0.889*
P (column)	*0.002*	*0.938*	*0.884*	

Table 2. Effects of time since fire and grazing on *Speyeria idalia* population densities (individuals/ha) in 2007. Different letters within a row indicate $P < 0.05$ for pairwise comparisons.

Period and Treatment	Time since fire (years)			P (row)
	0	1	2	
(A) Early June				
Ungrazed	21.7	9.0	7.0	*0.067*
Grazed	0.5	8.9	13.9	*0.009*
P (column)	*0.001*	*0.808*	*0.252*	
(B) Late June				
Ungrazed	11.4a	21.8b	25.1b	*0.013*
Grazed	1.5	1.2	6.5	*0.138*
P (column)	*0.073*	*0.001*	*0.008*	
(C) Late July				
Ungrazed	21.8a	5.6b	8.9b	*0.009*
Grazed	0.4	2.3	2.0	*0.647*
P (column)	*0.001*	*0.367*	*0.132*	

Table 3. Effects of time since fire and grazing on the abundance of floral resources (# of flowering ramets/ha) in 2007. Different letters within a row indicate $P < 0.05$ for pairwise comparisons.

Period and Treatment	Time since fire (years)			P (row)
	0	1	2	
(A) Early June				
All Forbs and Legumes				
Ungrazed	3841	2681	2034	0.444
Grazed	899a	3491b	3565b	0.018
P (column)	0.026	0.498	0.273	
Echinacea pallida				
Ungrazed	625a	188ab	1b	0.029
Grazed	25	248	50	0.421
P (column)	0.059	0.786	0.643	
(B) Late June				
All Forbs and Legumes				
Ungrazed	3426	4788	5457	0.505
Grazed	1433a	7780b	5982b	0.016
P (column)	0.185	0.412	0.867	
Monarda fistulosa				
Ungrazed	0	0	380	0.150
Grazed	72.5	8.7	0.0	0.767
P (column)	0.482	0.812	0.086	
(C) Late July				
All Forbs and Legumes				
Ungrazed	2487	2655	2749	0.957
Grazed	1941a	5185b	3101ab	0.042
P (column)	0.577	0.073	0.600	
Liatris pycnostachya				
Ungrazed	608a	71b	215b	0.006
Grazed	77	119	81	0.645
P (column)	0.001	0.503	0.228	

a

b

● Taberville
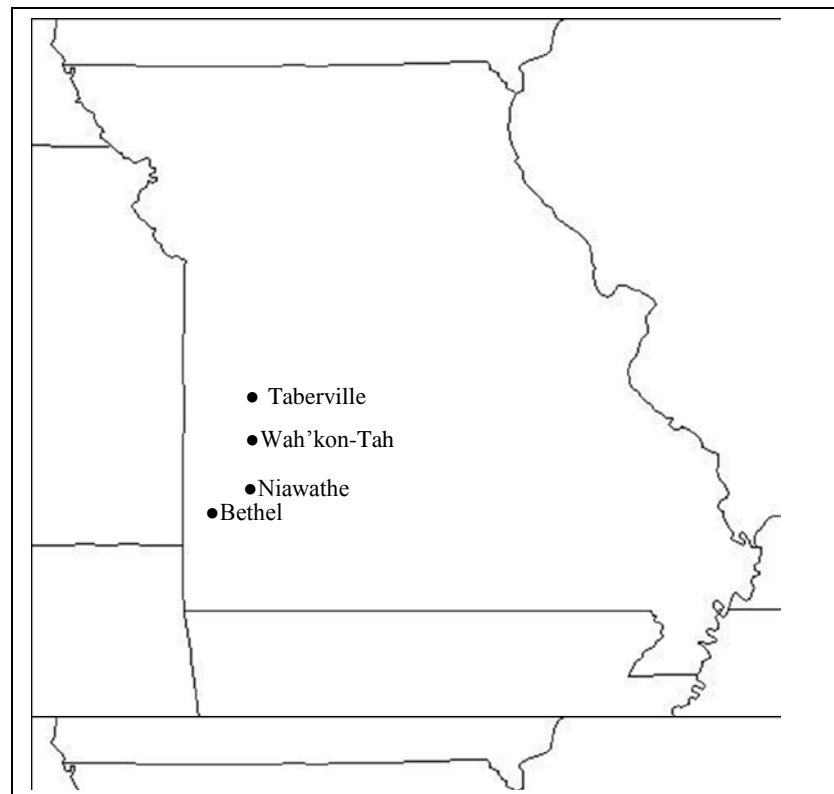
●Wah'kon-Tah

●Niawathe
●Bethel

Figure 1. Maps showing (a) the location of Missouri within the U.S.A., and (b) the locations of *Speyeria idalia* study sites in southwestern Missouri. Three of the conservation areas (Taberville, Wah'kon-Tah, and Niawathe) are native, unplowed prairies, whereas Bethel Prairie Conservation Area has been plowed and restored to tallgrass prairie.
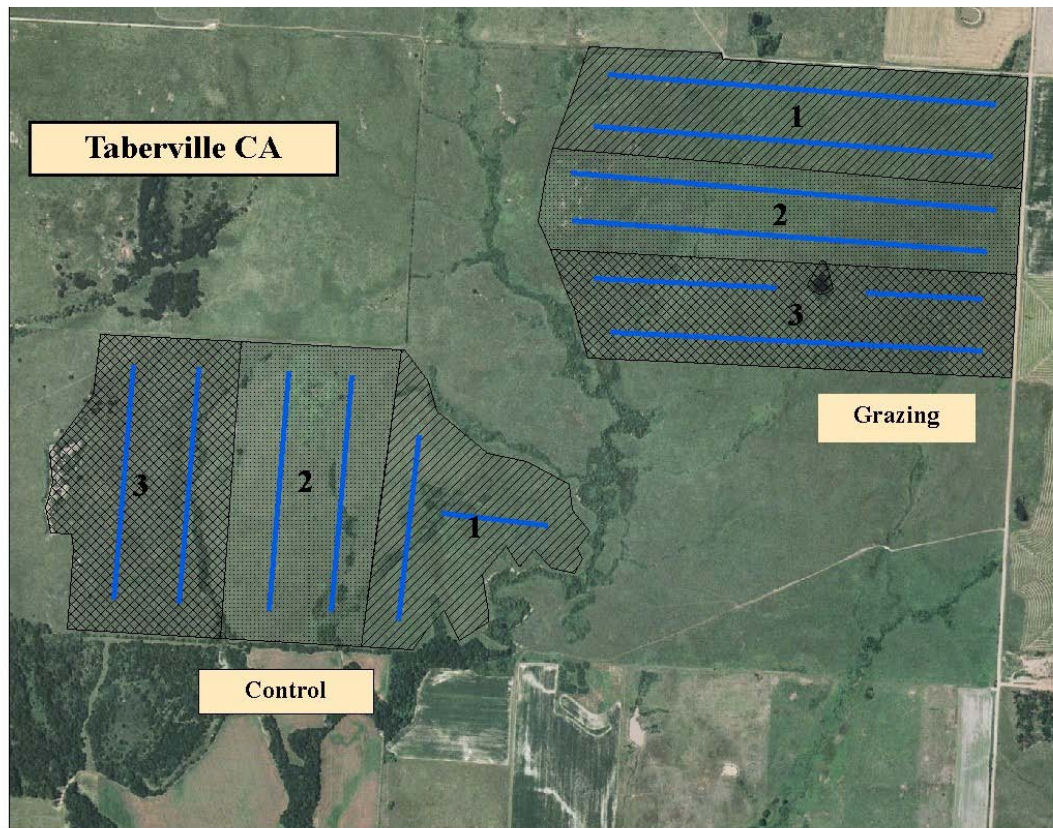
Figure 2. Map showing the experimental design at the Taberville Prairie Conservation Area in southwestern Missouri. Burn units denoted by the number 1 were burned in 2005, number 2 in 2006, and number 3 in 2007. Transects for butterfly and nectar source sampling are indicated by bold lines within each burn unit.

VITA

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Doctor of Philosophy

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Title of Study: THE EFFECTS OF ECOLOGICAL MANAGEMENT ON TALLGRASS
                PRAIRIE BUTTERFLIES AND THEIR NECTAR SOURCES

Pages in Study: 106   Candidate for the Degree of Doctor of Philosophy

Major Field: Natural Resource Ecology and Management

Scope and Method of Study:
        The primary goal of my dissertation research was to learn how disturbance-
sensitive butterfly species can persist in disturbance-dependent prairie ecosystems. I
conducted three studies, all at the same four tallgrass prairies in southwestern Missouri.
In Chapter 1, I examine the effects of habitat structure, butterfly species, and butterfly
size on butterfly detectability, and the corresponding role of distance sampling in
generating better estimates of abundance. In Chapter 2, I examine nectar use and nectar
source selectivity of tallgrass prairie butterflies. In Chapter 3, I examine the effects of
time since fire, grazing and sampling period on the abundance of *Speyeria idalia* (an
imperiled butterfly) and its nectar sources. Each prairie had two pastures: one
rotationally burned and grazed by cattle (also known as pyric herbivory), and one
rotationally burned but not stocked with cattle. Butterfly population density and floral
resource availability were assessed in early June, late June, and late July of 2006 and
2007.

Findings and Conclusions:
        Analyses of distance data revealed substantial variation in butterfly detectability
among species and among different behaviors, but not between different habitat
structures.   I recommend that biologists supplement line transect sampling with distance
sampling for butterfly research.
        Prairie butterfly taxa varied in use of nectar sources. *S. idalia* showed strong
selectivity for a different nectar source during each sampling period. Multiple butterfly
taxa were highly selective in for *Echinacea pallida*. My findings demonstrate the
important role that a few subdominant forbs play in conservation of tallgrass prairie
butterflies.
        S. idalia and its nectar sources show complex responses to time since fire,
grazing, and sampling period. In 2007, *S. idalia* population density was a function of a
three-way interaction of these factors. Grazing reduced abundance of *S. idalia* and two
preferred nectar sources, *Echinacea pallida* and *Liatris pycnostachya*, particularly in
recently burned patches. In ungrazed pastures, recent fire appeared to enhance
abundance of *S. idalia* and its preferred nectar sources.

ADVISER'S APPROVAL: Samuel D. Fuhlendorf