

A multi-scale examination of the distribution and habitat use patterns of the regal fritillary

by

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Abstract

The regal fritillary (*Speyeria idalia*) was once an abundant butterfly species of North American prairie communities. Despite its once broad geographic distribution, populations have declined by ~99% in the prairie region for reasons that are poorly understood. The rapid, range-wide declines and persistent threats to extant populations from habitat loss and mismanagement prompted the U.S. Fish and Wildlife Service to initiate a species status review of the regal fritillary as a potential candidate for listing under the endangered species act in September 2015. Due to the uncertain status and contention regarding the effects of management practices (i.e., burning, grazing, and haying) on regal fritillary, my research objectives were to assess the effects of management practices and habitat features on the distribution and density of regal fritillary and their preferred larval host plant for the Midwest, prairie violet (*Viola pedatifida*). I generated species distribution models (SDM) of prairie violet to readily identify potential areas across the landscape containing patches of host plants and subsequently facilitate the location of regal fritillary larvae. The SDM produced maps of the probabilistic occurrence distribution of prairie violet throughout my study area and highlighted habitat features and management practices important to the occurrence of prairie violet. The seven final variables used to create the SDM and identified as important to the occurrence of prairie violet were elevation, slope, hillshade, slope position, land cover type, soil type, and average fire frequency. Using the SDM for prairie violet, I located eight areas to conduct surveys for regal fritillary larvae that were managed using various management (grazing and haying) regimes and fire-return intervals (low ≥ 10 years, moderate 3-5 years, and high 1-2 years). I used a binomial generalized linear model to determine the effects of management, host plant density, months since burn, and the interaction between months since burn and management on the occurrence distribution of regal

fritillary larvae. My results indicate that greater host plant density and short fire-return intervals are important to the occurrence of regal fritillary larvae and, despite current management recommendations, larvae may be negatively impacted by a lack of fire. Finally, I surveyed tracts of prairie within my study area using a distance sampling approach along line transects stratified by overall management (burned, grazed, and hayed) and fire-return interval (low ≥ 10 years, moderate 3-5 years, and high 1-2 years) for adult regal fritillary. My results indicated that adult density was at least 84% greater in areas that received moderate fire-return intervals and greatest in areas that were grazed and burned on a moderate fire-return interval. However, density estimates of adult regal fritillary did not differ among overall management practices (i.e., burned, grazed, hayed). Additionally, adult density increased as percent cover of grass, litter, and prairie violets increased. In contrast, adult density decreased as percent cover of woody vegetation and forbs increased. These results support the use of prescribed fire in a shifting mosaic or patch-burning practice as a viable management strategy for maintaining and conserving regal fritillary populations within the Flint Hills region.

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Chapter 1 - Predicting the Occurrence of the Larval Host Plant for the Regal Fritillary in Tall-grass Prairie Using a Species Distribution Modeling Approach

Introduction

The regal fritillary, *Speyeria idalia* (Drury, 1773) (Nymphalidae), a once abundant butterfly of North American prairie communities had an historic range that extended from Oklahoma, USA, to the border of Canada and east to the Atlantic coast (NatureServe 2005). Despite its once broad geographic distribution, populations have declined by approximately 99% (NatureServe 2005). Both eastern and western populations have experienced dramatic declines, with *S. idalia* nearly extirpated from the eastern portion of its former range (Selby 2007). *S. idalia* was listed as a Category II species under the United States Endangered Species Act (ESA) until this category was removed in 1996 (U.S. Fish and Wildlife Service 1996). The rapid, range-wide decline of this species prompted the U.S. Fish and Wildlife Service to initiate a status review of *S. idalia* under the Endangered Species Act (ESA) in September 2015. While the direct causes of local population declines of *S. idalia* are unclear, it appears the species decline is a result of habitat loss and fragmentation along with incompatible grassland management practices such as intensive grazing, frequent and intensive burning, and haying (Schultz and Crone 1998, Davies et al. 2005, Ferster and Vulinec 2010).

S. idalia is an oligophagus butterfly species that consumes only violets (*Viola* spp.) during the immature stages (Klots 1951, Hammond 1974, Ferris and Brown 1981). Although the species uses a variety of *Viola* species, immature *S. idalia* tend to be associated with specific *Viola* species in different parts of their range (Selby 2007). Populations in the central Great Plains are reported to selectively feed on *Viola pedatifida* (Swengel 1997, Kelly and Debinski

1998, Dole 2004). *V. pedatifida* is a small perennial plant characteristic of native tall-grass communities within Kansas, USA (Kopper et al. 2000). It consists of a rosette of basal leaves, from which one or more flowering stems may emerge that are somewhat taller. The basal leaves have a deeply lobed palmate structure, and are “fan” shape in appearance. *V. pedatifida* typically blooms from mid- to late-spring, but it can also bloom during fall under favorable conditions (Figure 1.1).

Large conspicuous adult butterflies such as *S. idalia* are difficult to miss as they search for nectar sources, mates, or oviposition locations. Conversely, larvae are inconspicuous and cryptic, making them difficult to locate in the field (Scudder 1889, TNC 2001, Kopper et al. 2001). Consequently, assessments of habitat quality are often measured as the habitat features and resources associated with the presence and abundance of adults (Britten and Riley 1994, Smallidge et al. 1996, Grundel et al. 2000, Collinge et al. 2003). However, resources used by adults may not adequately reflect requirements of immature stages, and assessments of habitat quality are generally improved if both adult and immature stages are included (Bergman 1999, Lane and Andow 2003, Albanese et al. 2008). Challenges associated with detecting *S. idalia* larvae have limited the ability to study this ambiguous and precarious life-history stage. The inability of Lepidoptera larvae to move great distances usually restricts them to the area in which they hatched (Tilmon 2008). The distribution of *S. idalia* larvae across the landscape is restricted to the patchy distribution of its larval host plant *V. pedatifida*. Therefore, the ability to readily locate patches of *V. pedatifida* should expedite discovery of *S. idalia* larvae in the field and facilitate research and conservation of this cryptic life-history stage.

Predictive ability is fundamental for conservation planning and forecasting (Ferrier 2002, Funk and Richardson 2002, Rushton et al. 2004) and understanding relationships between spatial

pattern and process (Rosenzweig 1995, Brown and Lomolino 1998, Ricklefs 2004, Graham et al. 2006). Recently, prediction has seen an increased role in applied ecology largely due to the threats to biodiversity from global climate change (Clark et al. 2001). However, the complexities of ecosystems such as historical legacies, nonlinearities, interactions, and feedback loops among other factors inhibit efforts directed at prediction (Levin 1998). Thus, researchers are plagued by the need to understand and predict complex ecological processes and patterns (Olden et al. 2008).

Species distribution models are numerical tools that relate observations of species occurrence or abundance with environmental predictor variables (Elith and Leathwick 2009). They are an innovative approach commonly used to overcome issues associated with prediction (i.e., nonlinearities) and explore diverse questions in ecology, evolution, and conservation (Elith et al. 2006). For example, species distribution models have been employed to study relationships among predictor variables and species richness (Mac Nally and Fleishman 2004), invasive potential of non-native species (Peterson 2003, Goolsby 2004), historic species distribution (Hugall et al. 2002, Peterson et al. 2004), and future climates (Bakkenes et al. 2002, Skov and Svenning 2004, Araújo et al. 2004, Thomas et al. 2004, Thuiller et al. 2005).

My objective was to construct probabilistic maps of the predicted distribution of *V. pedatifida* and identify the habitat features and management practices associated with *V. pedatifida* occurrence. Specifically, I used four of the leading species distribution modeling techniques and *V. pedatifida* presence-absence data from my study area in northeastern Kansas to generate probabilistic maps of the potential distribution of *V. pedatifida* based on physical landscape attributes, environmental variables, and land management practices. I used an

ensemble approach to combine probabilistic predictions from the top models produced by the four individual modeling techniques.

Methods

Study Area

Surveys for *V. pedatifida* were conducted in northeastern Kansas, in Clay, Geary, Riley and Pottawatomie counties. This study area is nestled within the Flint Hills, encompasses both the Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) and bisected by a number of drainages and flanked by two large reservoirs (Figure 1.2). The Flint Hills are characterized by large rolling hills and rocky flint filled soils (Anderson and Fly 1955). The flint contained within the bedrock for which the region is named depressed erosion and left the Flint Hills higher than the surrounding areas, with an elevation relief of 91-152 m. In addition to preventing soil erosion the underlying flint and limestone formations made this region undesirable for crop cultivation making this region home to the largest remaining contiguous tract of tall-grass prairie in North America (Reichman 1987). Subsequently, the vegetative community is commonly associated with dominant grasses such as big bluestem (*Andropogon gerardii*), indiagrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), however, perennial grasses, woody species and a wide variety of native herbaceous forbs comprise the remainder of the plant community (Anderson and Fly 1955, Owensby and Smith 1979). The climate in this region is driven by its interior location and characterized by hot, dry summers and cold winters with temperatures ranging from -40° C to 49.44° C (Abrams and Hulbert 1987). Precipitation varies drastically and droughts are common. Average annual precipitation in this region is 83.82 cm (Abrams and Hulbert 1987).

The FRMR is located on the northern edge of the Flint Hills between the cities of Manhattan and Junction City. The FRMR is one of the nation's largest U.S. Army posts comprising of ~41,000 ha. Approximately 29,000 ha are managed for a number of uses including conservation and outdoor recreation activities. The FRMR is divided into training areas that are managed using a combination of burning and haying regimes.

The KPBS is a 3,487 ha tract of tall-grass prairie co-owned and operated by the Division of Biology, Kansas State University and The Nature Conservancy. The KPBS has been a part of the National Science Foundation Long-Term Ecological Research (LTER) network since 1981 and experimentally managed with various grazing and burning regimes (Knapp et al. 1998). Grazing treatments are varied by native bison (*Bison bison*), cattle (*Bos taurus*), or no grazing. Prescribed burns occur on an annual to every 2, 4, and 20-year intervals.

Field Surveys for *V. pedatifida*

V. pedatifida presence-absence data were obtained through field surveys. Surveys were conducted in spring (March – May) during 2014 and 2015. Each year of the study I generated ~350 random points distributed throughout the study site using Environmental Systems Research Institute's (ESRI) ArcMap 10.3.1 Geographic Information System (GIS) ArcMap 10.3.1 software. These randomly distributed points were used to survey for the presence-absence of *V. pedatifida*. I used a Garmin 64s global positioning system (GPS) receiver and the survey points associated UTM coordinates to locate points in the field. Once a survey point was reached, I created a 10-m X 10-m plot using marking flags, measuring tape, and compass. I set the first marking flag at the initial survey point location. From this point, I used the compass and measuring tape to set a second flag 10-m due north from the initial marking flag. From the second marking flag, I used the compass and measuring tape to set a third flag 10-m due east

from the second marking flag. Finally, from the third flag I used the compass and measuring tape to set a fourth and final flag 10-m due north from the third flag creating a 100-m² survey plot. After creating the survey plot, I systematically searched for *V. pedatifida* recording both presence and absence. I also selected a random subset of 20 plots to resurvey each year to account for detection error.

Predictors

I considered 16 predictor variables for predictive spatial modeling of *V. pedatifida* (Table 1.1). I obtained National Elevation Dataset (NED) data, ortho-National Agriculture Imagery Program (NAIP) images, and gridded Soil Survey Geographic (gSSURGO) data from the Geospatial Data Gateway (GDG) (<http://datagateway.nrcs.gov>). I used GIS software to process, calculate, and derive the 16 predictor variables from the raw datasets obtained from the GDG.

I derived 12 variables from the NED dataset using the spatial analyst and geomorphometry and gradients metrics toolboxes in ArcMap. I derived aspect, compound topographic index, curvature, hillshade, heat load index, roughness, slope area ratio, slope, slope aspect cosine, mean slope, slope position, and topographic radiation aspect index. The NAIP image was used to generate a fine resolution (1-m) land cover layer by performing a supervised classification in ArcMap on the NAIP image. Using this method, I delineated five major land cover types: water, cropland, urban, forest, and grassland. I reclassified the raw SSURGO data into 13 different soil classes using ArcMap. The reclassified soil classes included sand, loamy sand, sandy loam, sandy clay loam, loam, clay loam, sandy clay, clay, silty clay, silty clay loam, silt loam, silt and complex soils. Finally, I created an average fire frequency layer in ArcMap. This layer was produced by calculating the number of burns that took place over a 16 -year period (2001-2016). The average fire frequencies for the FRMR and KPBS were calculated

using their respective records. However, burn data for private lands in Kansas are not readily available. Therefore, to estimate average fire frequency for the areas outside of the FRMR and KPBS, I used remotely sensed data obtained from Mohler and Goodin (2012 a,b).

All predictors were resampled to a 10-m x 10-m spatial resolution. This scale was selected because it was the size of a *V. pedatifida* survey plot. In addition, any predictor variables that were not inherently continuous in nature (i.e., land cover type and soil type) were resampled using a 3-m x 3-m moving window analysis in an effort to create continuous variables from naturally categorical layers. To avoid problems associated with multicollinearity, predictors were compared in a pairwise fashion to evaluate their correlation. Correlation among variables was compared using the maximum of the Pearson, Spearman and Kendall coefficient. Variables that had a $r \geq |0.70|$ were considered highly correlated. When two or more predictors were correlated, the choice of which variable to remove was somewhat subjective. If one variable was outperforming another in terms of its percent deviance explained, then that variable was retained. However, if variable performance was similar, I removed the variable that I felt was less interpretable. Because correlated variables were essentially providing the same information to the predictive model, the somewhat subjective variable selection process should not influence model results.

In addition to eliminating correlated variables, I also removed variables that were not contributing to the model. Variable contribution was determined at the covariate selection stage and model fitting stage. At the covariate selection stage, variables that had low percent explained deviance (< 1.0%) were removed. At the model fitting stage, variable contribution was assessed by including and removing variables. If a variable did not contribute to the model

(i.e., the inclusion of the variable had little to no effect on evaluation metrics such as Area Under the Curve) then the variable was removed from the model.

Statistical Modeling Methods

The number of statistical modeling tools available to model a species distribution has rapidly increased over the last decade (Cushman et al. 2010). Basic logistic regression was once the most common analytical tool (Guisan and Zimmermann 2000). However, currently there are a broad range of analytical approaches (Cushman et al. 2010). Recent model comparisons and applications in several ecological studies have indicated that boosted regression trees (BRT), generalized linear models (GLM), multivariate adaptive regression splines (MARS), and random forests are among the top performing species distribution modeling techniques (Elith et al. 2006, Guisan et al. 2007, Evangelista et al. 2008, among others). I selected these species distribution modeling techniques based on their strong performance in other studies to predict the potential probabilistic distribution of *V. pedatifida* within my study area.

While previous studies have demonstrated that these techniques perform quite well for modeling species distributions, each approach has associated strengths and weaknesses. The GLM is a parametric technique that allow errors to be distributed following a number of distributional families including binomial, Poisson, or negative-binomial (Cushman et al. 2010). Unlike GLM, MARS is a non-parametric technique that models nonlinear relationships by combining regression and recursive partitioning methods (Friedman 1991, Elith et al. 2006). MARS is also an effective tool for assessing and describing specific interactions, a problem that plagues GLMs. However, MARS models seem to weaken when used to predict outside the areas where response data were collected (F. Huettmann unpublished cited in Cushman et al. 2010). BRT and random forest approaches are both ensemble techniques, producing a final model that

is a combination of many different trees (Stohlgren et al. 2010). Random forests have been proven useful for large-scale predictions and make a robust algorithm for projective modeling (Rehfeldt et al. 2006, Cushman et al. 2010).

Selection of a modeling approach and ultimately a final model output may be based on a number of factors including the availability and resolution of predictor variables, cost, convenience, or species occurrence data (i.e., presence-absence versus presence-only or abundance) (Stohlgren et al. 2010). However, model interpretation can be confused by the varying results produced by the different modeling approaches despite using the same set of response data and predictor variables (Stohlgren et al. 2010). The inconsistent results from approach to approach could be due to differences in model assumptions or algorithms, or different data requirements (Stohlgren et al. 2010). Discrepancies among the results from different modeling approaches led Araújo and New (2007) to suggest using ensembles of models for species distribution modeling, versus relying on model outputs from a single modeling approach. Ensemble species distribution models combine the strengths of several modeling approaches, while minimizing the weaknesses of any one model (Stohlgren et al. 2010). Despite claims of superiority for any one approach (Busby 1986, Walker and Cocks 1991, Lehmann et al. 2003, among others), independent evaluations of models have been unable to demonstrate the dominance of any one technique (Araújo and New 2007). Therefore, I generated individual probabilistic maps of potential *V. pedatifida* occurrence using four of the current leading individual modeling techniques BRT, GLM, MARS, and random forest and then combined the final outputs to create an ensemble model.

I created the four individual models using Software for Assisted Habitat Modeling (SAHM) for VisTrails version 2.2.3 using the default settings established for each technique

(Talbert 2012). The ensemble model was produced by combining the probabilistic maps from the four individual models and taking the mean value of the probability of potential *V. pedatifida* occurrence. To identify which models best explained observed patterns among analyses, I used a multi-model inference approach where I compared alternative competing models (Johnson and Omland 2003). Model performance was assessed for individual models by simultaneously applying both a 10-fold cross validation and 70/30 test training split. In this case, only the training data (70%) were partitioned into folds. I used six statistics - the area under the receiver-operating curve (AUC), Cohen's kappa, true skills statistic (TSS), sensitivity, specificity, and the percent correctly classified - to assess agreement between the presence-absence records and the predictions.

The AUC is a measure of model fit commonly used in model comparison studies (Elith et al. 2006, Guisan et al. 2007, Evangelista et al. 2008, among others). In general, AUC values > 0.90 indicate high accuracy, values between 0.70-0.90 indicate good accuracy, and values ≤ 0.50 (random) indicate low accuracy (Roura-Paseual et al. 2009). The AUC values for the 10-fold cross-validation correspond to the mean of the AUC measures obtained following the 10-fold cross-validation methodology. Cohen's kappa is a measure that corrects the overall accuracy of model predictions by the accuracy expected to occur by chance. The kappa statistic ranges from negative one to positive one, where positive one indicates perfect agreement and values of zero or less indicate a performance no better than random (Cohen 1960). Similar to kappa, TSS accounts for both omission and commission errors and ranges from negative one to positive one, where positive one indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche et al. 2006). Sensitivity quantifies the proportion of observed presences correctly predicted as presences. Therefore, a poor sensitivity indicates high omission

error (i.e., incorrect true positive fraction). Conversely, specificity is the measure of the proportion of observed absences correctly predicted as absence. A low specificity indicates high commission error (i.e., incorrect predictions of presence) (Fielding and Bell 1997). Finally, I used percent correctly classified to quantify the percentage of sites where the models correctly predicted the presence or absence of *V. pedatifida*.

Results

Probabilistic Maps

Throughout the course of this study I surveyed a total of 1,248 locations for the presence-absence of *V. pedatifida* (Figure 1.3). Of the 1,248 surveyed locations, 495 had *V. pedatifida* present while 795 had no *V. pedatifida* present. I re-surveyed a sub-set of plots each year to determine my detectability of *V. pedatifida*. I accurately detected the presence of *V. pedatifida* 82.5% of the time. Distributions from the four individual modeling techniques within the study area were used to display mapped probabilistic predictions of *V. pedatifida* occurrence and indicated that projection varied among modeling techniques (Figure 1.4a-d). An ensemble model was created from the mean probabilistic values from the four individual techniques (Figure 1.4e). The six evaluation metrics used to assess model performance and accuracy for both the 70/30 test training split and the 10-fold cross-validation indicated that performance among modeling techniques varied (Table 1.2). The ensemble model was the most conservative in terms of predicting high probabilities of *V. pedatifida* occurrence while the GLM was the most generous. The total hectares predicted by the ensemble, GLM, random forest, MARS and BRT models to have a probability of *V. pedatifida* occurrence >0.60 were 2,518, 3,929, 3,390, 3,809, and 2,852 respectively out of the 157,454 ha that comprise the study area.

Predictor Variables

The seven final predictor variables used to model the predicted occurrence of *V. pedatifida* were average fire frequency, elevation, hillshade, land cover type, slope, topographic radiation aspect index (TRASP), and soil type. While variable importance differed across modeling techniques, due to variation in modeling algorithms, elevation was consistently the most important variable among models and had the greatest percent explained deviance among predictors (Table 1.3). Elevations throughout the study area ranged from 298 – 447 m above sea level. The presence of *V. pedatifida* was associated with elevations that ranged from 380 – 420 m above sea level. Average fire frequency was calculated as the number of burns occurring over a 16-year period (2001 – 2016). *V. pedatifida* presence was associated with sites that had a 2-4 year fire-return interval. Hillshade is a metric that takes on values from 0 to 255, where values of 0 correspond to dark (lots of shade) and 255 corresponds to bright (lots of sun). *V. pedatifida* presence was associated with hillshade values of 180 – 190. Land cover type was classified into five cover classes: grassland, cropland, water, developed, and forest. *V. pedatifida* presence was nearly exclusively in the grassland cover type. Slope is a variable that can take on values from zero to essentially infinity, where a flat surface is 0%, a 45-degree surface is 100%, and as the surface becomes more vertical, the percent rise becomes increasingly larger. *V. pedatifida* presence was associated with 0 – 10% slopes. TRASP is a measure of slope direction that can take on values that range from zero to one. Values of one correspond to south-southwest facing slopes while values of zero correspond to north-north east facing slopes. *V. pedatifida* presence was most associated with north-northeast facing slopes. Soil type was classified into 13 different soil classes: sand, loamy sand, sandy loam, sandy clay loam, loam, clay loam, sandy clay, clay, silty clay, silty clay loam, silt loam, silt, and complex soils. *V. pedatifida* presence was

associated with silty clay loams and two complex soils, Benefield – Florence complex and Dwight – Irwin complex. All three of these soil types are associated with well-drained uplands and gentle to moderate slopes. The two complex soils often contain top soil layers consisting of silty clay loams.

Discussion

Ecological Implications

The ability to find *S. idalia* and other cryptic Lepidoptera larvae is an issue that plagues research directed at this life history stage. *S. idalia* larvae have been particularly difficult to locate in the field and efforts to find them have resulted in very small sample sizes and even failures (Barton 1995; TNC 2000, 2001). Consequently, research and inferences regarding the larval stages of *S. idalia* and other species of Lepidoptera are often limited and lacking. The ability to focus search efforts to areas that have a high probability of containing larvae would undoubtedly facilitate their location and enhance conservation and management recommendations.

Larvae of Lepidoptera are often constrained to specific host plant species. For example, *S. idalia* consume only *Viola* species as larvae while monarchs (*Danaus plesippus*) consume *Asclepias* species during the immature stages. Without the presence of these specific host plant species, larvae of these Lepidoptera would be unable to survive. In contrast to larvae, host plants are much easier to locate. Thus, the ability to efficiently locate patches of host plants across the landscape should facilitate the location of larvae. The probabilistic maps of the occurrence of *V. pedatifida* produced in this study can be used to more efficiently locate *V. pedatifida* and subsequently *S. idalia* larvae.

While the probabilistic maps produced in this study provide a visual depiction of the occurrence distribution of *V. pedatifida* within the study area, the seven final predictor variables used to generate models provide the specific habitat features and requirements of *V. pedatifida*. The predictor variables used here suggested that *V. pedatifida* is a prairie upland species that requires moderate fire disturbances and full sun to part shade. These findings align with descriptions of *V. pedatifida* habitat requirements in the literature and supports their use and relevance in the final models. Furthermore, it indicates that they could be valuable starting points if used to model the predicted occurrence distribution of *V. pedatifida* in other areas of the species range. Although the specific variables used in this study performed well for describing the occurrence distribution of *V. pedatifida* in this region, extrapolation outside of the Flint Hills should consider the use of additional predictors that are biologically relevant to other study areas. For instance, climatic and remotely sensed variables have been shown to improve predictions and link underlying ecological relationships of species (Zimmermann et al. 2007). However, these data are typically only available at large spatial resolutions (e.g., Daymet climate data has a 1-km² native spatial resolution). Given the relatively small extent of the study area used here, I assumed that climate (i.e., precipitation, temperature, etc) would not vary greatly and elected not to use such variables. However, if the occurrence distribution of *V. pedatifida* were to be modeled across a broader extent of its range where there is likely to be a precipitation and temperature gradient then inclusion of such variables would likely prove useful.

Model Limitations: Interpretation and Extrapolation

There are a few important caveats that are worth discussing related to model interpretation. The models produced in this study were generated based on the presence-absence of *V. pedatifida* and variables suspected to be relevant to *V. pedatifida* occurrence within the

study area. For instance, elevation is a relative variable and undoubtedly differs across the range of *V. pedatifida* and other *Viola* host plant species of regal fritillary larvae. Consequently, the elevation range that is associated with the presence of *V. pedatifida* in other parts of the species range or the elevation range that is associated with the presence of other *Viola* host plant species will likely differ from the elevations relevant to the presence of *V. pedatifida* in this study. Additionally, some of the variables used in this study may serve as proxies for one another. For example, hillshade which quantifies shaded relief was correlated with variables such as aspect and slope aspect cosine which quantify slope direction. Subsequently, these variables are likely proxies for one another and could be used interchangeably depending on their performance in the model (i.e, percent deviance explained). Thus, variable interpretation should be done with respect to potential *S. idalia* larvae distribution and with careful consideration.

I am making an assumption that because *S. idalia* rely heavily on violets as larvae to survive and their relative immobility restricts them to patches of *V. pedatifida* that a model of potential distribution of *V. pedatifida* will serve as a relevant and meaningful substitute for *S. idalia* distribution. However, it is unrealistic to assume that all areas that contain *V. pedatifida* will also harbor *S. idalia* larvae or contain microhabitat conditions necessary for *S. idalia* growth and development. Yet, all areas that support *S. idalia* larvae growth to adulthood contain violet species such as *V. pedatifida*. Consequently, at some level, the requirements of both species overlap and therefore, support the use of potential distribution models of *V. pedatifida* as a suitable surrogate for *S. idalia* distribution in this region.

The primary objective of this study was to capture a regional extent of *V. pedatifida*. It was not my objective to produce models that predict the occurrence distribution of *V. pedatifida* across its entire range. However, *V. pedatifida* occurs outside my area of interest, and restricting

the models to a portion of the overall species range may bias the models (Thuiller et al. 2004). It is important to recognize that models created for various “areas of interest” may produce different results due to environmental layers used for prediction, additional occurrence points at larger extent, among other factors (Stohlgren et al. 2010). Thus, models produced in this study are likely only relevant to the distribution of *V. pedatifida* and *S. idalia* larvae maximally within the Flint Hills region, but most certainly within the bounds of the study extent. Furthermore, *V. pedatifida* was selected for this study because it is the preferred larval food plant for *S. idalia* larvae in this region (Swengel 1997, Kelly and Debinski 1998, Dole 2004). If the study extent was increased or encompassed a different part of *S. idalia*'s range, then the host plant species being modeled should be taken into consideration. For instance, *S. idalia* larvae of New England populations prefer *V. sagittata* (arrowleaf violet), *V. pedata* (birdfoot violet), and *V. lanceolata* (bog white violet) (Wagner et al. 1997). Therefore, if *Viola* species were to be used as a surrogate in these areas for the potential distribution of *S. idalia* larvae, then models should be created based on the presence-absence of the preferred host species or modelers should consider combining models of multiple host species as warranted by availability and preference.

Currently, the standard method for evaluating accuracy of species distribution models is the AUC. It is generally thought that AUC values >0.90 indicate high accuracy, values 0.70 - 0.90 indicate good accuracy, and values 0.50 – 0.70 indicate low accuracy (Swets 1988). However, Fielding and Bell (1997) have suggested that models with AUC >0.60 can be useful. While evaluation metrics such as AUC provide a quantitative measure of model accuracy and performance and should certainly be considered when assessing model performance, recent studies have questioned its reliability. For example, AUC scores can be inflated simply by increasing the geographical extent of the study beyond the area where presence locations were

obtained (Lobo et al. 2007). This led Lobo et al. (2007) to suggest reporting a suite of evaluation metrics such as sensitivity and specificity in concert with AUC values to make a robust assessment of model performance and accuracy. Although a model comparison is beyond the scope of this study it is worth noting that the BRT technique was the most accurate and best performing modeling method while random forest was the weakest technique. Nonetheless, the evaluation metrics suggested that all models performed well and better than random. The AUC for all models were >0.70 , which suggested that all models were useful. The TSS and kappa values for all models were greater than zero (random) and percent specificity and sensitivity for all models were greater than 60%.

Conclusions

The approach presented here demonstrates a unique method that facilitates the location of *S. idalia* larvae in the field by identifying the probabilistic distribution of their larval host plant. This approach constrains search efforts for host plants and ultimately larvae by concentrating searches to areas of high probability of host plant occurrence. If we can more readily locate patches of host plants, we can subsequently spend more time locating and studying the cryptic larval stages of *S. idalia*. While the maps and output presented here can guide conservation efforts, their inferences are limited to the Flint Hills. To further guide conservation efforts and management recommendations, it would be of great value to adopt this technique and expand upon the models presented here into larger extents of *S. idalia*'s range. Similarly, this approach could be applied to other species such as the monarch (*Danaus plexippus*) and facilitate conservation and management of other imperiled Lepidoptera species. Conservation and management recommendations for *S. idalia* and Lepidoptera populations alike, will benefit from having a more comprehensive understanding of all life history stages.

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Figure 1.1 Images of *Viola pedatifida* in native prairie within northeastern Kansas, USA, 2014. Image (a) displays the fan shape appearance and deeply lobed leaves of *V. pedatifida* and image (b) displays *V. pedatifida* flowers.

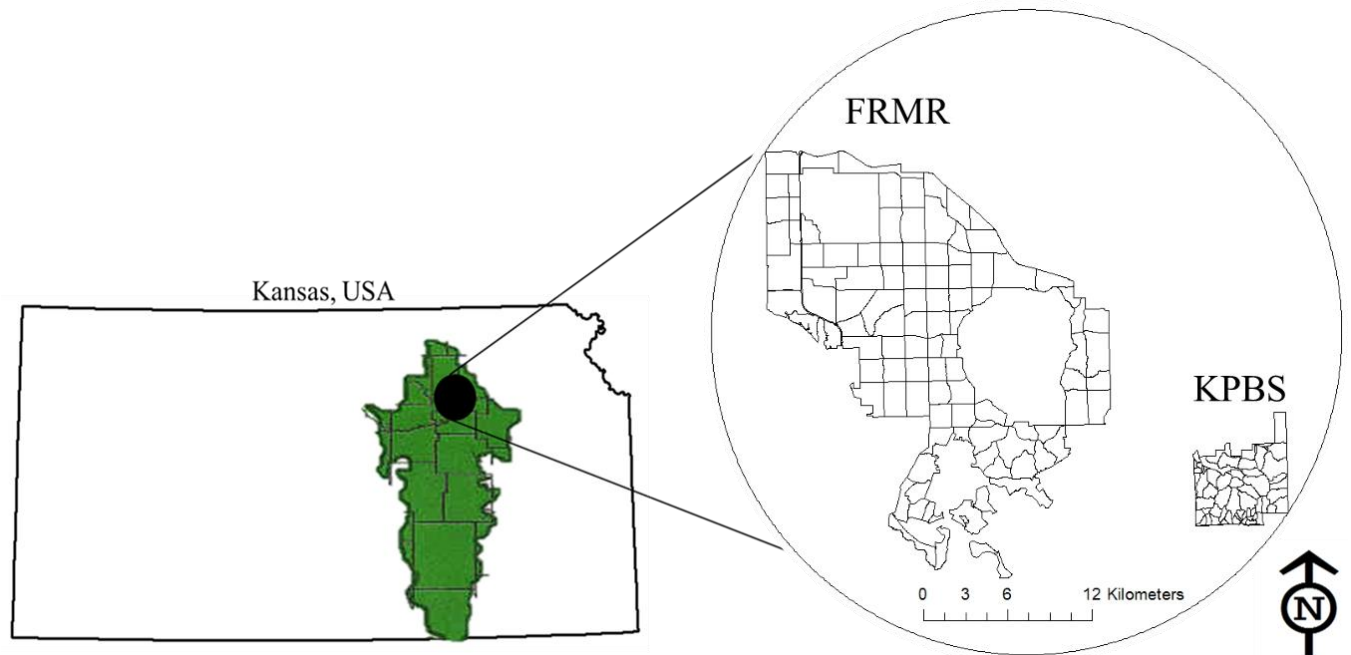


Figure 1.2 Illustration of the study area for *Viola pedatifida* surveys conducted during 2014 - 2015. The Flint Hills are marked by the green region spanning across the eastern edge of Kansas, USA, while the black dot within the Flint Hills marks the study area. The Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) are marked within the enlargement of the study area.

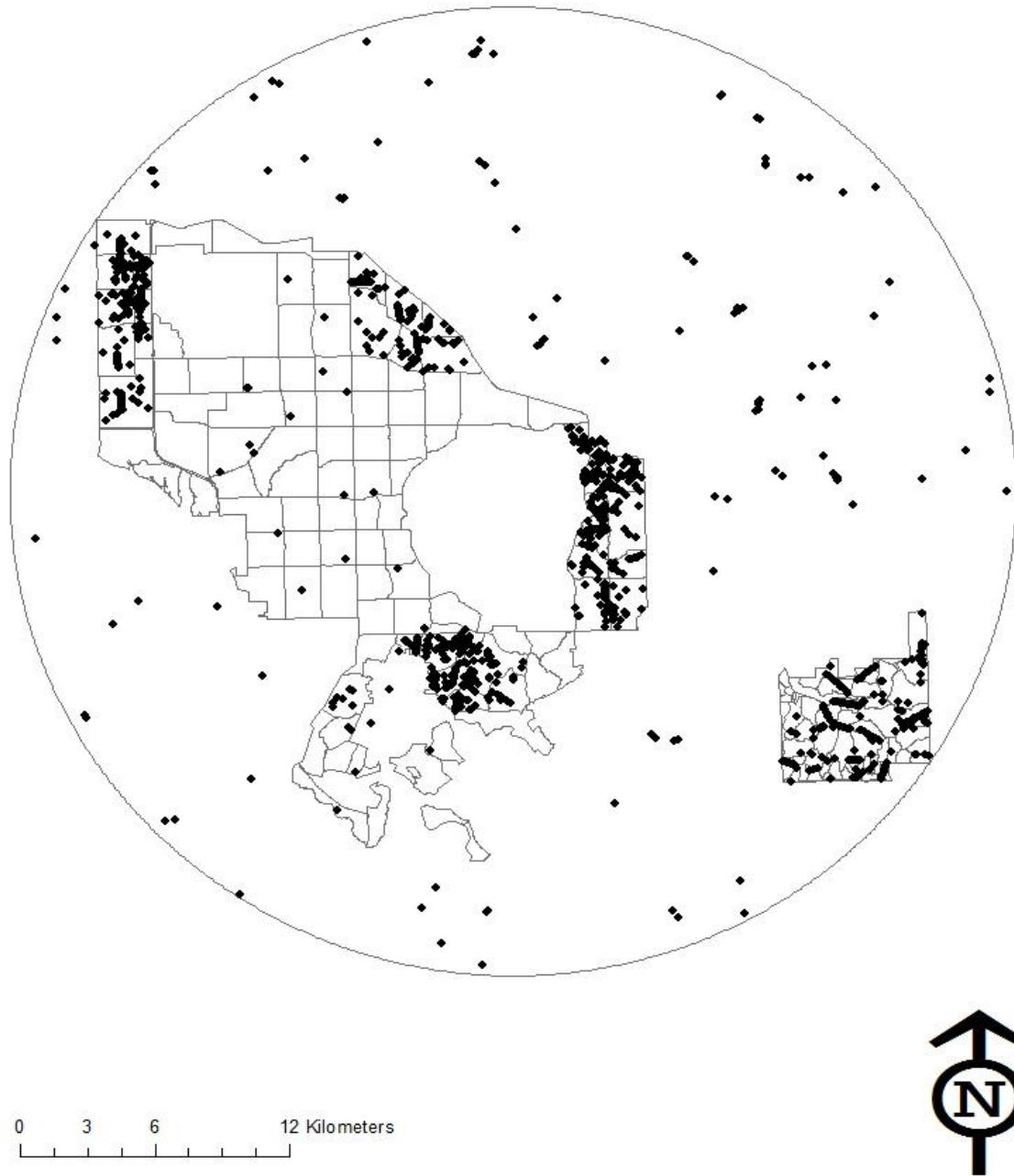


Figure 1.3 Point locations of the 1,248 locations surveyed during 2014 -2015 in northeastern Kansas, USA, for *Viola pedatifida*. The black dots indicate the 1,248 locations surveyed for the presence-absence of *Viola pedatifida*. The Fort Riley Military Reserve is marked on the western edge of the study area and Konza Prairie Biological Station is marked on the eastern edge of the study area.

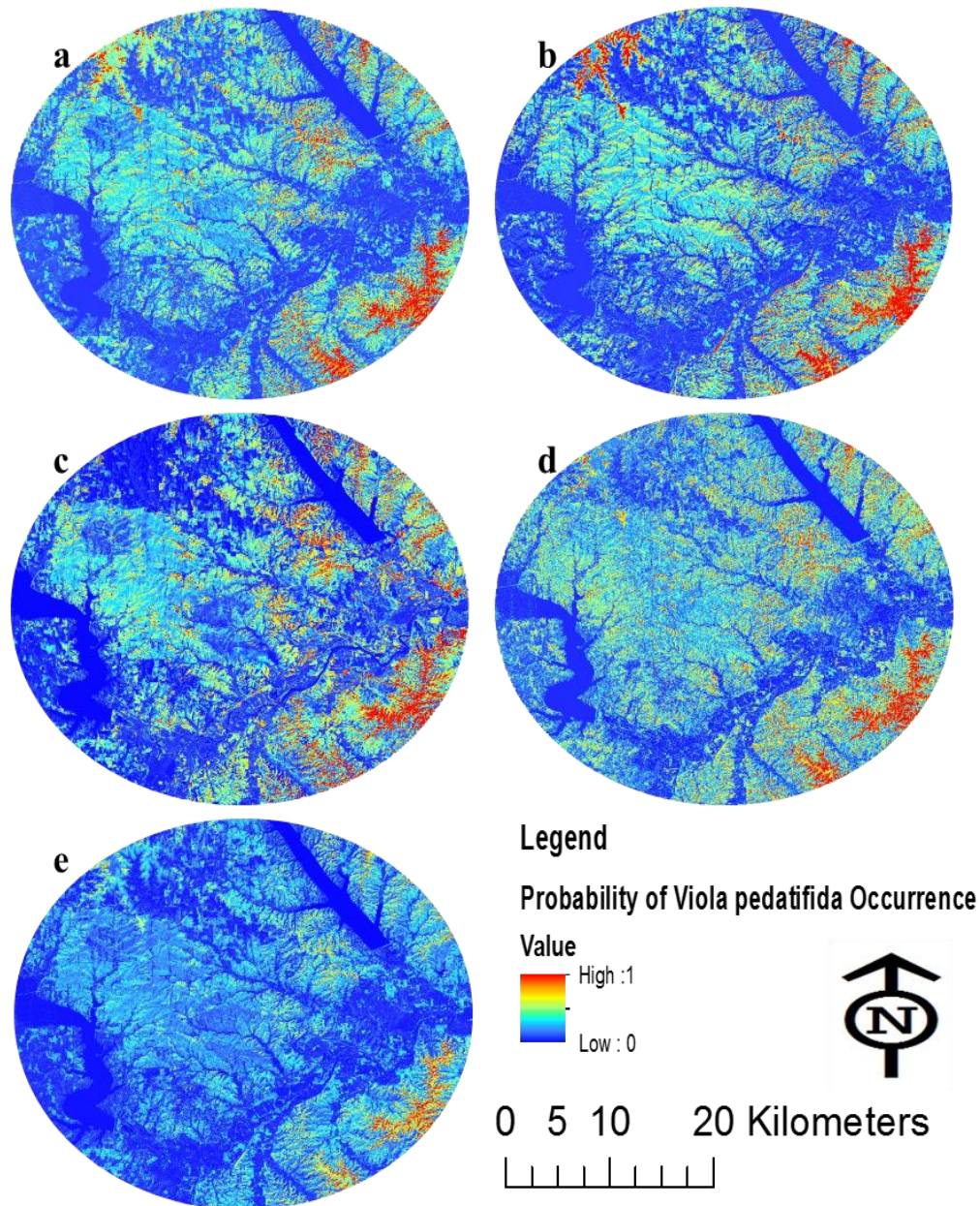


Figure 1.4 Probabilistic maps of the distribution of *Viola pedatifida* in northeastern Kansas USA, using boosted regression tree (a), multivariate adaptive regression splines (b), generalized linear model (c), random forest (d), and ensemble (e) species distribution modeling approaches. Models a –d were generated using *V. pedatifida* presence-absence data collected in northeastern Kansas in 2014 -2015 as the response variable and a suite of seven predictors as the explanatory variables in the Software for Assisted Habitat Modeling for VisTrails. The ensemble model (e) was created by taking the mean probabilistic values from each of the four individual techniques (a –d). On maps, red correlates with values of one or high probability of *V. pedatifida* occurrence while blue correlates with values of zero or low probability of *V. pedatifida* occurrence.

Table 1.1. Description of predictor variables considered for use in predictive distribution models of *Viola pedatifida* occurrence in northeastern Kansas, USA, 2014 – 2015 including native spatial resolution.

Predictor Variable	Description	Native Resolution
Elevation	Height above sea level in meters	3m
Soil Type	A quantification of the thirteen soil types present within the study area	10m
Land Cover Type	A quantification of five land cover types present within the study area	1m
Aspect	Aspect identifies the downslope direction of the maximum rate of change in value from each cell to its neighbors. Aspect can also be thought of as slope direction	3m
Average Fire Frequency	A measure of the average fire frequency (# of burns/16yrs) for sites within the study area	250m
Compound Topographic Index	A steady state wetness index that is strongly correlated with soil moisture	3m
Curvature	Surface curvature (concavity/convexity) is the second derivative of the surface, or the slope-of-the-slope	3m
Hillshade	A measure of shaded relief	3m
Heat Load Index	Represents a slope/aspect interaction that is scaled to represent solar isolation	3m
Roughness	Surface roughness is a component of surface texture that is quantified by deviations. Essentially this is unscaled variance	3m
Slope Area Ratio	Calculates the ratio of the slope to the specific contributing area	3m
Slope	Identifies the slope (gradient), also referred to as the percent slope	3m
Slope Aspect Cosine	A transformation of percent slopes that takes into account the effects of aspect	3m
Mean Slope	Takes the mean of the slope within a specified window	3m
Slope Position	A continuous variable that represents slope position of a given cell and its relative position between valley floor and ridgetop	3m
Topographic Radiation Aspect Index (TRASP)	A linear transformation of the circular aspect variable that quantifies north-south facing slopes	3m

Table 1.2 Evaluation statistics for the four individual modeling techniques used to predict *Viola pedatifida* occurrence in northeastern Kansas, USA, 2014–2015. Evaluation statistics include results from both the 70/30 training split and the 10-fold cross-validation. The area under the curve (AUC) values from the cross-validation are the mean AUC values with the standard deviations in parenthesis.

Method	Evaluation Statistics Applied to Training Split						Evaluation Statistics Applied to Cross-Validation					
	AUC	% CC	Sensitivity	Specificity	Kappa	TSS	AUC	% CC	Sensitivity	Specificity	Kappa	TSS
BRT	0.88	80.1	0.77	0.81	0.55	0.58	0.73 (0.06)	66.7 (5.95)	0.60 (0.10)	0.69 (0.08)	0.27 (0.10)	0.29 (0.11)
GLM	0.77	67.9	0.67	0.68	0.32	0.35	0.71 (0.07)	63.7 (7.99)	0.62 (0.13)	0.63 (0.10)	0.23 (0.14)	0.26 (0.15)
MARS	0.75	66.3	0.67	0.65	0.29	0.33	0.71 (0.07)	64.6 (6.46)	0.66 (0.11)	0.63 (0.07)	0.26 (0.12)	0.30 (0.14)
Random Forest	0.71	63.3	0.64	0.62	0.23	0.27	0.69 (0.07)	73.3 (6.51)	0.47 (0.09)	0.84 (0.09)	0.34 (0.12)	0.32 (0.11)

*Percent correctly classified (% CC), True Skill Statistic (TSS), Area Under the Curve (AUC), Boosted Regression Tree (BRT), Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS)

Table 1.3 Final predictor variables used to predict the probabilistic distribution of *Viola pedatifida* occurrence within northeastern Kansas, USA, 2014 – 2015, and deviance explained by each predictor.

Variable	Deviance Explained (%)
Elevation	7.7%
Hillshade	6%
Land Cover Type	4.6%
Soil Type	2.8%
Slope	2.7%
Topographic Radiation Aspect Index (TRASP)	2%
Average Fire Frequency	1.4%

Chapter 2 - Scale and the Impact of Disturbance on Regal Fritillary (*Speyeria idalia*) Larvae: Re-Thinking Regal Fritillary Conservation and Management.

Introduction

Native prairie communities have become uncommon and fragmented in the Central Great Plains succumbing to development, plant succession, and invasion of exotic species among other factors (Samson and Knopf 1996). For example, tall-grass prairie historically covered > 68,796,559 hectares of the Great Plains, but only 3-5% remains (Samson and Knopf 1996). Factors associated with the loss of native prairie in the Central Great Plains are the leading cause of the decline and extirpation of several formally abundant and iconic butterfly species (Oates 1995, Schlicht and Orwig 1998). In particular, regal fritillary (*Speyeria idalia*) populations have declined by approximately 99% during the last few decades (NatureServe 2005) prompting the U.S. Fish and Wildlife Service to initiate a status review of *S. idalia* under the Endangered Species Act (ESA) in September 2015.

Wide-spread pyric-herbivory was and still remains a key process to the development and the maintenance of the ecological structure and function of many of the world's largest grassland ecosystems including the Great Plains of North America (Fuhlendorf and Engle 2001). The largest remaining contiguous expanse of North American tall-grass prairie is found within the Flint Hills region stretching from Kansas to Oklahoma, USA (Reichman 1987). This region is dominated by rocky soils and rolling hills with unrestricted fire and grazing by large mammalian herbivores being key drivers of vegetation patterns for millennium (Milchunas et al. 1988). While other regions of the Great Plains were converted to croplands or developed, much of the Flint Hills region remains sparsely settled, unplowed, and predominately used for domesticate

cattle grazing. The flint and limestone deposits underlying the Flint Hills coupled with its topography made this region largely undesirable for crop cultivation. This helped preserve the region's prairie ecosystem and facilitated continuous wide-spread occurrence of large herbivores coupled with fire as a grassland management tool. Effects of current fire and grazing practices on this landscape undoubtedly differs from the historic disturbance regime in many important ways (Fuhlendorf and Engle 2001). However, the ecological legacy of the processes of wide-spread fires coupled with grazing by large, native herbivores is continued through grassland fire applied by land managers and cattle producers (Fuhlendorf and Engle 2001). This has maintained landscape-scale, ecosystem structure and functions that were important in the evolution and thus, to the continued persistence of native flora and fauna populations that have been lost in other regions of the Great Plains (Fuhlendorf and Engle 2001). For example, *S. idalia* have become uncommon throughout much of the Central Great Plains but relatively large, stable populations persist in the Flint Hills region (Selby 2007).

Insects are an extremely diverse animal phylum dominating terrestrial systems around the world in biomass and abundance (May 1988, Gaston 1991, Groombridge 1992). The importance of insects makes them a necessary but often overlooked measure of ecosystem health because immense diversity and minute characteristics make efficient species-level identification difficult. Although a complete understanding of the ecological factors important to the successful conservation management of all of the life history stages of endangered vertebrate species is widely accepted, much basic life history and ecological information is often lacking during insect conservation efforts.

Butterflies are readily identifiable to species in contrast to other insect groups making research on the status, population trends, and habitat requirements of butterflies a plausible

measure of ecosystem condition and sustainability for insects (New 1997, Oostermeijer and van Swaay 1998, Blair 1999, van Swaay et al. 2006). The quality of a habitat to support butterfly populations is often characterized in terms of the presence and abundance of adults and resources adults use for foraging and reproduction (Britten and Riley 1994, Smallidge et al. 1996, Grundel et al. 2000, Collinge et al. 2003). However, habitats and resources used by adults may not adequately reflect the requirements of the often longer but less mobile larval stages of these insects (Bergman 1999, Lane and Andow 2003, Albanese et al. 2007). Consequently, conservation research studies directed at identifying ecological factors necessary to support persistent, wild butterfly populations should include those factors potentially important to the survivorship of larvae to adults. Organisms function within a range of scales, especially within and among different life history stages (Addicott et al. 1987, Wiens 1989, Lindenmayer 2000, Moore 2000). To understand species-habitat relationships, researchers must consider how species are affected by environmental patterns at different scales (Wiens 1989, Levin 1992, Turner 2005). While the importance of understanding these factors is necessary to effectively guide conservation and management efforts, few field research studies collect data on the larval life history stage of *S. idalia* because unlike adults, larvae are cryptic and difficult to locate in the field (Scudder 1889, TNC 2001, Kopper et al. 2001; D. Debinski, Iowa State University, pers. com.). Identifying resource patterns and scales at which larvae respond to these patterns will better facilitate butterfly conservation efforts. In particular, knowledge of the spatial scale at which developing larvae utilize host plant resources will lead to more accurate and efficient census and research techniques and improved refuge design and management practices.

Butterflies can be large, brightly colored, and vagile with several species even capable of intercontinental migration. In contrast, larvae are immobile with a utilization distribution

typically restricted by a limited dispersal capacity to the location of egg deposition and surrounding host plants on which it must feed to survive (Bergman 1999, Lane and Andow 2003, Albanese et al. 2008). Lepidoptera larvae are also relatively small and cryptic, making even larger larvae difficult to locate on known host plants. Field mark/recapture studies on butterflies are labor intensive, time consuming, and difficult especially for larvae because direct observations and effective, development-wide, field marking techniques are limited (Singer and Wedlake 1981, Gall 1984, Murphy 1987, Mattoni et al. 2001, Haddad et al. 2005). However, conceptual and technical advances in geographic information systems (GIS) and spatially explicit species distribution and gradient modeling offer new opportunities to more efficiently and effectively study this important life history stage in the field across broad-scale areas. For example, the occurrence and survival of butterfly larvae depends on the presence of a host and the abundance of many species increases with host plant availability (Bourn and Thomas 1993, Bergman 1999, Lane and Andow 2003). Species distribution models (SDMs) are particularly useful for mapping the probabilistic occurrence distribution of plant species even when referenced with sparse but appropriate data (Elith and Leathwick 2009, Chapter I). Maps of the distribution of host plant species can be used to efficiently locate stands of host plants and thus larvae within broad-scale regions of a butterfly species range (Chapter I). Additionally, the majority of Lepidoptera larvae activity is spent grazing or moving among food resources within their dispersal capacity and consumption and mobility increase with maturity. If distinct evidence of the spatial distribution of feeding larvae can be identified, this may potentially serve as a surrogate of direct observations of larvae and their movement patterns (Albanese et al. 2007, Appendix A). Maps of the occurrence distribution of late-instar larvae (i.e., butterfly larvae that have survived to the final stages of development before pupation) and their foraging locations

combined with further refined maps of the abundance distribution of potential host plants could be used to identify scale-dependent relationships between late-instar larvae and host plant availability without direct, repeated field observations.

S. idalia butterflies are univoltine, non-migratory, and considered a North American prairie specialist (Kelly and Debinski 1998). The species was once abundant across the prairie biome with a range that extended from the border of Canada to Oklahoma and east to the Atlantic coast (NatureServe 2005). Populations declined rapidly with the widespread and dramatic loss of native prairie and are now restricted to remnant prairie tracts (Selby 2007, NatureServe 2005). *S. idalia* butterflies begin to emerge each year in late spring (Klots 1951, Tilden and Smith 1986, Wagner et al. 1997). This butterfly is a flower generalist and in early summer, adults forage among nectar rich flowers and mate (Klots 1951, Tilden and Smith 1986, Wagner et al. 1997, Selby 2007). Adult females outlive males and begin to lay single eggs in proximity to host plants in late summer with some persisting until early fall (Scott 1986, Swengel and Swengel 2001). Larvae hatch during fall but enter a winter diapause, with development resuming early the following spring when they begin feeding on freshly emerged host plants (Hammond 1974, Wagner et al. 1997). Larvae then develop through six instars before pupating by late spring (Edwards 1879, Hammond 1974, Wagner et al. 1997). Late-instar larvae voraciously consume and denude leaflets and leaves of their relatively small host plants, leaving only stems before moving on to locate and graze on a neighboring host plant cluster (Appendix A). Larvae rest on the stems of host plants, nearby vegetation, and underneath litter and rocks when not foraging (Appendix A). Larvae feed on different violet species (*Viola* spp.) throughout their range, but the violet species fed on by local populations tend to have distributions that are primarily restricted to remnant tracts of native grassland (Hammond and McCorkle 1983). For

example, birdfoot (*V. pedata*) and prairie violet (*V. pedatifida*) are small perennial plants characteristic of native prairie and reported to be the preferred larval host plants of *S. idalia* populations in the Central Great Plains (Swengel 1997, Kelly and Debinski 1998, Dole 2004).

Prairie fires can facilitate many important ecosystem functions and services that include among others increasing structural heterogeneity, forage production for large herbivores, and diversity among native small mammals, birds, and plants (Fuhlendorf and Engle 2001). Managed fire and grazing can, however, have negligible to negative effects on some native grassland species of flora and fauna (Fuhlendorf and Engle 2001). It has been proposed that *S. idalia* populations are negatively affected by fire management practices that may reduce adult nectar sources, host plant abundance, or cause direct egg and larvae mortality (Hammond and McCorkle 1983, Royer and Marrone 1992, Dana 1997, Fritz 1997, Selby 2007). Current habitat management recommendations have therefore favored low intensity grazing (NatureServe 2005) and mechanical cutting to maintain *S. idalia* habitat given limited information on the influence of fire and grazing relative to current *S. idalia* population trends (Swengel 1996). The role of fire in ecology of *S. idalia* is contentious especially considering its close association with native tall-grass prairie in which fire is a vital process (Dana 1991; Swengel 1996, 1998; Panzer 1998, 2002; Schwartz 1998; Swengel and Swengel 1999, 2001). This uncertainty is understandable especially considering that knowledge of the effects of land management regimes on insect population persistence and appropriate land management practices for restoring and maintaining habitat for insects are often lacking (Swengel and Swengel 2006). This information may be especially important for native prairie and grassland butterfly conservation management efforts because relatively frequent disturbance is often necessary to suppress the growth and establishment of woody plants (Vogl 1974, Shuey 1997).

I used a combination of Environmental Systems Research Institute's (ESRI) ArcMap 10.3.1 Geographic Information System (GIS) software technologies, spatial modeling techniques and field surveys to assess effects of land management practices and prairie host plant density on late-instar *S. idalia* larvae. Specifically, I used an ensemble of SDMs to map the spatial distribution of the *S. idalia*'s larval host plants across a large tract of native tall-grass prairie in northeastern Kansas, USA (Chapter I). I used these maps to efficiently locate distinct larvae survey areas managed using different burn frequencies with cattle grazing or haying. I then used field data collected during rapid host plant counts with spatial kriging models to further map the fine-scale density distribution of host plants within survey areas. I surveyed each area for late-instar *S. idalia* larvae and then compared models of the spatially explicit occurrence distribution of larvae across multiple scales of host plant density and between management treatments.

Methods

Study Area

This study was conducted in northeastern Kansas, USA, at the Fort Riley Military Reserve (FRMR) (Geary and Riley counties) and Konza Prairie Biological Station (KPBS) (Geary County) (Figure 2.1). Both areas were located in the northern portion of the Flint Hills region and less than 11 km separated the boundaries of the FRMR and KPBS, but the intervening land tract contained the Kansas River and a mosaic of developments and agricultural fields. The climate in this region is dry (average total annual precipitation = 83.82 cm) and windy, but temperate (Abrams and Hulbert 1987). Most precipitation occurs in spring and temperatures can range from -40 °C to 49.44 °C (Abrams and Hulbert 1987). The landscape of the Flint Hills is characterized by large, remnant tracts of native tall-grass prairie with intensively-managed agricultural areas, grassland, small stands of shrub and forest, several large rivers and reservoirs,

and broadly distributed suburban and rural developments. The vegetative community was commonly associated with dominant grasses such as big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*); however, other perennial grasses, woody species, and a wide variety of native herbaceous forbs comprise significant proportions of the plant community (Anderson and Fly 1955, Owensby and Smith 1979).

The FRMR included ~41,000 contiguous ha, making it the largest military reservation in the USA. Approximately 29,000 ha were used for military training, wildlife management, hunting, conservation, and other outdoor recreational activities. Land management was planned, prescribed to primarily control the establishment and spread of woody vegetation and included broad-scale regimes of applied fire and hay removal. Fires were applied to large land units annually starting in late-winter and continuing through fall with the majority occurring in early spring. Managed fire frequency within land units ranged from <1 to >20 years and the FRMR also experienced occasional wildfires throughout the year from lightning strikes and more frequent fires from the detonation of munitions during military training exercises. Prairie hay was cut and removed mechanically from 15 July – 15 August.

The KPBS is a 3,487 ha contiguous tract of tall-grass prairie co-owned and operated by the Division of Biology, Kansas State University, and The Nature Conservancy and part of the National Science Foundation's Long-Term Ecological Research Program (LTER). The KPBS has been experimentally managed with a mixture of fire and large herbivore grazing regimes since 1981 with a mixture of prescribed burns and native bison (*Bison bison*) or cattle grazing (*Bos taurus*) applied annually to different land units within the KPBS (Knapp et al. 1998). Land

units were either grazed or not and fire is typically ignited in the spring and applied on a one to twenty year return interval within land units.

Host Plant Distribution Maps

I generated an ensemble SDM to predict the probabilistic occurrence distribution of *S. idalia*'s preferred larval food plant for this region, *V. pedatifida* (Chapter I; Figure 2.2). I used the generated SDM as a tool to (1) effectively and efficiently locate patches of host plants within the FRMR and KPBS study sites and (2) facilitate the location of larvae survey areas within different treatments (grazing and haying) and fire-return intervals (low ≥ 10 years, moderate 3-5 years, and high 1-2 years) within these sites. I generated the SDM of *V. pedatifida* occurrence using four of the current leading individual modeling techniques: boosted regression tree, generalized linear model, multivariate adaptive regression splines, and random forest. I created an ensemble model from these four individual techniques by taking the mean value of the probability of potential *V. pedatifida* across all four individual models.

I obtained the *V. pedatifida* presence-absence data used to create the SDM through field surveys. Over the course of my study, I surveyed 1,248 spatially balanced, random locations from March – May for the occurrence of *V. pedatifida*. These randomly distributed locations were located in the field using a Garmin 64s global positioning system (GPS) receiver. Once a survey point was located, I systematically surveyed for the presence or absence of *V. pedatifida* within a 10 m X 10 m plot. In addition to these initial surveys, I selected a random subset of 20 plots each year to re-survey to account for detection error, I accurately detected *V. pedatifida* 82.5% of the time.

Finally, I used GIS to process, calculate, and derive predictor variables hypothesized to be biologically relevant to the occurrence of *V. pedatifida* within the study area (Chapter II). The

seven final predictor variables used to model the predicted probabilistic occurrence of *V. pedatifida* in the SDM model were average fire frequency, elevation, hillshade, land cover type, slope, topographic radiation aspect index and soil type.

Late-Instar *S. idalia* Surveys

I used the ensemble SDM output of the predicted probabilistic occurrence of *V. pedatifida* to locate potential larval survey areas across the study area within different treatments and fire-return intervals. Surveys for late-instar *S. idalia* larvae were conducted in April and May during 2014 and 2015. Larval survey plots contained a gradient of violet density (Figure 2.3) and stratified by management regime (grazing and haying), and fire-return interval (low ≥ 10 years, moderate 3-5 years, and high 1-2 years; Table 2.1). Each larval survey plot was 2500 m² and partitioned into grids of 100-m² sub-plots. After establishing the larval search plots and setting up the search grids, I randomly selected 15, 100-m² sub-plots within the larger 2500-m² grids to count all of the *Viola* host plant species contained within the randomly selected sub-plots. I then used kriging models in GIS to estimate host plant density in the remaining 100-m² sub-plots not surveyed. After obtaining estimates of host plant density within each larval survey site, I randomly selected a spatially balanced sample of 15, 100-m² sub-plots from each of the 8. 2500-m² larval survey plots to survey for late-instar *S. idalia* larvae. I searched for late-instar larvae by systematically examining each host plant located within the plot. I also examined the surrounding vegetation and litter in search of late-instar *S. idalia* larvae. In addition to searching for late-instar *S. idalia* larvae, I also surveyed host plants within each sub-plot for late-instar *S. idalia* larvae distinct feeding sign. I used this distinct feeding sign as a surrogate in the analysis for the presence of late-instar *S. idalia* larvae even when one could not be detected within a sub-plot (see Appendix A). Lastly, I characterized habitat features within each randomly selected

sub-plot. I used a module-nested plot method to estimate six cover variables within sub-plots selected to survey for late-instar *S. idalia* larvae (Table 2.2). Cover was estimated using nine cover classes that were converted to mid-points in the analysis (cover classes: 0 – 1%, 1 – 2%, 2 – 5%, 5 – 10%, 10 – 25%, 25 – 50%, 50 – 75%, 75 – 95%, >95%). Cover classes and module-nested plot methods were adopted from the North Carolina Vegetation survey (Peet et al. 1997), which is a variation of the more traditional, cover class scheme (e.g., Domin 1928, Braun-Blanquet 1964, Daubenmire 1968).

Spatial Scaling

To determine the scale that best described the occurrence distribution of late-instar *S. idalia* larvae or their feeding sign, I created a 70 m X 70 m grid of 100-m² cells in GIS for each of the eight larval search areas delineated in my study. Although I only searched for larvae within a subset of 100-m² plots in the “core” 50 m X 50 m or 2500-m² grid a “boundary” on all sides of the larval search areas was required for the moving window analysis, spatial scaling technique to work properly, thus I made a 70 m X 70 m grid in GIS. Additionally, during my counts of host plants within the 2500-m² larval search areas, I also extended these counts outside of the “core” 2500-m² areas into the 70 m X 70 m “boundary” area. I then took the host plant count data and applied the number of violets counted within each 100-m² sub-plot to GIS, this yielded the density (number of host plants/100-m²) of host plants within larval search areas. However, host plants were not counted in every 100-m² sub-plot within the eight larval search areas (See Late-Instar *S. idalia* Surveys). Therefore, to generate estimates of host plant density for the unsurveyed plots both within the “core” larval search area and within the “boundary”, I used kriging models in GIS to estimate host plant density for sub-plots with no host plant data collected. The kriging models generated in GIS provided estimates of violet density for each

100-m² sub-plot within each of the 8, 2500-m² larval search areas. These estimates of host plant density were then applied to the larvae search results for each 100-m² sub-plot surveyed for late-instar *S. idalia* larvae or their feeding sign. I then used four different moving window sizes in GIS to calculate the density of host plants within larval search areas at different scales. The four scales were (1) a larvae survey sub-plot or 100-m² (2) a Von Nuemann 4-neighbor moving window or 500-m² (3) a Moore 3 X 3 moving window or 900-m² and (4) a larval search area or 2500-m².

Statistical Analysis

All data were analyzed using R (version 3.3.1; R Development Core Team 2016). To identify which models best explained observed patterns in the occurrence distribution of late-instar *S. idalia* larvae or their feeding sign, I used an information-theoretic framework to compare and select the best fitting models (Burnham and Anderson 2002). I used the second-order variant of Akaike's information criterion adjusted for small sample sizes (AIC_c) to compare the relative ability of alternative models to fit observed data. I calculated Delta AIC_c (ΔAIC_c) and Akaike weights (w_i), to evaluate the support for each model given the data (Burnham and Anderson 2002). I used AIC_c to rank models and selected the best fitting models as those with the lowest AIC_c scores (Buckland et al. 2001). I considered all models with a $\Delta AIC_c < 2$ to have support, but selected only models for which the AIC_c values was less than the AIC_c values of all the simpler models within which they were nested (Richards 2008).

I first conducted an analysis using a generalized linear model (GLM) and classification tree model of the occurrence of late-instar *S. idalia* larvae or their feeding sign and host plant density at each of the four spatial scales (100-m², 500-m², 900-m², and 2500-m²) to determine which scale best described the occurrence distribution of late-instar *S. idalia* larvae. For each

model, I quantified and compared model relative fit statistics using different approaches to empirically estimate which scale best described the occurrence distribution of late-instar *S. idalia* larvae or their feeding sign. The fit statistics used to compare models were Kappa, Δ AIC, percent deviance, and McFadden's R^2 .

After the analyses to determine the scale at which the relationship between host plant density and the occurrence of late-instar larvae or their feeding sign was greatest using the moving window, scaling technique, I then ran an analysis on late-instar *S. idalia* larvae occurrence or their feeding sign and the full set of predictor variables using a GLM with logit link function. Late-instar *S. idalia* larvae occurrence was considered the occurrence of late-instar *S. idalia* larvae in combination with their feeding sign in a sub-plot or just the occurrence of feeding sign but no actual detection of a late-instar *S. idalia* larvae within a sub-plot. Predictor variables used to explain the response or occurrence of late-instar *S. idalia* larvae or their feeding sign were host plant density at the key scale identified by the moving window analysis, months since burn, management regime (grazed or hayed), and interaction between management regime and months since burn. I first ran this analysis using a Quasi binomial distribution to account for zero inflation (Welsh et al. 1996, Ridout et al. 1998, Cunningham and Lindenmayer 2005, Martin et al. 2005); however, I also analyzed these data using the same methods but with a simpler binomial distribution as this technique is robust to the violation of the unequal sample size assumption and the AIC results are reliable. The simpler binomial distribution results were the same as the Quasi binomial distribution, validating the use of the simpler binomial modeling technique.

Estimating the abundance, occurrence, and distribution of organisms is of great interest to ecologists and a central goal in ecology, conservation, and management (Royle and Dorazio

2008). Unfortunately, logistical constraints and the cryptic nature of many species make complete censuses or counts virtually impossible (MacKenzie et al. 2005). However, imperfect detection of organisms can confuse measures of abundance, occupancy, and distribution (Bayley and Peterson 2001, Mackenzie et al. 2002, Gu and Swihart 2004), and failure to account for organisms present but not detected can result in biased estimation and erroneous conclusions (Kellner and Swihart 2014). Moreover, detection is seldom perfect or constant due to a number of reasons that include observer error (Nichols et al. 2000), species rarity (Dettmers et al. 1999), or because detection varies with confounding variables such as environmental conditions (Gu and Swihart 2004). Subsequently, numerous methods exist to account for counts of organisms when detection is imperfect, including distance sampling (Buckland et al. 2001, Johnson et al. 2001), time removal (Farnsworth et al. 2002, Etterson et al. 2009), repeated counts (Royle and Nichols 2003, Royle 2004), double observer (Cook and Jacobson 1979, Nichols et al. 2000), mark-recapture (Laake et al. 2011), double sampling (Bart and Earnst 2002), among others.

While these more traditional methods of accounting for differing detection probability have worked well for addressing the detection dilemma, these techniques were either impossible or unrealistic to execute in this study. For instance, mark-recapture techniques were not well suited in this case because every few days *S. idalia* larvae molt and shed their exoskeleton where a tag would be attached. Furthermore, the short time period I had to detect late-instar *S. idalia* larvae within selected sub-plots and the amount of time it took to thoroughly search sub-plots made repeated surveys of sub-plots in a season unrealistic to accomplish. Despite the inability to employ some of the more traditional techniques that have been developed to deal with imperfect detection probability, I was able to overcome this limitation by determining a distinct and reliable feeding sign exhibited by late-instar *S. idalia* larvae that queued me to their presence

within sub-plots even when a larva could not actually be detected (see Appendix A). Other studies have demonstrated that a distinctive and consistent feeding sign can be beneficial in detecting the presence of a larva on a host plant and used as a surrogate for direct observations of larvae during research on rare and cryptic Lepidoptera (Swengel 1995, Smith et al. 2002, Albanese et al. 2008). Using this approach, I was able to calculate detection probability as the difference between sub-plots with larvae and feeding sign and sub-plots where only feeding sign was detected but not larvae.

The detection probability of occupancy or occurrence can be influenced by features of the local habitat or surrounding landscape (Nupp and Swihart 1996, Mancke and Gavin 2000, Odell and Knight 2001). Subsequently, non-detection is more likely to happen when population sizes are small and habitat features interfere with the detection of species (Gu and Swihart 2004). For example, variation in vegetation structure among patches, even when patches contain similar densities can cause variability in detection probability (Gu and Swihart 2004). Therefore, I determined if detection probability varied among the larvae survey areas, observers, years and between 100-m² sub-plots with differing percent cover of the habitat variables measured. Preliminary analyses revealed detection probability remained relatively constant and did not differ significantly between these comparisons. The greatest difference among all detection probabilities compared was <0.09. Thus, I elected not to conduct more logistically challenging repeated larvae surveys and more data hungry modeling techniques to account for detection probability in my analysis. Additionally, my examination indicates that if there were detection bias in my sample, it was consistent across time and space and therefore, should not be problematic (Buckland et al. 2001). I also integrated these detection probability estimates as prior probabilities into random forest and classification tree models. These techniques again

yielded the same results as the much simpler binomial GLM, further validating the use of the simpler technique.

Results

Over the course of this study, I surveyed 208, 100-m² sub-plots for late-instar *S. idalia* larvae or their feeding sign. Of these surveyed plots, 47 (22%) contained late-instar larvae with feeding sign or just their feeding sign, while 161 (77%) had no feeding sign or larvae. All plots that contained late-instar *S. idalia* larvae had their accompanying feeding sign. The difference between sub-plots with late-instar *S. idalia* larvae and their feeding sign and sub-plots with just feeding sign or detection probability was 0.42.

Host plant density at the 500-m² scale best described the occurrence distribution of late-instar *S. idalia* larvae (Figure 2.4). Subsequently, models including host plant density as a predictor variable was host plant density at this key 500-m² scale. The global model included the occurrence of late-instar *S. idalia* larvae or their feeding sign as the response variable and host plant density at the 500-m² scale, months since last burn, management regime (grazed and hayed), and the interaction between management regime and months since burn. I ran all combinations of the global model, which resulted in 25 total alternate models including a null model. The top model included the predictor variables months since last burn and host plant density at the 500-m² scale (Table 2.3).

The top model coefficients revealed that there was a positive relationship between the occurrence of late-instar *S. idalia* larvae or their feeding sign and host plant density at the 500-m² scale ($\beta = 0.11$, SE 0.02; Figure 2.5). There was a negative relationship between months since last burn and the occurrence of late-instar *S. idalia* larvae or their feeding sign ($\beta = -0.04$, SE 0.01; Figure 2.6). The coefficient 95% confidence intervals (95% CI) were (0.08 – 0.16) for host

plant density at the 500-m² scale and (-0.07 – - 0.02) for months since last burn. Although the 95% CI's did not include zero for these variables, the 95% CI's for management regime (-3.6 – 0.17) and interaction term months since last burn x management regime (-0.01 – 0.17) both included zero. Additionally, I converted these beta coefficients to odds. The host plant density odds at the 500-m² scale were 1.12 and the months since last burn were 0.95. These results reveal that for a unit increase in host plant density at the 500-m² scale the odds of the occurrence of late-instar *S. idalia* larvae or their feeding sign increased by 0.12 or 12% and for a unit increase in months since last burn the odds of the occurrence of late-instar *S. idalia* larvae or their feeding sign decreased by 0.05 or 5%. Finally, the percent deviance for the top models was 0.39 and the r² for logistic regression (adjusted McFadden or pseudo r²) was 0.64.

Discussion

Scudder (1889) first noted our lack of knowledge regarding the larval stages of *S. idalia*. Yet, over a century later, very few studies conducted on *S. idalia* have focused on this life history stage. One of the likely reasons is that *S. idalia* larvae are extremely cryptic hindering field identification and location (Scudder 1889, TNC 2001, Kopper et al. 2001; Chapter I, Appendix A). This study is one of very few focused on the larval stages of *S. idalia* and the first to examine the spatially explicit occurrence distribution of larvae across multiple scales of host plant density and between common grassland management treatments.

***S. idalia* Larvae and Management**

Numerous studies suggest that one of the reasons *S. idalia* are absent from recently burned sites is that the larvae are killed in the fire (Kelly and Debinski 1998, Swengel 1998, Huebschman and Bragg 2000, Swengel and Swengel 2001, Powell et al. 2007, Moranz et al. 2014, among others). In contrast, my results directly contradict these assumptions and indicate

that *S. idalia* larvae can in fact survive fire and demonstrate that the probability of late-instar *S. idalia* larvae occurrence actually decreases as months since burn increases (Figure 2.6). One of the potential reasons it is presumed that fire kills *S. idalia* larvae is that studies have shown that *S. idalia* and other grassland-obligate insects are greatly reduced or even eliminated from sites immediately following a burn (Swengel 1996, 2001, 2004; Swengel and Swengel 2001; Powell et al. 2007; Moranz et al. 2014). However, these studies focused on adult *S. idalia* not larvae, with the absence of adults in recently burned sites leading to the assumption or hypothesis that the burn eradicated the larvae from the sites as well as adults.

Previous studies have shown that high-intensity grazing may be a threat to populations of *S. idalia* (Hammond and McCorkle 1983; Royer and Marrone 1992; Dana 1997; Selby 2003, 2004, 2006) by removing essential nectar sources for adults (Moranz et al. 2014), with potential trampling of eggs and larvae as additional factors (Dana 1997, Fritz 1997). However, less intensive grazing may be “highly favorable” to *S. idalia* and their larval host plants (NatureServe 2005), which have been demonstrated to be more abundant in grazed areas (Mello 1989). It is speculated that the eradication of grazing throughout the New England states may have played a role in the loss and degradation of grassland habitats and subsequently led to the elimination of *S. idalia* from these states (Dunwiddie and Sferra 1991).

Haying or mowing area also processes that have aided in the preservation of prairie remnants by preventing excessive litter and depressing woody encroachment (Selby 2007). These processes also appear to favor prairie-specialist species, such as *S. idalia* (McCabe 1981, Swengel 1996). Nonetheless, haying or mowing can still be a threat to populations of *S. idalia*. For example, haying during mid-July is likely to eliminate nectar sources when they are needed by adults and mowing an area too short could leave the delicate overwintering larvae exposed to

harsh winter conditions (Selby 2007). Although haying and grazing are suspected to be important processes that effect the occurrence and distribution of populations of *S. idalia*, the results of my study indicated that neither haying or grazing significantly influenced the occurrence distribution of late-instar *S. idalia* larvae.

It is well documented that many of the world's grasslands butterfly species are sensitive to disturbance (Akite 2008, Kubo et al. 2009, Oates 1995, Swengel 1996). In continental North America, some species sensitive to disturbance, such as *S. idalia*, are confined in terms of their distribution to prairies, which rely heavily on disturbances such as fire, grazing, and haying to maintain their open structure and depress woody encroachment (Anderson 2006, Moranz et al. 2014). The sensitivity of butterflies to the disturbances that maintain their habitat is often referred to as the "prairie butterfly paradox" (Moranz et al. 2014). The apparent sensitivity of prairie-obligate butterflies has led to the suggestion that processes such as fire was an infrequent occurrence as these species evolved (Schlicht and Orwig 1998, Nekola 2002, Swengel et al. 2011). Yet, the overwhelming amount of evidence suggests that fire has been an essential process in maintaining and shaping prairies for many decades (e.g., Sauer 1950, Wright and Bailey 1982, Axelrod 1985, Collins and Steinauer 1998, Briggs et al. 2002, Anderson 2006). In fact, studies have indicated that since European settlement in North America, frequency of fire has actually decreased (Steinauer and Collins 1996, Samson et al. 2004). Furthermore, given the evidence that fire, grazing, and pyric herbivory were common disturbances in tall-grass prairie during most of prehistory, it would make sense that grassland-dependent butterflies such as *S. idalia* evolved with these disturbances as primary selective forces and subsequently have developed mechanisms for dealing with such disturbances (Moranz et al. 2014).

The discovery of *S. idalia* larvae in sites burned ≤ 61 days prior to their detection suggests that *S. idalia* larvae have developed mechanisms to survive fire and supports the hypothesis that *S. idalia* have evolved with processes like pyric herbivory (Appendix A). Additionally, greater density of *Viola* species in sites that have been recently burned (Debinski and Kelly 1998, Latham et al. 2007) further support the conclusion that *S. idalia*, specifically *S. idalia* larvae are fire adapted and evolved with this process. The inconsistencies when it comes to determining the effects of fire on *S. idalia* are likely due to a number of factors among which is the timing of the observation (Latham et al. 2007, Moranz et al. 2014; Chapter III). For example, Moranz et al. (2014) found a complex population response of adult *S. idalia* that was facilitated by the interaction of time since fire with grazing and timing of sample period. Unlike other studies, Moranz et al. (2014) found that *S. idalia* abundance in sites that were burned recovered within a few months post-burn. They hypothesized that either (1) fire did not kill *S. idalia* larvae or (2) recolonization of the burned sites occurred much faster than reported in other studies. They suggested the latter explanation was correct because others had concluded *S. idalia* larvae were destroyed by fire (Swengel 1996, 1998) and fires left few unburned microsites. Conversely, the results of my study indicate that fire may have not killed all of the *S. idalia* larvae and the depressed abundance or absence of adult *S. idalia* from the sites immediately following the burn was not because larvae were destroyed but for alternative reasons. Timing of observations of adults within sites can make a difference in terms of adult *S. idalia* abundance (Moranz et al. 2014). Most studies find that adult *S. idalia* are either absent or their abundance is greatly reduced during surveys of burned sites early in the adult flight. However, studies that have continued surveys for adult *S. idalia* beyond one sample bout following a fire and surveyed throughout the adult flight found that the burned sites had recolonized to pre-fire abundance

levels a few months post-burn (Moranz et al. 2014). This is likely due to the eventual replenishment of nectar sources to the burned sites as the time since fire increases and also to the enhanced blooming of preferred nectar sources in these sites (Moranz et al. 2014). Consequently, the timing of the observations could be one possible alternative explanation for why similar studies find adult *S. idalia* abundance to be depressed or non-existent in sites following burns and subsequently propagates the assumption that *S. idalia* larvae are incapable of surviving fire. These results highlight the importance of survey timing. Sampling during a small window of the overall flight period may lead to inaccurate conclusions regarding treatment effects on adult density. Moreover, sampling only one life history stage (e.g., adult) and extrapolating the findings of the effects of management on adults to larvae could also result in inaccurate conclusions regarding the effects of management.

***S. idalia* Larvae and Host Plant Density**

Habitat requirements of adult butterflies differ from immature stages and habitat features and resources necessary for adults may not adequately reflect the requirements of the immature larval stages (Bergman 1999, Lane and Andow 2003). *Viola* host plant species are an essential component of habitat availability for populations of *S. idalia*, especially during the immature stages when it is their sole source of food (Klots 1951, Hammond 1974, Ferris and Brown 1981, Selby 2007). However, the decline or absence of *S. idalia* in an area is not always related to the absence of *Viola* host plants (Bliss and Schweitzer 1987, Ferge 1990, Huebschman 1998, Ferster 2005, Selby 2007). At the Fort Indiantown Gap National Guard Training Center in Pennsylvania, USA, density of arrow leaf violets (*V. sagittata*) did not differ between areas where adult *S. idalia* were present and areas where adult *S. idalia* were not present (Zercher et al. 2002, Ferster 2005). Similarly, Swengel (1997) found there was no significant correlation

between *V. pedatifida* and adult *S. idalia* in prairies surveyed in the Midwest. Contrary to these studies, I found a positive relationship with *S. idalia* and *Viola* host plant density, where the probability of late-instar *S. idalia* larvae occurrence increased with increasing *Viola* host plant density. My results likely differ from other studies because I evaluated the relationship between *Viola* host plants species and *S. idalia* larvae, not the relationship between *Viola* host plants and adult *S. idalia*. After *S. idalia* larvae pupate into adults they no longer require *Viola* species to persist, instead their “food” needs shift to nectar sources (Latham et al. 2007). This shift in “food” requirements is likely why studies investigating the effects of *Viola* density on adult *S. idalia* find little to no relationships (Chapter III). It is probable that until female *S. idalia* begin oviposition in the fall, *Viola* are no longer an important habitat features for *S. idalia* and whether an area contains *Viola* or not has no significant influence on adult *S. idalia* habitat selection at this stage in their life history. Although *Viola* host plants appear to be less important to *S. idalia* adults they are nevertheless essential for larvae and my results indicate that late-instar *S. idalia* larvae require areas $\sim \geq 40$ host plants per 500-m². Subsequently, conservation and management should aim to conserve, maintain, and create areas that contain high densities of *Viola* host plants through the implementation of management practices such as prescribed burning and light to moderate grazing which have been shown to facilitate the growth and establishment of *Viola* host plants (Mello 1989, Latham et al. 2007).

Spatial Scaling

Understanding the response of organisms to spatial pattern across scales is arguably one of the central goals in ecology (Levin 1992, Turner et al. 2001, Turner 2005). However, applied challenges, such as assessing habitat features and management practices that influence the occurrence and distribution of a rare grassland butterfly at different life history stages (i.e., larval

and adult), require the interfacing of phenomena that occur on very different spatial and temporal scales. Because patterns are organism and scale dependent, it is therefore preferable to assess ecological patterns across multiple scales (Wu and Loucks 1995). The ability to identify points where processes and patterns change along a continuous scale could aid in the identification of key shifts in ecological processes and biologically relevant research scales (Wiens 1989). In this study, I demonstrated that the ability to predict the occurrence distribution of late-instar *S. idalia* larvae within patches of host plants depends on the scale at which host plant density is measured. When I quantified and modeled host plant density and the occurrence of late-instar *S. idalia* larvae at four scales, I found that the occurrence distribution of late-instar *S. idalia* larvae was best described by the four-neighbor moving window form or 500-m² scale. This suggests that the 500-m² scale represents the grain of resource configuration (i.e., host plant density) at which late-instar *S. idalia* interact with the landscape structure when searching for host plants and necessary resources for surviving this precarious life history stage. Subsequently, when I assessed the relationship of the occurrence distribution of late-instar *S. idalia* larvae and host plant density, I used the key 500-m² scale. I found that the probability of late-instar *S. idalia* larvae occurrence increased as host plant density increased at this scale.

Although evidence of spatial dependence of late-instar *S. idalia* larvae and their host plant density is interesting, other unmeasured factors certainly contributed to the occurrence patterns of late-instar *S. idalia* larvae in sites where they were found and should also be investigated. Other studies have shown that the restricted distribution of numerous imperiled butterflies is the result of factors other than host plant distribution (Quinn et al. 1998, Dennis et al. 2003, Konvicka et al. 2003). While butterfly abundance is commonly associated with the quantity of host plants, studies have demonstrated that butterfly abundance is often related to the

number of host plants growing under certain microhabitat conditions rather than overall host plant abundance (Bourn and Thomas 1993, Bergman 1999, Lane and Andow 2003). Therefore, the determination of the microhabitat conditions appropriate for larval development is also key to conserving rare and threatened butterfly populations (Albanese et al. 2008).

A number of factors can contribute to the quality of microhabitats for the larval stages of Lepidoptera, including: microenvironmental features, climatic conditions, and their interactions (Singer 1972, Ehrlich et al. 1980, Dobkin et al. 1987, Ravenscroft 1994), number and quality of host plants (Gilbert and Singer 1975, Rausher 1981, Zangerl and Berenbaum 1992, Grundel et al. 1998), effect of predators and parasites (Sato and Ohsaki 1987, Ohsaki and Sato 1994), and occurrence of associating ants (Thomas 1984, Baylis and Pierce 1991, Hochberg et al. 1994, Wagner and Kurina 1997). Furthermore, these features may be especially important for single generation Lepidoptera that are oligophagous and have restricted host plant species options and a narrow window for larval development (Albanese et al. 2008).

S. idalia do not begin oviposition behavior until late August to early September (Scott 1986, Wagner et al. 1997, Zercher et al. 2002). Oviposition behavior seems to be casual with eggs deposited singly near, but rarely on the *Viola* host plants themselves (Scott 1986, Swengel and Swengel 2001). In fact, females tend to deposit eggs on the underside of dead vegetation near the ground in shady areas, rather than placing eggs on the actual host plants (Kopper et al. 2000, Appendix A). This oviposition site-selection strategy displayed by females is speculated to be influenced by the need for larvae to survive extreme circumstances such as harsh winter conditions rather than by any benefits of depositing eggs directly on host plants (Kopper et al. 2000). Thus, a multi-scale assessment of the relative importance of the occurrence distribution of *S. idalia* larvae compared to potential determinants of their occupancy other than host plant

density would provide further insights into the influence of habitat features on *S. idalia* larvae and assist in the refinement of conservation and management recommendations.

Conclusions

Conservation and management efforts may be futile if one life history stage is examined but another is ignored (Ferster and Vulinec 2010). To preserve populations of *S. idalia* and their habitat it is imperative that research be conducted on both the immature and adult stages to make robust and informed conservation and management recommendations. Moreover, it is important to recognize the importance of both spatial and temporal dynamics within and among patches of *S. idalia* larvae habitat and identify scales that are relevant to this species at this perilous life history stage. My findings suggest that *S. idalia* larvae can endure fire and indicate that late-instar larvae are perhaps negatively impacted by a lack of fire. These results support the hypothesis that *S. idalia* have evolved with processes such as fire and pyric herbivory and developed adaptations to deal with fire disturbances, which have been a part of the legacy of the Flint Hills region. Further supporting this conclusion is the positive response of *S. idalia*'s larval host plant to disturbances such as fire (Latham et al. 2007) and grazing (Mello 1989). Although, *S. idalia* larvae seem to respond positively to fire, adults have different requirements that are affected by fire (i.e., nectar sources) and thus, require nearby areas that have remained unburned (Chapter III). Therefore, conservation and management for *S. idalia* should aim to implement fire using a patch-burn framework. This framework ensures that only a portion of the landscape is burned, which maintains the grassland and promotes the growth of *Viola* host plants; however, other portions of the landscape remains unburned providing the necessary resources (e.g., nectar sources) to *S. idalia* as they transition from larvae to adult butterflies. Although haying and grazing did not positively affect the occurrence distribution of late-instar *S. idalia* larvae, these

processes also did not negatively affect the occurrence distribution of late-instar *S. idalia* larvae. Suggesting patch-burn grazing or patch-burning in concert with haying are also suitable management strategies when implemented with caution and with respect to timing, frequency and intensity. Finally, conservation and management strategies should aim to conserve high density patches of host plants ($\sim >40$ plants) at the 500-m² scale to promote the development of *S. idalia* larvae into the late-instar stages and subsequently to adulthood.

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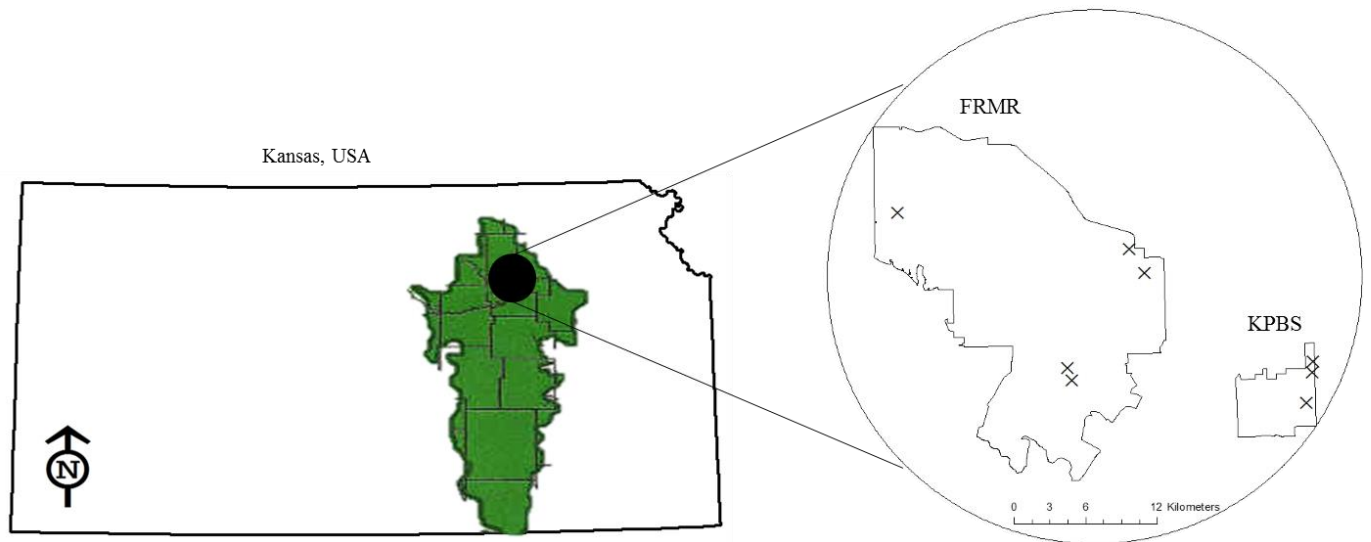




Figure 2.1 Illustration of the study area for late-instar *Speyeria idalia* larvae surveys conducted during 2014 -2015. The Flint Hills are marked by the green region spanning across the eastern edge of Kansas, USA, while the black dot within the Flint Hills marks the study area. The Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) are marked within the enlargement of the study area. The X's within the FRMR and KPBS mark the locations of the eight late-instar *S. idalia* larvae survey plots.

Legend

 FRMR/Konza Boundary

Probability of *V. pedatifida* Occurrence

Value
 High : 1
Low : 0

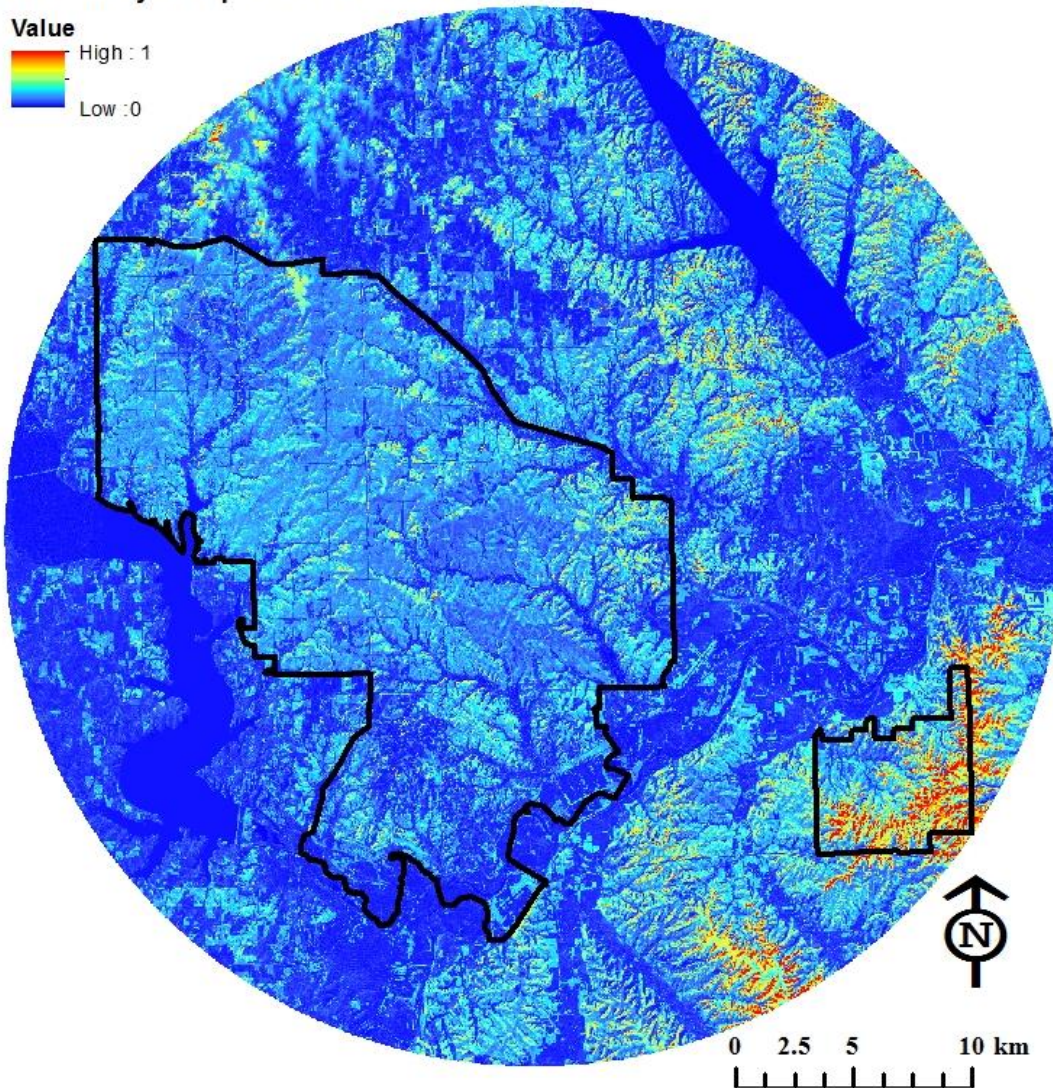


Figure 2.2 Probabilistic map of the occurrence distribution of *Viola pedatifida* in northeastern Kansas USA, using an ensemble species distribution modeling technique. The map was generated using *V. pedatifida* presence-absence data collected in northeastern Kansas in 2014 - 2015 as the response variable and a suite of seven predictors as the explanatory variables in the Software for Assisted Habitat Modeling for VisTrails. The ensemble model was created by taking the mean probabilistic values from four individual techniques: boosted regression tree, random forest, multivariate adaptive regression splines, and generalized linear model. On the map, red correlates with values of one or high probability of *V. pedatifida* occurrence while blue correlates with values of zero or low probability of *V. pedatifida* occurrence. The Fort Riley Military Reserve (FRMR) is the larger region outlined on the western edge of the map while Konza Prairie Biological Station (KPBS) is the smaller region outlined on the eastern edge of the map.

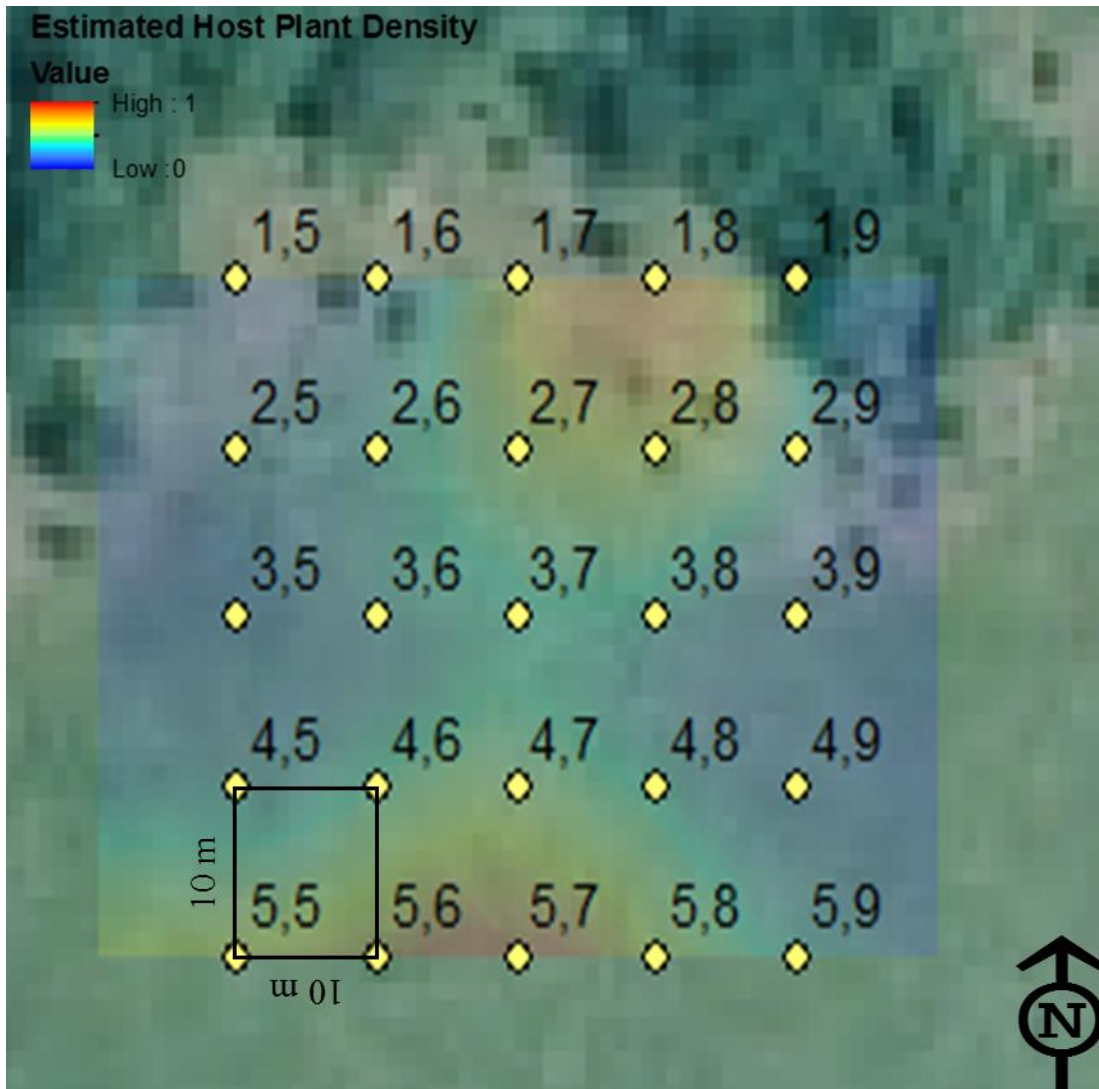


Figure 2.3 Illustration of one of the eight larval search areas selected to survey for the occurrence of late-instar *Speyeria idalia* larvae in northeastern Kansas, USA, at the Fort Riley Military Reserve and Konza Prairie Biological Station during 2014 – 2015. The image displays the gradient of *S. idalia* larvae host plant density within the 2500-m² search plot ranging from high violet density (red) and low violet density (blue). Host plant density was obtained through counts of host plants in a sub-set of 15, 10 m X 10 m plots within the search area. Host plant density for the remaining unsurveyed plots was estimated using kriging modeling in Geographic Information System (GIS) software. The yellow dots within the larval search plot mark the boundaries of 100-m² sub-plots. The numbers accompanying each dot are unique identification codes for the individual sub-plots.

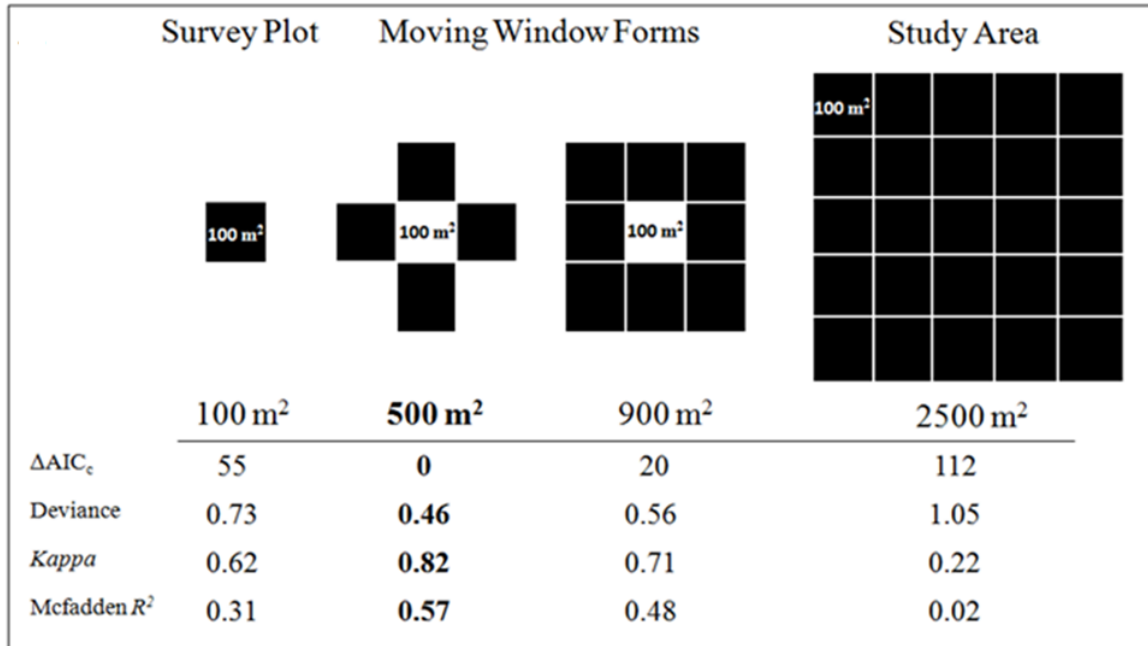


Figure 2.4 Illustration of the four moving window forms used to quantify and model the occurrence distribution of late-instar *Speyeria idalia* larvae and their larval host plant density from data collected in northeastern, Kansas, USA, at the Fort Riley Military Reserve and Konza Prairie Biological Station during 2014 -2015. Models were compared using delta AIC_c (ΔAIC_c), Deviance, Kappa, and McFadden R^2 . The scale that best described the occurrence distribution of late-instar *S. idalia* larvae is indicated in bold.

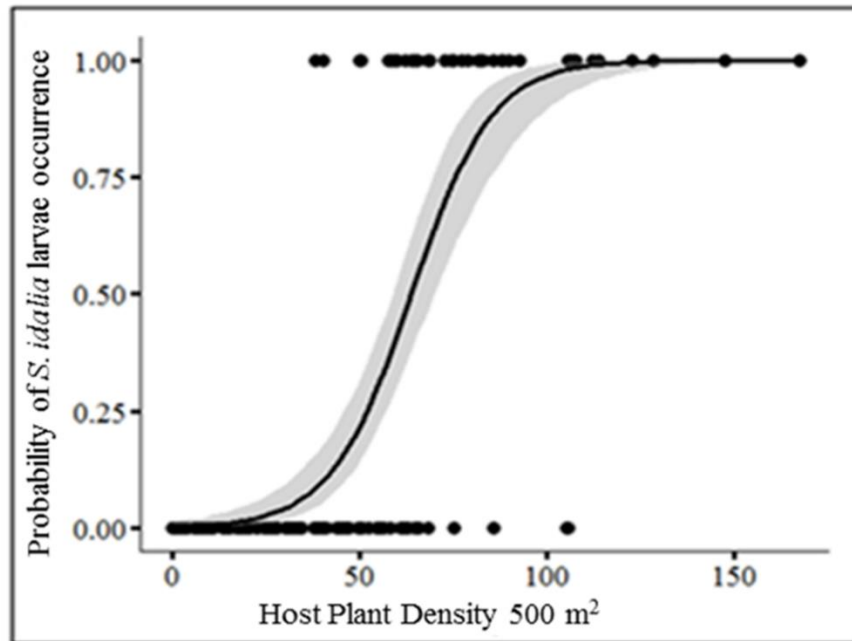


Figure 2.5 Relationship between the probability of occurrence of late-instar *Speyeria idalia* larvae and host plant density at the 500-m² scale with fitted generalized linear model line. The y-axis displays the probability of late-instar *S. idalia* larvae occurrence (or their feeding sign) and the x-axis displays host plant density at the key 500-m² scale. The black dots above and below the fitted line represent observations of late-instar *S. idalia* larvae or their feeding sign along the gradient of host plant density at the 500-m² scale. Surveys for late-instar *S. idalia* larvae were conducted within northeastern Kansas, USA, at the Fort Riley Military Reserve and Konza Prairie Biological Station during 2014 -2015.

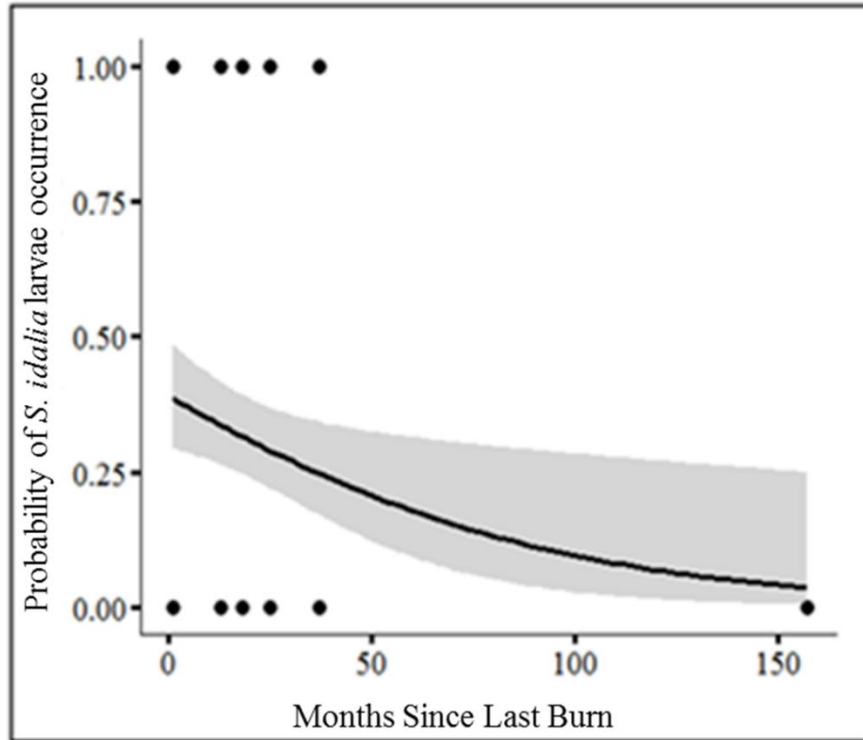


Figure 2.6 Relationship between the probability of late-instar *Speyeria idalia* larvae occurrence and months since last burn with fitted generalized linear model line. The y-axis displays the probability of late-instar *S. idalia* larvae or occurrence (or their feeding sign) and the x-axis displays the months since last burn. The black dots within the figure represent the larval search areas surveyed for late-instar *S. idalia* larvae. Surveys were conducted within northeastern Kansas, USA, at the Fort Riley Military Reserve and Konza Prairie Biological Station during 2014 -2015.

Table 2.1 The location of the eight larval search plots selected to survey for the occurrence of late-instar *Speyeria idalia* larvae in northeastern Kansas, USA, at the Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) during 2014 – 2015. Included is the management regime (grazed or hayed) and the fire-return interval (low ≥ 10 years, moderate 3-5 years, and high 1-2 years) received by each of the larval search areas.

Larval Search Plot	Location	Management	Fire-Return Interval
1	FRMR	Hayed	High
2	FRMR	Hayed	Moderate
3	FRMR	Hayed	Moderate
4	FRMR	- *	Low
5	FRMR	- *	High
6	KPBS	Grazed	High
7	KPBS	Grazed	Moderate
8	KPBS	Grazed	High

* Indicates that a larval search area did not receive either grazing or haying management and the only treatment of the area was fire-return interval at one of the intervals low, moderate or high

Table 2.2 Description of the habitat variables measured in the late-instar *Speyeria idalia* study at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern, Kansas, USA, 2014 – 2015.

Habitat Variable	Plot Size*	Description
Tree Cover	100 m ²	% Total woody plant canopy cover greater than 2.5 m in height
Shrub Cover	10 m ²	% Total woody plant cover less than 2.5m in height
Herb Cover	1 m ²	% Total herbaceous plant cover
Forb and Fern Cover		% Total herbaceous plant cover excluding graminoids
Bare Ground Cover		% Total exposed soils and rock cover
Litter Cover		% Total dead vegetative litter cover

*Data were collected within nested vegetation sampling modules within each randomly selected 100-m² late-instar *S. idalia* larvae survey sub-plot

Table 2.3 The top four models generated in program R using a generalized linear model approach testing the effect of predictor variables: months since burn, management regime (grazed or hayed), and host plant density (500-m² scale) on the occurrence distribution of late-instar *Speyeria idalia* larvae. Late-instar *S. idalia* larvae were surveyed in eight different larval search areas located at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern, Kansas, USA, during 2014-2015. Included are the degrees of freedom (df), second order variant of Akaike's information criterion (AIC_c), the difference in AIC_c (Δ AIC_c) and Akaike model weights (w_i) for each model. The top model is indicated in bold.

Model	df	AIC _c	Δ AIC _c	w_i
Months Since Burn + Host Plant Density	3	85.3	0.00	0.999
Host Plant Density	2	100.1	14.75	0.001
Months Since Burn	2	217.8	132.54	0.000
Null	1	224.3	139.01	0.000

Chapter 3 - Effects of Management Regime and Habitat Characteristics on the Abundance of the Regal Fritillary (*Speyeria idalia*) in Tall-grass Prairie

Introduction

The regal fritillary, *Speyeria idalia* (Drury, 1773) (Nymphalidae), is a large, showy and non-migratory butterfly that was once a common inhabitant of North American grassland ecosystems (Powell et al. 2007). *S. idalia* are univoltine, having a single generation per year with an adult flight from approximately late May – early October (Klots 1951, Tilden and Smith 1986, Wagner et al. 1997). Females emerge one to two weeks after males and mate soon after they emerge but oviposition is delayed until late August to September (Wagner et al 1997, Kopper et al. 2001, NatureServe 2005). Oviposition behavior is somewhat haphazard with eggs laid singly near, but not necessarily on the host plants themselves (Scott 1986, Swengel and Swengel 2001a). *S. idalia* is an oligophagous butterfly species that consumes only violets (*Viola* spp.) during the immature stages. While they are able to use a variety of violet species, *S. idalia* tend to be associated with specific *Viola* species in different parts of their range (Selby 2007). Birdfoot and prairie violet (*V. pedata*, *V. pedatifida*) are thought to be the preferred larval food plants throughout the Midwest and Great Plains (Swengel 1997, Kelly and Debinski 1998, Dole 2004).

The historic range of *S. idalia* extended from Oklahoma to the border of Canada and east to the Atlantic coast (NatureServe 2005). Despite its once broad geographic distribution, populations have declined drastically (NatureServe 2005). For reasons that are not well understood, eastern populations crashed during the early 1960s – 1990s (Powell et al. 2007). Currently, there are only two extant populations remaining east of Illinois: Fort Indiantown Gap,

Pennsylvania, and Radford Army Ammunition Plant in Virginia (Debinski and Kelly 1998, Swengel and Swengel 2001a, Williams 2002, NatureServe 2005). However, there are locally abundant populations west of Illinois, with the species considered “apparently secure” in Kansas (Ely et al. 1986, Marrone 2002, Selby 2007). *S. idalia* was listed as a Category II species under the United States Endangered Species Act (ESA) until this category was removed in 1996 (U.S. Fish and Wildlife Service 1996). The rapid, range-wide declines and ongoing threats to extant populations from habitat loss and mismanagement prompted the U.S. Fish and Wildlife Service to initiate a species status review in September 2015 of *S. idalia* as a potential candidate for listing under the ESA.

The greatest ongoing threats to populations of *S. idalia* appear to be habitat loss and fragmentation through grassland conversion to cropland along with inappropriate land management practices such as high-intensity grazing, frequent and intensive burning, and haying (Schultz and Crone 1998, Davies et al. 2005, Ferster and Vulinec 2010). It was estimated that the Great Plains region has lost 70% of its grasslands and tall-grass prairie is ~3-5% of its historic extent (Samson et al. 2004). Although the Flint Hills represents the largest remaining contiguous tract of tall-grass prairie, it has still suffered drastic losses with tall-grass prairie retaining as little as 37% of the historic extent in the Flint Hills/Osage Plains region (Samson et al. 2004). Native tall-grass prairie communities have succumbed to anthropogenic land conversion, development, invasive herbaceous and woody plant species, and plant community succession (Samson and Knopf 1996). Historically, unrestricted grazing by native herbivores and wildfire played important roles in the maintenance of prairie ecosystems in the Great Plains (Fuhlendorf and Engle 2001). However, in the absence of these ecological drivers, most

remaining tracts of remnant prairie are often maintained by prescribed land management (Vogl 1974, Shuey 1997).

Fire, grazing, and haying play critical roles in maintaining and shaping prairie remnants, and a complete lack of these processes can pose a serious threat to the extent and quality of remaining prairie remnants (Selby 2007). Depending on their timing and intensity, these management strategies can also constitute threats to *S. idalia* populations (Selby 2007). Several studies have suggested that fire is harmful to *S. idalia* and likely depresses prairie-specialist butterfly populations especially when applied aggressively at short return-intervals (Swengel 1996, 2001b, 2004; Swengel and Swengel 2001b, among others). While light to moderate intensity grazing may be “highly favorable” to *S. idalia*, high intensity grazing can be a threat (Hammond and McCorkle 1983, Royer and Marrone 1992, Dana 1997, among others). Haying and mowing have helped preserve prairie remnants by preventing excessive litter and woody encroachment (Selby 2007). These practices also appear to favor prairie-specialist butterflies (Swengel 1996). However, haying or mowing can still have negative effects on *S. idalia* by eliminating essential nectar sources when needed by adults and development of eggs and larvae can be negatively affected if an area is mowed too short (Selby 2007).

Despite the numerous studies examining the effects of fire on prairie butterflies and invertebrates, it remains a subject of great controversy (Dana 1991; Swengel 1996, 1998; Panzer 1998, 2002; Schwartz 1998; Swengel and Swengel 1999, 2001b). Information pertaining to the effects of fire on prairie specialist butterflies such as *S. idalia* would provide valuable insight and help guide conservation and management recommendations. Furthermore, there is a lack of information regarding the effect of the interaction of fire and other management practices such as grazing and haying on *S. idalia* (Selby 2007). Given the necessity of processes such as fire,

grazing, and haying to the persistence of prairie remnants and lack of knowledge regarding these processes and their effects on prairie obligate invertebrates, such as *S. idalia*, my objectives were to (1) quantify the effects of prairie management, particularly fire, grazing, and haying on adult *S. idalia* density and (2) determine the relative influence of habitat characteristics created by these management regimes on adult *S. idalia* density.

Methods

Study Area

This study was conducted in northeastern Kansas, United States, at the Fort Riley Military Reserve (FRMR) (Geary and Riley counties) and Konza Prairie Biological Station (KPBS) (Geary County) (Figure 3.1). Both the FRMR and KPBS are nestled within the northern portion of the Flint Hills. The surrounding landscape of the FRMR and KPBS encompasses numerous drainages, two large reservoirs and broadly distributed urban and rural developments. More generally, the Flint Hills are characterized by large rolling hills and rocky flint-filled soils (Anderson and Fly 1955). The flint contained within the bedrock for which the region is named depressed erosion and left the Flint Hills higher than the surrounding areas, with an elevation relief of 91-152 m. In addition to preventing soil erosion, underlying flint and limestone deposits made this region undesirable for crop cultivation making it home to the largest remaining contiguous tract of tall-grass prairie in North America (Reichman 1987). Subsequently, the vegetative community is commonly associated with dominant grasses such as big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) (Anderson and Fly 1955, Owensby and Smith 1979). The remainder of the plant community is comprised of perennial grasses, woody species, and a wide variety of native herbaceous forbs (Anderson and Fly 1955, Owensby and Smith 1979). The climate in this region is driven by its

interior location and characterized by hot, dry summers and cold winters with temperatures ranging from -40°C to 49.44°C (Abrams and Hulbert 1987). Annual precipitation varies drastically (average annual precipitation = 83.82 cm) and droughts are common (Abrams and Hulbert 1987).

The FRMR is one of the nation's largest army posts comprising ~41,000 ha. Approximately 29,000 ha are managed for multiple uses including conservation and outdoor recreation activities such as: military training, hunting, hiking, biking, and bird watching, among others. The FRMR is divided into training areas that are managed using a combination of burning and haying regimes. Prescribed burns at the FRMR are typically conducted during the spring and fall, but occasional wildfires from live fire military training do occur throughout the year. Haying at the FRMR is strictly regimented and must occur between 15 July – 15 August. The FRMR was partitioned into four study locations due to its large size and varying management regimes (Figure 3.1).

The KPBS is a 3,487 ha tract of tall-grass prairie co-owned and operated by the Division of Biology, Kansas State University, and The Nature Conservancy. The KPBS has been a part of the National Science Foundation Long-Term Ecological Research (LTER) network since 1981 and experimentally managed with various grazing and burning regimes (Knapp et al. 1998). Grazing treatments are varied by native bison (*Bison bison*), cattle (*Bos taurus*), or no grazing. Prescribed burns occur on an annual to every 2, 4, and 20-year intervals with most ignited during the spring. The KPBS was treated as a single study location (Figure 3.1).

Adult Surveys

During the annual flight period (late May – early August) in 2012, 2014, 2015, and 2016, I surveyed transects ($n = 44$) distributed throughout the five study locations for adult *S. idalia*

(Table 3.1). Transects were 500 m to >1 km in length and stratified by management regime (fire, grazing, or haying) and fire-return interval (low - ≥ 10 years, moderate - 3-5 years, and high - 1-2 years) (Table 3.2). Transects were surveyed twice in 2012, three times in 2014, and six times in 2015 and 2016. Successive survey bouts did not begin until all transects for the current bout had been surveyed. Surveys were conducted largely within the parameters of the British Butterfly Monitoring Scheme (Pollard and Yates 1993). All surveys were conducted between 0830 and 1830 CST, under sunny and warm conditions, when temperatures were $\geq 17^\circ\text{C}$ if there was overcast, and winds $< 20\text{km/h}$ on the Beaufort scale. Surveys were conducted by walking transect centerlines and recording the perpendicular distance from the transect centerline to each individual adult *S. idalia* within ≤ 30 m either side of the transect centerline. Distances to each individual adult *S. idalia* from the transect centerline were estimated in intervals of 0-5 m, >5 m-10 m, >10 m-20 m, and >20 m-30 m.

Vegetation Surveys

To characterize habitat features along transects, I used a module-nested plot method to sample vegetation data. Each module consisted of one 100-m² plot with two 10-m² and two 1-m² embedded sub-plots. I measured one density and six cover variables during field surveys (Table 3.3). Cover was estimated using nine cover classes that were converted to mid-points in the analysis (cover classes: 0 – 1%, 1 – 2%, 2 – 5%, 5 – 10%, 10 – 25%, 25 – 50%, 50 – 75%, 75 – 95%, >95%). The cover classes and module-nested plot methods were adopted from the North Carolina Vegetation survey (Peet et al. 1997), which is a variation of the more traditional, cover class scheme (e.g., Domin 1928, Braun-Blanquet 1964, Daubenmire 1968). Vegetation data were collected every 100-m along adult survey transects in 2014 – 2016. At each vegetation

survey point along a transect, I surveyed two module vegetation plots. Modules were placed at a 90° angle from the transect on both sides of the transect centerline.

Statistical Analysis

Distance sampling is a wildlife sampling technique that is commonly employed to estimate the size or density of a population (Chandler 2013). Distance sampling methods have demonstrated to be effective for sampling a wide variety of taxa, from butterflies (Brown and Boyce 1998, Powell et al. 2007) and birds (Catt et al. 1998, Oliveira et al. 1999) to desert tortoises (*Gopherus agassizii*; Swann et al. 2002) and badgers (*Meles meles*; Hounscome et al. 2005). To accurately estimate and model density, it is often necessary to account for individuals present but not detected (Chandler 2013). While conventional methods of analysis do not allow for explicit modeling of both density and detection probability, the function *distsamp* in program R employs the multinomial-Poisson mixture model of Royle et al. (2004), which was developed to overcome this limitation (Chandler 2013).

There are numerous options that exist for analyzing distance sampling data (Chandler 2013). I used Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance (R Development Core Team 2010, Fiske and Chandler 2011) to estimate adult *S. idalia* densities following the model of Royle et al. (2004), which assumes that multiple transects have been surveyed and distance data are recorded in discrete intervals. Package Unmarked, like other distance sampling software, provides a selection of candidate functions to describe the probability of detection and estimates the associated parameters using maximum likelihood estimation (Miller et al. 2016). I compared models using the key functions: uniform, half-normal, and hazard-rate. To identify which models best explained observed patterns in adult *S. idalia* density, I used an information-theoretic framework to compare and select the best fitting

models (Burnham and Anderson 2002). I used the second-order variant of Akaike's information criterion adjusted for small sample sizes (AIC_c) to compare the relative ability of alternative models to fit observed data. I calculated Delta AIC_c (ΔAIC_c) and Akaike weights (w_i), to evaluate the support for each model given the data (Burnham and Anderson 2002). I used AIC_c to rank models and selected the best fitting models as those with the lowest AIC_c scores (Buckland et al. 2001). I considered all models with a $\Delta AIC_c < 2$ to have support. Exploratory analysis revealed that the hazard-rate detection function consistently best fit the data according to accompanying AIC_c values (Table 3.4); subsequently, all data were modeled with the hazard-rate detection function. Model results include the number of AIC_c units from the top ranked model (ΔAIC_c), number of model parameters (K), and model AIC weight (w_i).

To evaluate the effects of fire-return interval and management on adult *S. idalia* density I developed four ecologically relevant models: null (no effect), global (fire-return interval+management), fire-return interval only, and management only. In the global model adult *S. idalia* density was estimated in the three levels of fire-return interval (low, moderate, high) and management (grazed, hayed, or burned). The resulting model estimated adult *S. idalia* density in nine possible treatment categories that included: grazed+high fire-return interval, grazed+moderate fire-return interval, grazed+low fire-return interval, hayed+high fire-return interval, hayed+moderate fire-return interval, hayed+low fire-return interval, and finally burned high fire-return interval, burned moderate-fire-return interval, and burned low fire-return interval. In the fire-return interval only model, management other than fire (i.e., grazing or haying) was ignored and adult *S. idalia* density was estimated in the three levels of fire-return interval (low, moderate, and high). Similarly, in the management-only model, fire-return

interval was ignored and adult *S. idalia* density was estimated in the three management treatments (grazed, hayed, burned).

Finally, I tested the relative influence of the seven measured habitat variables on adult *S. idalia* densities. Prior to testing the influence of the habitat variables on adult *S. idalia* density I employed Pearson's correlation coefficient to test for statistical correlation among the variables. Correlated pair-wise variables ($r > 0.60$) were not included in the same models. Following the removal of models with correlated variables, I constructed all possible combinations of additive models to test the effect of the habitat variables on adult *S. idalia* density. Additionally, I tested for differences for the seven habitat measurements among fire-return interval (low, moderate, high) and management practices (fire, grazed, hayed) using a randomized block design analysis of variance (ANOVA; Statistix version 8.0). I used survey transect as the experimental unit. Year was treated as a block and considered a nuisance variable in this analysis. Independent variables in the analyses were presence of *S. idalia* (detected or not), fire-return interval or management practice, and their respective interaction. Following a significant ANOVA ($P < 0.05$), I used a least significant difference test to separate levels of independent variables.

Results

Effects of Management and Fire-Return Interval on *S. idalia* Density

The highest ranked model among model sets testing the effect of fire-return interval and management on adult *S. idalia* density was fire-return interval+management (AIC_c 1668.12, $K = 7$, $w_i = 0.98$). The other models were ranked as follows: fire-return interval (AIC_c 1675.53, ΔAIC_c 7.41, $K = 5$, $w_i = 0.02$), management (AIC_c 1761.8, ΔAIC_c 93.65, $K=2$, $w_i = 0.00$), and the null model (AIC_c 1763.0, ΔAIC_c 94.87, $K=4$, $w_i = 0.00$). The highest ranked model revealed that adult *S. idalia* densities were greatest in areas that were grazed and burned on a moderate

fire-return interval (Table 3.5). Although the density estimate in this treatment category had 95% confidence intervals that overlapped with the hayed+moderate fire and moderate fire only categories, the density estimate was at least ~30% greater in the grazed and moderate fire-return interval (Table 3.5). Density estimates of adult *S. idalia* did not differ among management type, revealing that *S. idalia* adults responded similarly to disturbance type in tall-grass prairie (Table 3.6). Because the top two ranked models both included fire-return interval, I estimated adult *S. idalia* densities for each categorized fire-return interval. Adult *S. idalia* density was at least 84% greater in areas that received a moderate fire-return interval versus areas that received high fire-return intervals and low fire-return intervals (Table 3.7).

Effects of Vegetation Characteristics on *S. idalia* Density and Occurrence

The Pearson's correlation coefficient test indicated that among the habitat variables measured, percent grass and bare ground were negatively correlated ($r = -0.69$). Therefore, I did not consider models that included both grass and bare ground as candidates for further analysis. Tree and shrub cover were also negatively correlated ($r = -0.64$). However, instead of eliminating one of the variables from subsequent models, I combined these two variables into one variable labeled woody vegetation. This combined variable quantified the total average percent woody vegetation cover. Following these adjustments, I tested all possible combinations of additive models using the revised habitat variables. The model that best fit these data was the global model (Table 3.8). Among the variables included in the top model, grass had the greatest effect on adult *S. idalia* density ($\beta = 0.389 \pm 0.126$ [SE]); as average percent grass cover increased the estimated density of adult *S. idalia* also increased (Figure 3.2a). Average percent litter cover also had a positive effect on adult *S. idalia* density ($\beta = 0.297 \pm 0.089$), increasing with the estimated density of adult *S. idalia* (Figure 3.2b). While the effect size was relatively

small ($\beta = 0.128 \pm 0.075$), average density of *V. pedatifida* also had a positive effect on adult *S. idalia* density (Figure 3.2c). Conversely, both average percent woody cover and average percent forb cover had negative effects on adult *S. idalia* density ($\beta = -0.284 \pm 0.141$, $\beta = -0.278 \pm 0.126$). As average percent woody and percent forb cover increased, the estimated density of adult *S. idalia* decreased (Figure 3.2d, e).

Effects of Management and Fire-Return Interval on Habitat Characteristics

The presence of adult *S. idalia* did not interact with fire-return interval; however, there was a significant interaction between the presence of adult *S. idalia* and management for woody vegetation only (Table 3.9). When the habitat variables were grouped by fire-return interval average bare ground cover differed between transects with and without adult *S. idalia* (Table 3.10). Average woody cover, average litter cover, average forb cover, average grass cover, and violet density did not differ between transects where *S. idalia* was detected versus those where *S. idalia* was not detected (Table 3.10). When the habitat variables were grouped by overall management, there were no differences between transects with and without adult *S. idalia* for any of the habitat variables measured (Table 3.10).

Vegetation composition varied little among overall management treatments. Average percent woody cover differed among management treatments; however, all other vegetation characteristics were similar among management treatments (Table 3.11). Vegetation composition did vary among fire-return intervals. Average forb, grass, litter, and woody cover differed among fire-return intervals (Table 3.12). Average forb cover was at least 1.5 times greater in sites that received a high fire-return interval compared to sites that received low or moderate fire-return intervals (Table 3.12). Average grass cover was greatest in sites burned on a moderate fire-return interval and at least 1.2 times greater than sites burned with low or high

fire-return intervals (Table 3.12). Average litter cover was nearly 2 times greater in sites that received a low fire-return interval compared to sites burned on a high or moderate fire-return-interval (Table 3.12). Finally, average woody vegetation cover was 4.5 times greater in sites that received a low fire-return interval (Table 3.12). There was no effect of fire-return interval on average bare ground and violet density (Table 3.12).

Discussion

Management, Fire-Return Interval and the Effect on *S. idalia* Density

My results suggest that adult *S. idalia* require some form of disturbance to maintain and conserve populations and the open native prairie habitat they exclusively inhabit. The greatest response was to fire as a disturbance, with additional positive responses when fire and managed grazing were applied in combination with one another. Among fire-return intervals, adult *S. idalia* density was greatest in sites that had a moderate (3 – 5 year) fire-return interval. This finding concurs with a large majority of the *S. idalia* literature, which suggests that less aggressive and more moderate fire regimes are favorable to adult *S. idalia* and other prairie-specialist species (Swengel 1996, 2001a, 2004; Huebschman and Bragg 2000; Swengel and Swengel 2001b; Wright et al. 2003; Powell et al. 2007). While the effect of grazing in concert with a moderate fire-return interval had 95% confidence intervals that overlapped with haying combined with a moderate fire-return interval and moderate fire only, these results nonetheless indicated that managed grazing along with a moderate fire-return interval supported the greatest densities of adult *S. idalia*.

Unlike the findings of Swengel (1996), which indicated that adult *S. idalia* and other prairie-specialists were more abundant in hayed rather than burned prairies, I found adult *S. idalia* density to be similar among management treatments – grazed, hayed, and burned.

Although I found these three management treatments to contain similar densities of adult *S. idalia*, it is important to consider that all study sites received some level of fire management at either the low, moderate or high fire-return intervals; however, for the initial analysis, sites were grouped based on overall management (burned only, grazed+burned, hayed+burned) regardless of fire-return interval. The lack of a difference in densities of adult *S. idalia* among the overall management treatments (grazed, hayed, burned) and the inclusion of fire-return interval in the top two ranked models further supports the conclusion that the most important driver of adult *S. idalia* density among sites was fire-return interval.

Results from previous studies regarding the effect of fire on prairie-specialist butterfly populations have been somewhat mixed but are often positive (Swengel 2001a, Panzer 2002). For example, Huebschman and Bragg (2000) also found that burning on a 3- to 4-year frequency while leaving contiguous areas unburned was a viable and realistic long-term management plan for *S. idalia* populations present at the Nine-mile Prairie in Nebraska. Conversely, Swengel (1997) determined that adult *S. idalia* was most abundant in larger prairie remnants managed by haying or grazing versus burning. I suggest two factors that explain such inconsistencies when it comes to determining the effects of fire on populations of *S. idalia*. First is the scale of the observation and second is the timing of the observation (Latham et al. 2007, Moranz et al. 2014). Due to the extensive conversion and fragmentation of the grassland ecosystems, it is common for research conducted on populations of adult *S. idalia* to be done within very small remnant patches of prairie. For instance, surveys conducted by Powell et al. (2007) investigating the effects of management, particularly prescribed burning, on adult *S. idalia* densities in northeastern Kansas were in prairie remnants that ranged in sizes from only 0.9-53 ha with a mean survey site of 7.1 ha. Similarly, the study site size at the Nine-mile Prairie

in Nebraska, where Huebschman and Bragg (2000) conducted their study on the effects of spring burning on adult *S. idalia* densities, was only 97 ha. While both studies indicated that adult *S. idalia* abundance declined drastically or were absent from areas directly affected by a burn, sites that were managed with patch-burning were reported to have the highest densities of adult *S. idalia* among burned sites (Huebschman and Bragg 2000, Powell et al. 2007). Therefore, it would be beneficial to integrate observations across a much larger scale where just a portion of the overall habitat is burned in a given year, successive fires occur in a patch-burn mosaic, and several years elapse between fires (Latham et al. 2007). In this scenario, the immediate decline following the fire would likely prove to be only a small fraction of the total population (Latham et al. 2007).

The second explanation for discrepancies regarding the effect of fire on adult *S. idalia* is the timing of the observations. Similar, to most other studies conducted on adult *S. idalia* Moranz et al. (2014) found that adult *S. idalia* abundance was negatively affected immediately following a burn. However, within five months of burning, the burned units had been recolonized and had large adult *S. idalia* populations (Moranz et al. 2014). These results are in contrast to the findings of Swengel (1996) who sampled adult *S. idalia* in the same region as Moranz et al. (2014) but earlier in the adult *S. idalia* flight period. While Swengel (1996) only sampled once from 14 June – 19 June, Moranz et al. (2014) sampled adult *S. idalia* populations during three periods – early June, late June and late July. The early sampling period of Swengel (1996) may not have provided adult *S. idalia* with enough time to recolonize the burned sites and also prohibited observations of adult *S. idalia*'s positive response to fire of late-season nectar sources (Moranz et al. 2014). Thus, sampling during a single portion of the flight period might lead to inaccurate conclusions regarding treatment effects on butterfly densities.

The problem with burning appears to arise when small relatively unconnected remnants are burned in their entirety and adult *S. idalia* abundance declines or they disappear from such sites (Swengel et al. 2011). Although a burn promotes the growth of grass and depresses woody encroachment, which are habitat features selected by adult *S. idalia*, immediately following the burn, the site has not had the chance to rejuvenate all vegetative features required by adult *S. idalia* and likely lacks the necessary nectar resources and heterogeneity that the species requires at this life history stage (Moranz et al. 2014). Presumably they abandon the site in search of sites that contain the needed resources. Although adult *S. idalia* are strong flyers and have the ability to disperse >7 km (Zercher et al 2002), they are not readily equipped to survive in the heavily developed matrix of urban developments and croplands that commonly surround remaining prairie remnants (Selby 2007). Consequently, the probability of successfully reaching distant prairie remnants and repopulating them is unlikely (Selby 2007). Therefore, small satellite populations of *S. idalia* are most vulnerable to disturbances that might have been overcome in the historic prairie landscape (Selby 2007). However, both Huebschman and Bragg (2000) and Powell et al. (2007) found that even among the relatively small prairie remnants surveyed in their studies, patch-burning was a feasible management strategy. These results suggest that as long as unburned areas are in close proximity adult *S. idalia* are able to recolonize the burned areas (Moranz et al. 2014). Nonetheless, management such as prescribed burning, grazing, and haying need to be implemented with caution and the timing, intensity, and extent should be altered to ensure the security of vulnerable populations (Selby 2007).

Habitat Characteristics and the Effect on *S. idalia* Density

I found that average percent grass cover had the greatest positive effect on adult *S. idalia* densities while average percent woody cover had the greatest negative effect on adult *S. idalia*

densities. These relationships are relatively unsurprising given the descriptions of *S. idalia* habitat in the literature. It is common for *S. idalia* to be described as a “prairie-specialist” dependent on grasslands (Swengel 1996), thus my results support previous descriptions that adult *S. idalia* habitats are profoundly defined by the presence and cover of grass and trees. Dole (2004) described *S. idalia* habitat in the Great Plains region as “pristine tallgrass prairie”. In fact, *S. idalia* have been identified as an indicator species of native tall-grass prairie (Hammond and McCorkle 1983). Although adult *S. idalia* can occur in sites that contain trees, studies have suggested that they are sensitive to habitat edges or boundaries, such as trees (Ries and Debinski 2001) and areas that contain dense tree cover are avoided (NatureServe 2005). These results elucidate the necessity of management such as fire, grazing, and haying to maintain the openness of prairie habitats and depress woody encroachment. Despite requiring some disturbance to maintain its openness and prairie flora, the positive relationship between average litter cover and adult *S. idalia* densities suggests that adult *S. idalia* do in fact select areas that have not been recently disturbed, particularly by prescribed fire. Powell et al. (2007) noted a similar relationship with adult *S. idalia* densities and litter accumulation. Powell et al. (2007) reported that sites that had greater densities of *S. idalia* typically had dense litter, which suggested that they had not been recently burned. The combination of these findings highlight that burning an entire site homogeneously on an annual basis is not an appropriate management strategy for populations of *S. idalia*. Burning annually decreases the accumulation of litter, and likely depresses the variety and abundance of nectar sources. Alternatively, not burning or a lack of any management at all is also not recommended for conserving and managing populations of *S. idalia* because the lack of management would facilitate woody encroachment. Thus, burning

contiguous tracts of prairie in a shifting mosaic is likely a suitable management strategy for promoting and maintaining both populations of *S. idalia* and the prairie habitat they depend on.

It has been suggested that the availability of “suitable” nectar sources during adult flight is as critical to an area's ability to support populations of certain butterfly species as the presence of larval host plants (Opler and Krizek 1984). This habitat requirement is particularly important for long-lived butterflies such as *S. idalia* (Selby 2007), which not only utilize nectar sources for energy, but also likely use these food sources for the production of eggs (Opler and Krizek 1984). Due to the importance of nectar sources suggested by the *S. idalia* literature, I *a priori* hypothesized that forb cover would be an important habitat feature in describing adult *S. idalia* densities. While average percent forb cover was one of the variables included in the top model, the negative relationship between *S. idalia* density and average forb cover was surprising. However, this result is likely due to the “broad” measurement of forbs in this study. I measured average percent forb cover as percent total herbaceous cover excluding graminoids. Accordingly, the resulting average percent forb cover estimates include all forbs including those forbs that are not selected or unusable by adult *S. idalia*. Although, adult *S. idalia* use a number of plant species as nectar sources, studies have indicated that the species has strong preferences for specific nectar plants. In observations of 1,058 individuals from across several states, Swengel (1993) found that adult *S. idalia* “strongly preferred” thistles; plants with pink flowers were selected as nectar sources 85% of the time. Throughout *S. idalia*'s range, milkweeds (*Asclepias* spp.) also appear to be a commonly preferred nectar source (NatureServe 2005, Heitzman and Heitzman 1987, Fritz 1997, Royer 2004, Marrone 2002). Previous studies have indicated that milkweeds accounted for $\geq 50\%$ of nectar plants used (Huebschman 1998, Nagel et al. 1991). Other important nectar sources include: thistles (*Cirsium* spp.), coneflowers

(*Echinacea* spp.), blazing-stars (*Liatris* spp), bergamots (*Mondarda* spp.), goldenrods (*Solidago* spp.), clovers (*Trifolium* spp.), and ironweeds (*Vernonia* spp.) (NatureServe 2005). The negative relationship between adult *S. idalia* density and average forb cover in my results is likely due to adult *S. idalia*'s strong propensity for specific nectar sources and illustrates the need for a finer scale measurement of forbs in future studies.

Viola species are a critical habitat feature for populations of *S. idalia*, particularly during the immature stages when *Viola* species are the sole food plant of *S. idalia* larvae (Klots 1951, Hammond 1974, Ferris and Brown 1981; Chapter I). Several studies have shown a positive correlation between the abundance of *Viola* species and adult *S. idalia* (Swengel 1997, Debinski and Kelly 1998). Although the relationship was slight, I also found a positive relationship between adult *S. idalia* density and density of its preferred larval host plant for this region, *V. pedatifida*. While adult *S. idalia* do not necessarily “require” *Viola* species unlike the larval stages, Nagel et al. (1991) suggested that adult *S. idalia* males tend to remain near their natal areas where *Viola* species are expected to be more abundant to be in the “right place” at the right time when females emerge a couple weeks after the males. However, their high mobility, propensity to “wander” (Selby 2007), and shifting requirement for resources besides *Viola* species at this stage in their life might explain the relatively “weak” relationship that I found between adult *S. idalia* and *V. pedatifida*.

Survey-Wide Adult *S. idalia* Density

I found *S. idalia* to be a common inhabitant of both the FRMR and KPBS occurring at 41 of 44 (95%) transects surveyed throughout the course of this study. Survey-wide density estimates produced in package unmarked in R for the FRMR and KPBS reported adult *S. idalia* density to be ~0.60 individuals per ha at the FRMR and ~0.51 individuals per ha at the KPBS.

These estimates are lower than estimates produced in other studies. The species' survey-wide density estimate in a study conducted in northeastern Kansas by Powell et al. (2007) was 7.6 individuals per ha. Kelly and Debinski (1998) had density estimates ranging from 1.1 individuals per ha to 15.7 individuals per ha in prairies surveyed throughout Iowa, Kansas, and the Dakotas.

One of the causes for the stark contrast in density estimates from this study to others is the size and connectedness of the sites surveyed. The mean size of the tall-grass prairie study sites described as small tracts mixed among agricultural and other development surveyed in Powell et al. (2007) was 7.1 ha with the smallest site surveyed being 0.9 ha and largest being 53 ha. In contrast, the smallest site surveyed in this study was 12 ha and the largest was 636 ha with a mean survey site size of 207 ha. Moreover, the tall-grass prairie areas surveyed in this study were highly connected, facilitating movement of adult *S. idalia* between sites. While adult *S. idalia* are robust flyers (NatureServe 2005), they strongly avoid prairie edges, such as row crop agriculture (Ries and Debinski 2001). Consequently, the relatively small isolated patches of prairie surveyed in Powell et al. (2007) could have restricted the adult *S. idalia* to these small areas and prohibited movement out of these sites resulting in greater density estimates. Another potential factor that could have inflated density estimates in these studies is the placement of transects in close proximity to one another. The transects in Powell et al. (2007) consisted of two parallel segments located >60 m apart. Presumably these parallel segments were surveyed on the same day and placed >60 m apart to avoid double counting. However, adult *S. idalia* can readily fly distances >1 km (Nagel et al. 1991, Selby 1992, Zercher et al. 2002, Barton 1993, 1994). Subsequently, it is plausible that individuals were double counted, despite efforts to avoid this issue and densities were overestimated.

Conclusions

The results of this study elucidate the need for disturbance applied at a landscape scale to maintain and conserve populations of *S. idalia* and their habitat. I found that adult *S. idalia* densities were greatest in sites that were burned on moderate (3-5 year) fire-return intervals regardless of other management applied to the site (i.e., haying or grazing). However, densities were slightly greater for sites that were grazed and burned on a moderate fire-return interval compared to sites that were just treated with fire on a moderate return-interval and sites that were hayed and burned on a moderate fire-return-interval. These results suggest patch-burning, patch-burn grazing, and patch-burning in concert with haying as viable long-term management plans for the maintenance and conservation of populations of *S. idalia*. Furthermore, the increasing densities of adult *S. idalia* in habitats that contained high grass cover, minimal woody cover, some litter accumulation and the presence of *V. pedatifida* demonstrated that the habitat features created by the implementation of these management regimes are favorable to adult *S. idalia*. Therefore, conservation management of adult *S. idalia* should aim to implement prescribed fire in a patch-burn mosaic thereby increasing grass cover, promoting *V. pedatifida* density, depressing woody vegetation, and allowing litter accumulation in unburned patches. Although patch-burning has been applied to relatively small, isolated prairie remnants with success (Huebschman and Bragg 2000, Powell et al. 2007) implementation should be done with caution and with respect to timing, intensity and frequency (Selby 2007). Comparable research should be conducted in other parts of *S. idalia*'s range to assist in the refinement of these management recommendations. Future research of adult *S. idalia* ecology should aim to be conducted on large scales (e.g., landscape) and respect to timing to fully assess the effects of processes such as fire, grazing and haying on populations of *S. idalia*. Determining how close patches of remnant

prairie should be for successful dispersal and recolonization would also be beneficial. My results highlight the need for further research on how adult *S. idalia* respond to sites that are managed with patch-burning versus sites that are managed exclusively with haying or mowing, which in previous studies have been suggested to be more favorable. Additionally, knowledge of how habitat characteristics important to adult *S. idalia* especially grass, forbs, *Viola* species and woody vegetation respond to different management treatments would be valuable.

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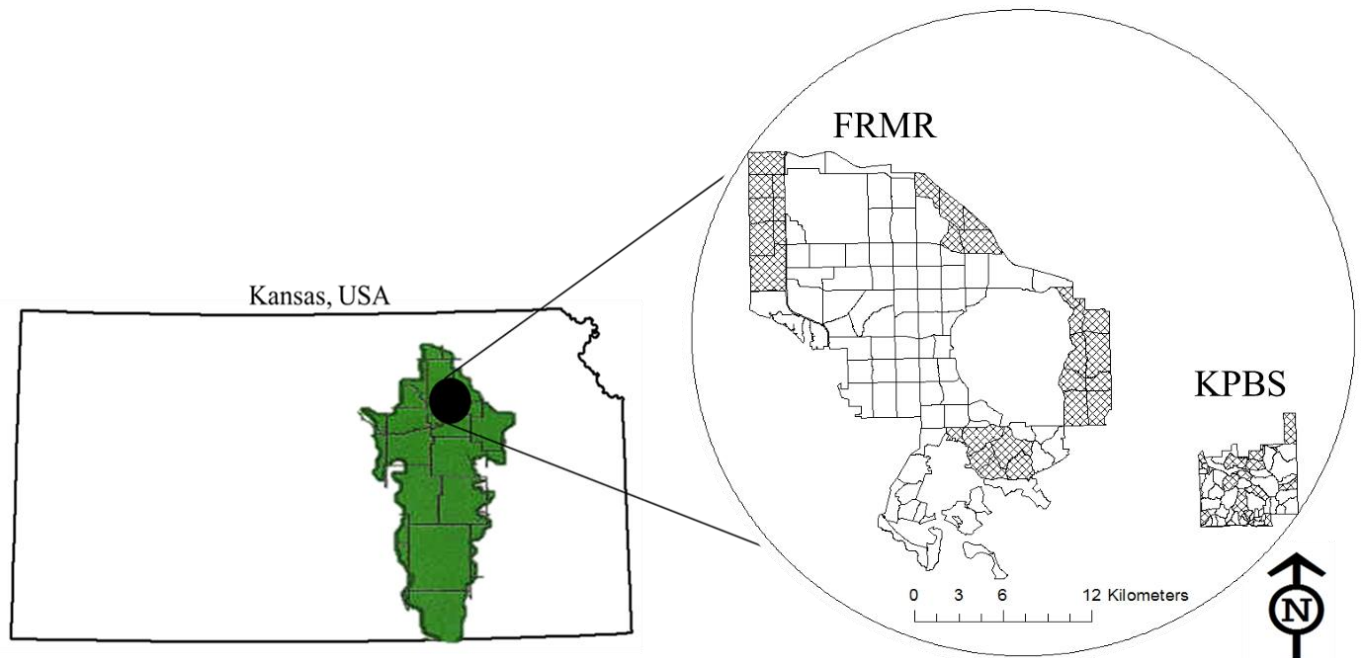


Figure 3.1 The study area for adult *Speyeria idalia* surveys conducted during 2012, 2014-2016. The Flint Hills are marked by the green region spanning across the eastern edge of Kansas, USA, while the black dot within the Flint Hills marks the study area. The Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) are marked within the enlargement of the study area. The cross-hatched sections within the FRMR and KPBS indicate the sites within each where adult survey transects were located.

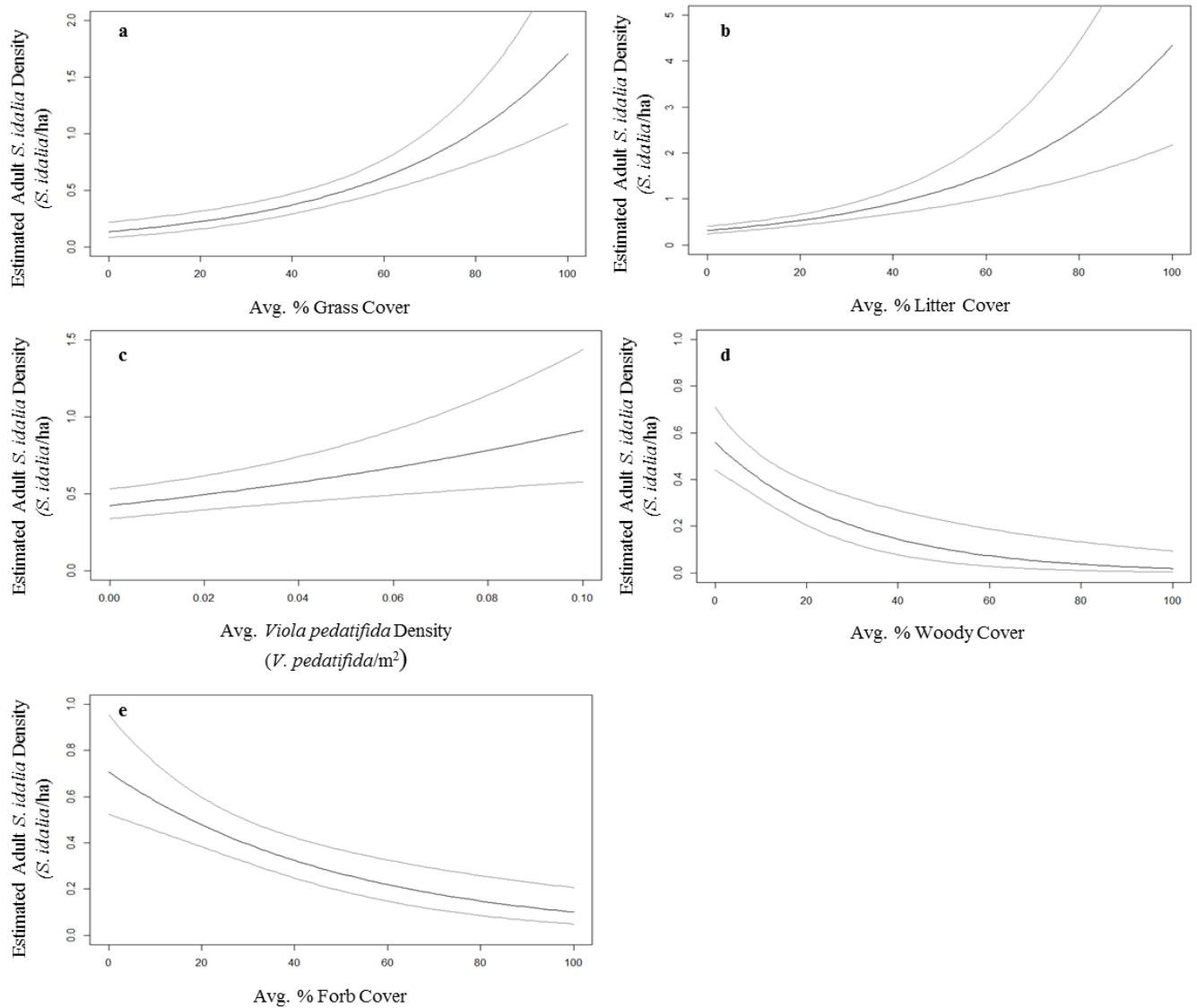


Figure 3.2 Relative influence of the habitat features contained in the top vegetation model on *Speyeria idalia* density. The habitat features were measured using a module-nested plot method every 100-m along adult *S. idalia* survey transects located at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA, 2014 – 2016. All habitat variables were estimated as average percent cover except for *Viola pedatifida*, which was estimated as average density of *V. pedatifida* (*V. pedatifida*/m²). Adult *S. idalia* density was estimated in package Unmarked in R and displayed on the y – axis. The average percent cover of the habitat features for panels a, b, d, and e are displayed on the x –axis. The x-axis on panel c displays the average density of *Viola pedatifida*.

Table 3.1 Number of transects surveyed for adult *Speyeria idalia* and total number of adult *S. idalia* observed each year at the Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA during 2012, 2014–2016.

Year	No. Transects Surveyed		Total No. <i>S. idalia</i>
	FRMR	KPBS	
2012	0	12	80
2014	23	3	142
2015	28	10	274
2016	16	7	36

Table 3.2 The number of transects surveyed in each treatment for adult *Speyeria idalia* at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern, Kansas, USA, 2012, 2014 – 2016. Included in the table is the total area in each treatment group and the total number of *S. idalia* observed in each treatment group.

Treatment	No. Transects	Total Area (ha)	Total No. <i>S. Idalia</i>
Fire High	7	876	34
Fire Moderate	8	1856	116
Fire Low	2	60	2
Grazed + High	4	398	71
Grazed + Moderate	1	135	17
Grazed + Low	1	84	10
Hayed + High	8	2431	58
Hayed + Moderate	12	3063	217
Hayed + Low	1	191	7

Table 3.3 Description of the habitat variables measured in the adult *Speyeria idalia* study at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern, Kansas, USA, 2014 – 2016.

Habitat Variable	Plot Size*	Description
<i>Viola pedatifida</i> Density	100 m ²	Number of <i>V. pedatifida</i>
Tree Cover		% Total woody plant canopy cover greater than 2.5 m in height
Shrub	10 m ²	% Total woody plant cover less than 2.5m in height
Herb Cover	1 m ²	% Total herbaceous plant cover
Forb and Fern Cover		% Total herbaceous plant cover excluding graminoids
Bare Ground Cover		% Total exposed soils and rock cover
Litter Cover		% Total dead vegetative litter cover

*Data were collected within nested vegetation sampling modules every 100-m along transects surveyed for adult *S. idalia*.

Table 3.4 Exploratory models developed in package Unmarked in R evaluating the fit of key detection functions tested (hazard-rate, half-normal, uniform) to candidate models. Models were built to estimate adult *Speyeria idalia* density in northeastern Kansas, USA, at the Fort Riley Military Reserve and Konza Prairie Biological Station during 2012, 2014 –2016. The second-order variant of Akaike’s Information Criterion (AIC_c) was used to rank models.

Model	Detection Function	K	AIC _c	ΔAIC _c	w _i
Fire-Return Interval	Hazard-Rate	5	1675.53	0.00	1
	Half-Normal	4	1706.93	31.40	0
	Uniform	3	1807.24	131.71	0
Management	Hazard-Rate	5	1761.77	0.00	1
	Half-Normal	4	1793.17	31.40	0
	Uniform	3	1893.48	131.71	0
Fire-Return Interval + Management	Hazard-Rate	7	1668.12	0.00	1
	Half-Normal	6	1699.42	31.30	0
	Uniform	5	1799.64	131.51	0
Null	Hazard-Rate	3	1763.00	0.00	1
	Half-Normal	2	1794.49	31.49	0
	Uniform	1	1894.89	131.89	0

The detection function that best fit the data for each candidate set of models is indicated in bold.

K-The number of estimated parameters for each model in the candidate model set.

AIC_c-Second order derivative of Akaike’s Information Criterion that accounts for small sample sizes.

ΔAIC_c .The difference in AICc among models in the candidate set.

w_i-The Akaike weights.

Table 3.5 Density estimates of adult *Speyeria idalia* grouped by fire-return interval (low \geq 10 years, moderate 3-5 years, and high 1-2 years) and management treatment (grazed, hayed, burned) from surveys during 2012, 2014–2016 at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA. Density estimates were calculated using package Unmarked in R. Estimates were weighted by transect length (i.e., survey effort) and accompanied by their respective standard errors (SE) and 95% confidence intervals (95% CI).

Fire-Return Interval + Management	Unmarked Density Estimates		
	Density	SE	95% CI
Fire High	0.41	0.06	0.31 – 0.54
Fire Moderate	0.82	0.10	0.64 – 1.05
Fire Low	0.16	0.04	0.09 – 0.27
Grazed + Fire High	0.55	0.08	0.40 – 0.74
Grazed + Fire Moderate	1.1	0.18	0.80 – 1.51
Grazed + Fire Low	0.21	0.05	0.13 – 0.36
Hayed + Fire High	0.34	0.05	0.25 – 0.46
Hayed + Fire Moderate	0.69	0.09	0.53 – 0.90
Hayed + Fire Low	0.41	0.03	0.08 – 0.22

Table 3.6 Density estimates of adult *Speyeria idalia* grouped by overall management from surveys during 2012, 2014–2016 at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA. Density estimates were calculated using package Unmarked in R. Estimates were weighted by transect length (i.e., survey effort) and accompanied by their respective standard errors (SE) and 95% confidence intervals (95% CI).

Management	Unmarked Density Estimates		
	Density	SE	95% CI
Grazed	0.55	0.08	0.41 – 0.73
Hayed	0.62	0.07	0.49 – 0.79
Burned	0.49	0.06	0.38 – 0.64

Table 3.7 Density estimates of adult *Speyeria idalia* grouped by fire-return interval from surveys during 2012, 2014–2016 at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA. Density estimates were calculated using package Unmarked in R. Estimates were weighted by transect length (i.e., survey effort) and accompanied by their respective standard errors (SE) and 95% confidence intervals (95% CI).

Fire-Return Interval	Unmarked Density Estimates		
	Density	SE	95% CI
High (1-2 years)	0.43	0.06	0.33 – 0.55
Moderate (3-5 years)	0.79	0.09	0.63 – 1.00
Low (≥ 10 years)	0.17	0.04	0.10 – 0.28

Table 3.8 The top ten highest ranking models generated in package Unmarked in R testing the effect of habitat variables measured and their relative influence on adult *Speyeria idalia* density. The habitat variables were collected using a module-nested plot method every 100-m along adult *S. idalia* survey transects located at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern, Kansas, USA, and collected during 2014–2016. Habitat variables considered in models included average percent cover of: grass, forb, woody vegetation, litter, bare ground, and average violet density (*Viola pedatifida*/m²).

Model	K	AIC _c	ΔAIC _c	w _i
Forb+Grass+Woody+Violet+Litter	8	1330.76	0.00	0.98
Forb+Grass+Woody+Litter	7	1338.20	7.44	0.02
Grass+Woody+Violet+Litter	7	1346.72	15.95	0.00
Forb+Grass+Litter+Violet	7	1347.38	16.62	0.00
Grass+Woody+Litter	6	1347.46	16.69	0.00
Forb+Grass+Litter	6	1353.79	23.03	0.00
Forb+Bare+Woody+Violet+Litter	8	1355.71	24.95	0.00
Litter+Grass+Violet	6	1364.55	33.79	0.00
Grass+Litter	5	1364.61	33.85	0.00
Forb+Grass+Woody+Violet	7	1366.26	35.50	0.00

The top model is indicated in bold.

K-The number of estimated parameters for each model in the candidate model set.

AIC_c-Second order derivative of Akaike's Information Criterion that accounts for small sample sizes.

ΔAIC_c-The difference in AICc among models in the candidate set.

w_i-The Akaike weights.

Table 3.9 Interaction between the presence of adult *Speyeria idalia* and habitat variables grouped by fire-return interval (low ≥ 10 years, moderate 3-5 years, and high 1-2 years) and overall management (grazed, hayed, and burned). Habitat variables were recorded in module-nested plots every 100-m along adult *S. idalia* survey transects located at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern, Kansas, USA, during 2014–2016. Bare ground, grass, forbs, litter, and woody vegetation were estimated in plots as average percent cover while *Viola pedatifida* was estimated as average *V. pedatifida* density (*V. pedatifida*/m²).

Habitat Variable	<i>S. idalia</i> *Fire-Return Interval		<i>S. idalia</i> *Management	
	F _{2,79}	P	F _{2,79}	P
Avg. % Bare Ground	0.12	0.89	1.45	0.24
Avg. % Forb	1.31	0.28	0.65	0.53
Avg. % Grass	2.74	0.07	0.43	0.65
Avg. % Litter	0.47	0.63	0.31	0.74
Avg. % Woody	0.59	0.56	4.15	0.02
Avg. <i>Viola pedatifida</i> density (<i>V. pedatifida</i> /m ²)	0.30	0.74	1.20	0.31

*S. idalia**Fire-Return Interval-Analysis of variance results testing the interaction of adult *S. idalia* presence and habitat variables grouped by fire-return interval.
*S. idalia**Management-Analysis of variance results testing the interaction of adult *S. idalia* presence and habitat variables grouped by management.

Table 3.10 Mean and standard errors of habitat variables along transects with and without adult *Speyeria idalia*. Included are results from the factorial analysis of variance testing the occupancy of *Speyeria idalia* against habitat variables grouped by fire-return interval (low ≥ 10 years, moderate 3-5 years, and high 1-2 years) and overall management (grazed, hayed, and burned). Habitat variables were measured every 100-m along adult *S. idalia* transects located at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA, during 2014-2016. Habitat variables were estimated using a module-nested plot method. Bare ground, grass, forbs, litter, and woody vegetation were estimated in plots as average percent cover while *Viola pedatifida* was estimated as average *V. pedatifida* density (*V. pedatifida*/m²).

Habitat Variable	<i>S. idalia</i> Occupancy ¹		<i>F</i> ² _{1,79}	<i>P</i>	<i>F</i> ³ _{1,79}	<i>P</i>
	0	1				
Avg. % Bare Ground	19.5 (2.47)	14.9 (1.23)	5.01	0.03	2.54	0.12
Avg. % Forb	19.4 (2.45)	24.2 (1.86)	9.31	0.75	0.86	0.36
Avg. % Grass	44.1 (2.97)	49.1 (1.94)	0.34	0.56	1.84	0.18
Avg. % Woody	6.06 (1.52)	6.41 (1.09)	0.08	0.78	0.72	0.40
Avg. % Litter	11.28 (1.89)	14.48 (1.50)	0.49	0.49	0.25	0.62
Avg. <i>Viola pedatifida</i> Density (<i>V.pedatifida</i> /m ²)	0.0026 (0.0010)	0.010 (0.0024)	3.25	0.08	4.13	0.05

Habitat variables that differed significantly among transects with and without adult *S. idalia* are indicated in bold.

¹0-Mean of habitat variable along transects without adult *S. idalia* with standard error in parenthesis; 1-Mean of habitat variable along transects with adult *S. idalia* with standard error in parenthesis.

²Results from the factorial analysis of variance testing adult *S. idalia* occupancy against habitat variables grouped by fire-return interval.

³Results from the factorial analysis of variance testing adult *S. idalia* occupancy against habitat variables grouped by overall management.

Table 3.11 Mean and standard error (SE) of the habitat variables collected along adult *Speyeria idalia* survey transects at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA, 2014 – 2016. Habitat variables were measured using a module-nested plot method every 100-m along adult *S. idalia* transects. Habitat variables were estimated as average percent cover for bare ground, forb, litter, grass and woody vegetation. *Viola pedatifida* were measured as average *V. pedatifida* density (*V. pedatifida*/m²). Habitat variables are grouped by their mean percent cover/density in each management treatment (grazed, hayed, and burned).

Variable	$F_{2,79}$	P	Grazed		Hayed		Burned	
			Mean	SE	Mean	SE	Mean	SE
Avg. <i>Viola pedatifida</i> Density	0.20	0.82	0.017 ^A	0.0097	0.009 ^A	0.0021	0.005 ^A	0.0021
Avg. % Woody	5.94	0.004	16.18^A	5.34	3.58^B	0.45	7.74^A	1.50
Avg. % Bare Ground	0.27	0.76	21.86 ^A	3.62	15.42 ^A	1.32	15.28 ^A	2.33
Avg. % Forb	1.61	0.21	27.44 ^A	4.38	20.62 ^A	2.16	25.66 ^A	2.27
Avg. % Litter	1.59	0.21	11.30 ^A	1.93	15.59 ^A	1.78	10.87 ^A	1.89
Avg. % Grass	1.10	0.34	37.18 ^A	5.32	49.38 ^A	2.04	48.75 ^A	2.92

Habitat variables that differed significantly between overall management treatments are indicated in bold.

^{A,B}Habitat variables with means that have the same capital letter (A or B) as a superscript indicate the means did not differ for that variable among overall management treatments. Habitat variables that have different capital letter superscripts indicate that the means differed between that habitat variable and overall management.

Table 3.12 Mean and standard error (SE) of the habitat variables collected along adult *Speyeria idalia* survey transects at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA, 2014 – 2016. Habitat variables were measured using a module-nested plot method every 100-m along adult *S. idalia* transects. Habitat variables were estimated as average percent cover for bare ground, forb, litter, grass and woody vegetation. *Viola pedatifida* were measured as average *V. pedatifida* density (*V. pedatifida*/m²). Habitat variables are grouped by their mean percent cover/density in each fire-return interval (low, moderate, and high).

Variable	$F_{2,79}$	P	Low (≥ 10 years)		Moderate (3 – 5 years)		High (1 – 2 years)	
			Mean	SE	Mean	SE	Mean	SE
<i>Viola pedatifida</i> Density	0.12	0.89	0.0032 ^A	0.004	0.0083 ^A	0.002	0.0075 ^A	0.003
Avg. % Woody	22.35	<0.01	22.12^A	5.84	4.69^B	0.63	4.23^B	0.51
Avg. % Bare Ground	0.42	0.655	15.86 ^A	3.45	14.68 ^A	1.59	18.14 ^A	1.81
Avg. % Forb	8.98	0.01	23.95^B	3.66	17.94^B	1.84	29.56^A	2.60
Avg. % Litter	6.59	0.002	24.16^A	4.61	13.93^A	1.70	10.36^A	1.50
Avg. % Grass	3.85	0.025	35.45^B	4.74	53.07^A	2.13	43.94^B	2.43

Habitat variables that differed among managements are indicated in bold.

^{A,B}Habitat variables with means that have the same capital letter (A or B) as a superscript indicate the means did not differ for that variable among fire-return intervals. Habitat variables that have different capital letter superscripts indicate that the means differed between that habitat variable and fire-return interval.

Appendix A - Fire Adaptations, Larval Feeding Behavior and Host Plant Use in the Regal Fritillary Butterfly (*Speyeria idalia*): Novel Observations from the Central Great Plains

Introduction

The regal fritillary, *Speyeria idalia* (Drury, 1773) (Nymphalidae), is a large univoltine and non-migratory butterfly. Adult *S. idalia* flight begins with the emergence of males in late May and continues through September when females begin to oviposit (Klots 1951, Tilden and Smith 1986, Wagner et al. 1997). *S. idalia* mate shortly after they emerge in late May – early June, however, females postpone oviposition until late August to early September (Scott 1986, Wagner et al. 1997, Zercher et al. 2002). Oviposition site selection appears to be somewhat casual with eggs deposited near, but rarely on the host plants themselves (Scott 1986, Kopper et al. 2000, Swengel and Swengel 2001). Because most host plant species are senesced when females begin oviposition it is generally suspected that they cue on factors other than the presence of host plants when determining oviposition locations (Wagner et al. 1997, Kopper et al. 2000).

After oviposition, *S. idalia* eggs hatch in approximately 25 days and the 1st instar larvae emerge, consume the chorion, and enter a winter larval diapause. Larval development resumes in early spring with the emergence of host plants. There are six larval instars followed by a pupal stage that lasts 2.5 to 4 weeks (Edwards 1879, Hammond 1974, Wagner et al. 1997). Throughout their life cycle, all *S. idalia* larvae are oligophagous and feed on a variety of violet (*Viola* spp.) host plant species (Klots 1951, Hammond 1974, Ferris and Brown 1981). Local populations are often associated with specific violet species and larvae in the central Great Plains are reported to preferentially feed on birdfoot (*V. pedata*) or prairie violet (*V. pedatifida*) (Swengel 1997, Kelly and Debinski 1998, Dole 2004).

The historic range of this once abundant butterfly of North American prairie communities extended from Oklahoma to the border of Canada and east to the Atlantic coast. Despite its once broad geographic distribution, populations have declined by approximately 99%. Both eastern and western populations have experienced dramatic declines and *S. idalia* are nearly extirpated from the eastern portion of their former range (NatureServe 2005). However, there are some locally abundant populations in the west and the species is considered stable in Kansas (Ely et al. 1986, Marrone 2002). *S. idalia* was listed as a Category II species under the United States Endangered Species Act (ESA) until this category was removed in 1996 (U.S. Fish and Wildlife Service 1996). The rapid, range-wide declines of this species prompted the U.S. Fish and Wildlife Service to initiate a status review of *S. idalia* under the ESA in September 2015.

While the direct causes of local population declines of *S. idalia* are unclear it appears their decline is a result of habitat loss and fragmentation along with inappropriate land management practices such as heavy grazing, frequent and intensive burning, and haying (Schultz and Crone 1998, Davies et al. 2005, Ferster and Vulinec 2010). It is estimated that the Great Plains region has lost 70% of its grasslands, with tallgrass prairie in the Flint Hills of Kansas retaining as little as 37% of the historic extent (Samson et al. 2004). Native tall-grass prairie communities have succumbed to anthropogenic land conversion, development, invasive weeds, and plant succession (Samson and Knopf 1996). Historically, unrestricted grazing by herbivores and wildfire played important roles in the maintenance of prairie ecosystems in the Great Plains (Fuhlendorf and Engle 2001). However, in the absence of these ecological drivers, remnant tracts of prairie that remain are often maintained by prescribed land management (Vogl 1974, Shuey 1997). Prescribed fire is considered one of the primary tools used to maintain the openness of grasslands by controlling invasive species and woody encroachment (Sauer 1950,

Stewart 1956, Vogl 1974, Nuzzo 1986). Prescribed management is crucial to maintaining grassland ecosystems and a lack of management can threaten the persistence of remaining prairie remnants along with *S. idalia* populations (Vogl 1974, Shuey 1997).

The effect of fire on prairie insects is a contentious subject. Several studies suggest that prescribed fire benefits many prairie specialist butterflies (Selby 2007) while others argue that it is harmful (Swengel 1996, 2001, 2004; Swengel and Swengel 2001). It is thought that regular extensive burning likely depresses prairie specialist butterfly populations (Swengel 1996, 2004; Swengel and Swengel 2001, among others). In particular, *S. idalia* literature often reports that fires reduce or even eliminate the species from sites by directly or indirectly killing larvae (Kelly and Debinski 1998, Swengel and Swengel 2001, Powell et al. 2007, among others). Therefore, management recommendations for populations of *S. idalia* suggest greater reliance on alternative management such as mowing, haying, light grazing, and the implementation of permanent non-fire refugia (Schlicht and Orwig 1992, Swengel 1996, Schlicht 2001, among others).

The uncertainty of the effects of fire on *S. idalia* populations is likely facilitated by the lack of information on the immature stages. *S. idalia* larvae are inconspicuous and cryptic, making them difficult to locate in the field (Scudder 1889, TNC 2001, Kopper et al. 2001, Debinski pers. com). The challenges associated with detecting *S. idalia* larvae have limited our ability to study this ambiguous and precarious life history stage. Consequently, assessments of habitat quality are often measured as the habitat features and resources associated with the presence and abundance of adults (Britten and Riley 1994, Smallidge et al. 1996, Grundel et al. 2000, Collinge et al. 2003). However, adult mobility can confound assessments of how a management practice affects presence and abundance (Swengel 1996). Adults can readily move in or out of areas as resources and conditions change. In contrast, larvae are restricted to the area

and microhabitat in which they hatched; thus, habitat features and resources used by adults may not reflect the requirements of the immature stages (Bergman 1999, Lane and Andow 2003, Albanese et al. 2008).

The goal of my study was to investigate the effects of management practices and habitat features on the presence and abundance of *S. idalia* larvae and adults. During the course of this study, I made several novel observations of late-instar larvae and post-diapause females. The observations I present and discuss here include: a distinct and reliable feeding sign exhibited by late-instar larvae, the use of an alternative host species *V. sororia* by post-diapause females and late-instar larvae, cathemeral larval activity, and finally the observation of numerous late-instar larvae in sites that had been recently burned. The findings I present in this paper provide insight to *S. idalia* ecology and behavior that contribute to our understanding and conservation efforts of populations of this imperiled species.

Methods

Study Area

I conducted field and laboratory studies from 2014 through 2015 at the Fort Riley Military Reserve (FRMR) and the Konza Prairie Biological Station (KPBS), in Geary and Riley counties within northeastern Kansas, USA. Both sites are nested within the Flint Hills, which is characterized by rolling hills stretching from Kansas to Oklahoma, rocky soil, and large tracts of tall-grass prairie (Anderson and Fly 1955, Reichman 1987).

Late-Instar Larvae Surveys

Late-instar larvae surveys were conducted in April and May during 2014 and 2015. The 8 larval survey plots were stratified by management regime (fire, grazing, and haying), and fire-return interval (low ≥ 10 years, moderate 3-5 years, and high 1-2 years). Five of the larval

survey plots were located at the FRMR and three were located at the KPBS. Each larval survey plot was 2500-m² and partitioned into grids of 100-m² sub-plots. The 100-m² sub-plots included a gradient of violet density. I randomly selected 15 100-m² sub-plots to be searched in each of the 10 2500-m² larval survey plots. I searched for late-instar larvae or their feeding sign in each of the 100-m² subplots by systematically examining each host plant located within the plot. Additionally, I examined the surrounding vegetation and litter in search of larvae. I use the terms early-and late-instar larvae to describe larvae when the exact instar was not determined. Relative to the six larval instars of *S. idalia*, early-instar refers to first through third instar and late instar refers to fourth through sixth instar.

Surveys for ovipositing females were conducted from late August to early October during 2014 and 2015. I surveyed 44 transects for ovipositing females. Each transect was at least 500 m to >1 km in length and stratified by management regime (fire, grazing, and haying), violet density, and fire-return interval (low, moderate, and high). I surveyed the standardized transects using a repeated modified Pollard walk method when weather conditions were appropriate for adult flight. The observer ceased the Pollard walk when a ovipositioning female was located and followed the female recording all oviposition locations.

Results

Larvae and Fire

I surveyed a total of 208 100-m² subplots for late-instar *S. idalia* larvae and their feeding sign during this study. Among the 208 plots surveyed, 46 were located in sites that had undergone a spring management burn. I detected late-instar larvae or their feeding sign in 10 (22%) of the 100-m² subplots that were located in the areas that had undergone spring management burns. A total of 20 late-instar *S. idalia* larvae were detected during this study.

Eleven (55%) of the larvae were observed in areas that had been burned ≤ 61 days prior to the detection. Six of these larvae were observed at the FRMR and five at the KPBS study sites.

Larvae Feeding Behavior

I collected a total of five *S. idalia* larvae from the field for observations. In 2014, I collected two late-instar *S. idalia* larvae on 19 April and a third on 19 May. In 2015, I collected two late-instar *S. idalia* larvae on 19 April. The larvae were reared on both *V. pedatifida* and *V. sororia* leaves. All five larvae produced a unique strip-style feeding sign on both host plant species. The larvae defoliated stems by consuming the leaves of host plant species in a “typewriter” fashion, feeding back and forth on a single leaf until all that remained was a small portion of the leaf and the stem (Figure A1). When larvae were not feeding, they spent most of their time resting either in the curls of dead vegetation provided or at the bottom of the enclosure near the base of vegetation. Contrary to previous reports, larvae were active during both day and night. This feeding behavior and combination of both diurnal and nocturnal activity was not unique to lab-reared larvae. Late-instar *S. idalia* larvae produced a distinctive and detectable feeding sign on host plants, and exhibited cathemerality in the field. I observed 17 larvae during daylight, two during twilight and one during night. These larvae displayed behaviors from actively feeding to resting. Feeding sign observed in the field was similar to that of captive-reared larvae. Late-instar larvae in the field defoliated host plants by stripping away and consuming the leaves, leaving only the stem of the host plant (Figure A2). This strip-style feeding sign was detected in each of the 100-m² sub-plots where larvae were found.

S. idalia* and *V. sororia

Among the 8 2500-m² larval survey plots, four contained both *V. pedatifida* and *V. sororia*, and one plot contained only *V. sororia*. Late-instar *S. idalia* feeding sign and larvae

were detected on *V. sororia* at three of these sites. The feeding sign exhibited on *V. sororia* plants resembled that of the feeding sign on *V. pedatifida* and was typical of late-instar *S. idalia* larvae (Figure A3). Additionally, I observed three post-diapause females oviposit in proximity to *V. sororia* during oviposition surveys (Figure A4). All females flew low to the ground and frequently dropped down into the vegetation. Upon landing, females maneuvered through the vegetation, tasting with their feet, and dragging their abdomens probing various substrates in search of oviposition sites. Eggs were deposited on the underside of dead vegetation or detritus near *V. sororia* plants. In two out of the three observations, the only host plant species within $\geq 2500\text{-m}^2$ of the oviposition site was *V. sororia*.

Conclusions

Previous studies conducted on *S. idalia* larvae have resulted in very small sample sizes (Barton 1995, $n=9$; Kopper et al. 2001, $n=12$; TNC 2000, 2001 $n=0$). The unique feeding sign I observed was a reliable sign of the presence of late-instar larvae and greatly improved my ability to detect this species within patches of *V. pedatifida* and *V. sororia*. Although it is known that *S. idalia* larvae are able to feed on a variety of *Viola* host plants direct field observations of feeding on *V. sororia* is not well documented for this region. Additionally, the selection of oviposition sites by adult females near *V. sororia* further stresses its potential importance and influence on *S. idalia* ecology and behavior. Among *Viola* species in the United States *V. sororia* is arguably the most common and is often considered a weed (Solbrig et al. 1980). While invasive, weedy species are often detrimental to Lepidoptera the spread of such plants are not always entirely damaging (Ferge 2008). The wild indigo duskywing (*Erynnis batisiae*) has been reported to switch from its native host plant, wild indigo (*Baptisia* spp.) to the invasive crown vetch (*Securigera varia*) (Opler and Malikul 1992). Consequently, *E. batisiae* is expanding its once

restricted range by utilizing *S. varia* along roadways and railroads (Ferge 2008). As global climate change, invasive species spread, and habitat loss and fragmentation continue to strain the persistence of native prairie fauna, more generalist species are certain to become more common. Thus, perhaps the use of *V. sororia*, a more generalist species of *Viola* than *V. pedatifida* by *S. idalia* is in response to *V. sororia*'s increasing availability throughout this region.

Adult *S. idalia* have been reported to be negatively affected by fire (Swengel 1996, Powell et al. 2007). However, these previous conservation recommendations were made based on research of the response of adult populations to fire, with the assumption that fire was fatal to *S. idalia* larvae (Royer pers. com. Cited in Moffat & McPhillips 1993, Kelly & Debinski 1998, Swengel 1998, Huebschman & Bragg 2000, among others). The response of many species particularly invertebrates, to fire is complex and inconsistent and driven by a number of different factors (Warchola et al. 2015). For instance, studies conducted on the Fender's blue butterfly (*Icaricia icarioides fenderi*) have shown that fire increases ant-tending of larvae and this mutualistic relationship actually increased larval survival in the year following the burn (Warchola et al. 2015). Additionally, studies have demonstrated that semi-fossorial behavior can facilitate the evasion of fire by larvae. Research conducted on the atala hairstreak (*Eumaeus atala*) and the frosted elfin (*Callophrys irus*), two species commonly faced with fire during the immatures stages were both found to survive fire when they were at least 1.75 cm below the surface (Thom et al. 2015). Our detection of late-instar *S. idalia* larvae at recently burned sites directly contradict this assumption about this species' ability to survive fire. Therefore, I hypothesize that *S. idalia* larvae have developed either physiological or behavioral mechanisms or perhaps a combination of both that facilitate their survival of low to moderate intensity surface fires. While in my study I did not observe any associations of *S. idalia* larvae with ants I did

observe larvae resting in dense ground cover and even underneath rocks. Perhaps the heat put off by the fire triggers a responsive behavior in *S. idalia* larvae to seek refuge under structures or even underground during fires. While semi-fossorial behavior may be one possible explanation for how *S. idalia* larvae evade direct mortality due to the burns the exact mechanisms *S. idalia* larvae employ to endure fire are still unclear.

If we want to understand and conserve populations of *S. idalia* and other rare Lepidoptera, their behavior and ecology at all life history stages must be investigated. The ready use of any *Viola* host plant species available and the numerous larvae found in sites shortly after burns suggest a dynamic relationship between *S. idalia* and their environment. Throughout prehistory *S. idalia* and their larval host plant have evolved in the Flint Hills with processes such as fire which have been a part of the legacy of this region for millennium. The ability of larvae to withstand fire supports the idea that this species has evolved with fire as a primary selective force and indicates that the relationship between fire and *S. idalia* larvae is not as simple as previously thought. The observation of *S. idalia* larvae shortly after a fire was previously undescribed and highlights the need for additional research directed at this life history stage. Furthermore, *S. idalia* conservation efforts would benefit from a mechanistic understanding of how larvae survive fire. Additionally, the documentation of a distinctive feeding sign exhibited by late-instar *S. idalia* larvae is not described in the literature and provides a unique tool that can facilitate the location of larvae and research on the cryptic immature stages of *S. idalia*. Although, the use of *V. sororia* by *S. idalia* has been documented it is often described as secondary to *V. pedatifida* in this region. However, in the face of stresses such as global climate change and the continued loss and fragmentation of prairie habitat the use of *V. pedatifida*, a prairie-obligate species may give way to increased use of *V. sororia*, which is a more common

generalist species of *Viola*. Therefore, widespread documentation of host plant species use and feeding sign exhibited by *S. idalia* larvae on host plants throughout *S. idalia*'s range would be informative. Moreover, laboratory experiments examining tradeoffs or consequences to the use of one host species over another would also provide valuable insight. Given the conservation concern for *S. idalia* throughout its range, our observations provide valuable knowledge to the life history of the species, which may facilitate future research and conservation management efforts directed towards populations of *S. idalia*, especially at the precarious larval stages.

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Figure A.1 Late-instar *Speyeria idalia* larva feeding on *Viola pedatifida* leaves in the Flint Hills of northeastern, Kansas, USA, 2015.



Figure A.2 Characteristic feeding sign exhibited by late-instar *Speyeria idalia* larvae on *Viola pedatifida* in the Flint Hills of northeastern Kansas, USA, 2014-2015. On the left is a *V. pedatifida* before being consumed and on the right is what remains of *V. pedatifida* after a late-instar larva strips away the leaves and leaves only a small portion of leaf and stem.



Figure A.3 Late-instar *Speyeria idalia* larva beginning to feed on the leaves of *Viola sororia* in the Flint Hills of northeastern, Kansas, USA, 2015.



Figure A.4 Adult *Speyeria idalia* female dragging her abdomen and probing various substrates in search of oviposition locations in the Flint Hills of northeastern, Kansas, USA, 2014. The broad-leaf plant in the picture is *Viola sororia*.