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DISTRIBUTION AND HABITAT ASSOCIATIONS OF THE GEORGIA SATYR (*NEONYMPHA*  
*AREOLATUS*) IN ARKANSAS

A Thesis Submitted  
to the Graduate College  
Arkansas Tech University

in partial fulfillment of requirements  
for the degree of

MASTER OF SCIENCE

in Fisheries and Wildlife

Department of Biological Sciences  
College of Science, Technology, Engineering, and Mathematics

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## Abstract

The Georgia satyr (*Neonympha areolatus*) is a small sedentary butterfly that is rare in Arkansas. Currently, the exact locations of this butterfly in Arkansas are unknown, along with the habitat characteristics associated with their presence. In order to determine these unknowns, I completed 104 surveys across seven different wildlife management areas in southern Arkansas. Pollard-Yates transects were conducted at each study site, and weather variables were recorded before each survey. Vegetation surveys were also completed at each site, and where each Georgia satyr was identified. Generalized linear models (GLM) were created to identify what parameters are important for determining the presence or absence of this butterfly. It was found that grasses, forbs, sedges, flowers, canopy cover, and burn history were important for determining the butterfly's presence, while cloud cover was important for detecting the butterfly. These results suggest that sedges and/or grasses are probable host plants for this butterfly, and that not only does this butterfly likely not nectar as an adult, but that nectar sources may increase interspecific competition. A Maxent model was also created using the location data collected along with climate data and various land data. Elevation and dominant soil drainage were determined to be the most influential factors. The resulting map identified the potential distribution of the satyr. This map, combined with the variables identified as important for determining presence, narrow the scope for future surveys.

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## I. Introduction

Habitat loss is commonly regarded as the main cause of the overall loss of biodiversity worldwide. Habitat loss can contribute to a species becoming endangered, and then continue to impede and limit any recovery efforts (Kerr and Deguise 2004). Degradation, fragmentation, and modification of habitats also contribute to species loss worldwide (Fischer and Lindenmayer 2007, Wallisdevries et al. 2012). One taxon that is affected by habitat alteration is butterflies (Polus et al. 2007, Forister et al. 2010, Choudhary and Chishty 2020). If a habitat is managed properly, threatened butterfly species could increase and population fluctuations could be minimized (Bergman 2001). Tracking population numbers could also illuminate any changes in their habitat quality, aiding in the management of the habitat (Schulz et al. 2020). Successfully connecting isolated populations to increase movement among patches can also help to counterbalance population declines that occur due to habitat fragmentation (Haddad and Baum 1999, Haddad and Tewksbury 2005, Wells et al. 2009, Milko et al. 2012).

One butterfly species of interest is the Georgia satyr (*Neonympha areolatus*; hereafter “the satyr”). The satyr’s range extends from Texas, all along the southern coastal states, and up into New Jersey (BAMONA 2021). While the satyr is not currently believed to be threatened (BAMONA 2021), this species is rare in Arkansas (Raney 2017), and proactive management of their habitat and other conservation efforts would be more cost-efficient than trying to recover the species if they become threatened in the future (Drechsler et al. 2011). While this species is not endemic to Arkansas (BAMONA 2021), butterflies are important to their ecosystems, acting as food sources, pollinators, and environmental indicators (Ghazanfar et al. 2016). Butterflies also have great

aesthetic, educational, economic, and health values to humans (Butterfly Conservation n.d.).

### **Georgia Satyr in Arkansas**

Records dating back to 1758 show that at least 1,891 species of Lepidoptera from 57 families have been documented in Arkansas (Lovely and Ettman 2013, Arkansas Lepidoptera 2018, BAMONA 2021). In the present day, 159 butterfly species from nine families have been recorded throughout the state. These species vary in their abundance, regions of occurrence, flight months, and the number of host plants. Of the 159 species, 24 are regarded as rare, with 13 being “highly fluctuant local species,” (Raney 2017). One of the nonlocal, rare species found in Arkansas is the Georgia satyr which is part of the family Nymphalidae and subfamily Satyrinae. Historically this butterfly has been identified in southern Arkansas, but there are currently no detailed records. Furthermore, while the life history, flight, and habitat have been informally documented, the caterpillar host is only assumed to be a sedge or grass (Robinson et al. 2010, Florida Native Plant Society 2018, BAMONA 2021), and the adult food of the butterflies is unknown. Conservation efforts are also noted to not usually be necessary, but the habitat of the butterfly may need to be managed with prescribed burnings (BAMONA 2021).

### **Habitat characteristics**

Adult butterfly populations tend to be found in areas with ample amounts of their larval food or host plant (Krauss et al. 2004, Grundel and Pavlovic 2007, Bried and Pellet 2012, Gompert et al. 2014, Schulz et al. 2020, Shepard et al. 2021). Though the host plant for the satyr has not been scientifically determined several sources have suggested what the host plant could be. The Butterflies and Moths of North America project (BAMONA)

(2021) identifies the host plant as sedges or grasses. Concurrently, the Florida Native Plant Society Broward Chapter (2018) identifies the host plant as *Cyperus planifolius* or flatleaf flatsedge. These host plant assumptions are reasonable since the order Poales, which contains sedges and grasses, is the primary host plant for the subfamily Satyrinae (Ferrer-Paris et al. 2013), and Satyrinae species have minimal variation in host plant usage (Janz et al. 2006). In contrast, HOSTS, a Database of the World's Lepidopteran Hostplants, specifically identifies the host plant as being from the genus *Digitaria* (Robinson et al. 2010). Currently, host plants under this genus have not been identified for any other butterflies under the subfamily Satyrinae or family Nymphalidae (Ferrer-Paris et al. 2013).

Beyond the host plant, butterfly populations may be associated with other habitat characteristics. These characteristics include nectar sources (Dennis 2004), sites used for safety from predators and the elements, resting locations, and mate location (Hanski et al. 2000). By determining the vegetation associated with selected habitat, areas of highest management concern can be established, and the effects of habitat changes can be predicted (Warren 1985). To ascertain the vegetation associated with occupancy, quantitative samplings are typically done. The sites selected for these samplings generally include occupied sites, previously occupied sites, and other areas that seem suitable based on the habitat (Warren 1985, Buckland et al. 2001). Establishing exactly which plants are used for which of the previously mentioned reasons requires more detailed observations (Hanski et al. 2000), and while making these establishments was not the aim of this study, knowing what vegetation is associated with the preferred habitat of this butterfly will pave the way for future research to do so.

The current literature on the satyr states that its preferred habitat in southern Arkansas is grassy, open pine woods (Rouse 1968). One area of pine flatwoods found in southern Arkansas is the Moro Big Pine Natural Area-Wildlife Management Area (MBPNA), which encompasses around 16,000 acres (Bragg et al. 2014). Surveys in August of 2021 completed by the Arkansas Natural Heritage Commission (ANHC) identified the satyr at three different locations the MBPNA in Calhoun County and along a roadside habitat north of Hampton, Arkansas. In congruence with the host plant suggestions previously discussed, one species of crabgrass, *Digitaria ischaemum*, has been identified in the MBPNA in Howard County, Arkansas. Furthermore, while flatleaf flatsedge has not been identified, *Cyperus sp.* has been identified in the MBPNA in both Howard County and Calhoun County along with two other species of sedges. The entire MBPNA also has a diverse array of many different species of grasses (The Nature Conservancy 2009).

### **Metapopulation**

Within habitats, the spatial distribution of species is generally influenced by an overall lack of homogeneously distributed resources (Singer and Thomas 1996). This lack of resource homogeneity can create patches within habitats that can be distinguished by their usability (McNamara 1982). Within these patchy habitats, spatial distribution is generally determined by behavioral decisions and population dynamics (Hanski and Gaggiotti 2004). For insects, the availability of host plants is one of the main drivers of patchiness and in turn distribution (Singer and Wee 2005). If the insects have multiple host plants that are available to them in a habitat patch or in close habitat patches, resource preferences, or behavioral decisions, will most likely determine distribution. In

comparison, if different host plants occur in separate, distant patches, insects will typically only encounter the host plant(s) of one patch. Distribution will thus tend to be determined by population success in the individual patches and migration, or population dynamics. Most species' distribution within habitats will be influenced by both factors. When population dynamics are the more influential factor, metapopulations can be observed (Hanski and Gaggiotti 2004).

Metapopulations are defined by multiple subpopulations within a habitat where migration occurs between suitable habitat patches (Levins 1969, Nowicki et al. 2008). If habitat patches are close enough and large enough, recolonizations of empty patches can counterbalance extinction rates, allowing a species to persist in an area, even if every subpopulation is at risk of extinction (Inchausti and Halley 2003). Based on the current observations of multiple small, discrete populations of the satyr in the pine flatwoods of southern Arkansas, this species may have a metapopulation structure in the MBPNA area. Such a structure could explain how this rare butterfly can persist in the area, despite the secluded populations, which increases the risk of extinction due to factors like inbreeding (Fahrig and Merriam 1985, Nieminen et al. 2001) and stochastic events or effects (Frankham 1998, Dennis et al. 2010). Furthermore, if this butterfly does exist in a metapopulation structure, management practices to reflect this structure could be enacted that focus on improving colonization rates and improving the quality and/or size of patches (Hanski et al. 1996).

### **Prescribed burns**

Butterflies tend to be especially vulnerable to fire when they are in the eggs or larvae stage due to their limited mobility (Kral et al. 2017, Jue et al. 2022), and it is

recommended that fires during these stages be avoided (Jue et al. 2022). Population recovery times post-fire can also differ based on the habitat and the population densities prior to the fire (Vogel et al. 2010). Grassland butterflies have been found to need typically between three and five years (Swengel 1996, Vogel et al. 2010), and the *Callophrys irus*, which inhabits longleaf pine forests, has been shown to need three to four years to recover (Jue et al. 2022). In contrast, multiple butterfly species found in a ponderosa pine and Gambel oak forest were observed having two to three times greater abundance just one year after burning and thinning treatments (Waltz and Covington 2004). For southern pines, prescribed burns are typically in two to four-year burn cycles (Sharma et al. 20202), which could allow for the satyr populations to recover much like the previously discussed species. However, if this population is only found at very low densities as it is a rare species, more time might be required for post-burn recovery. As stated previously, the habitat of the satyr may need to be managed with prescribed burnings (BAMONA 2021). Because fire can be deadly to butterflies, fire regimes must be catered to each species and environment in order to maximize the long-term habitat benefits and minimize the short-term population reductions (Warchola et al. 2018).

### **Justification**

The Georgia satyr is an under-studied species of butterfly found in Arkansas. This species is rare in Arkansas, and it may be threatened by habitat loss, pesticide usage, and certain management practices. In order to aid and manage this butterfly, its range in Arkansas along with that habitat characteristics it is associated with must be determined. This study will help identify where this butterfly occurs in Arkansas, as well as identify habitat associations to aid in further studies and searches for this butterfly.

### *Objectives*

1. To establish the current locations of the satyr in Arkansas.
2. To determine which habitat characteristics increase presence probability.
3. To describe the general behavior of the butterfly, including, but not limited to, flight patterns, landing locations, and flying seasons.



## **II. Methods**

### **Study Sites**

The satyr has been identified in recent years in the MBPNA and the Kingsland Prairie Preserve. Historically, the butterfly has been recorded in the following Arkansas counties: Bradley, Calhoun, Dallas, Drew, Lafayette, Miller, Nevada, and Ouachita. Within these known areas, this study focused on the MBPNA, Casey Jones Wildlife Management Area (WMA), Longview Saline Natural Area WMA, Kingsland Prairie Preserve, Big Timber WMA and Warren Prairie Natural Area (Warren Prairie), with special care given to searching Warren Prairie as the species was present there in recent years (S. Scheiman, pers. comm). To determine surveying locations, in the months leading up to the field season, preliminary field-based searches of the habitats were completed along with the use of topographic maps to identify potentially suitable sites within these areas. These suitable sites were identified based on the presence of open pine flatwoods. Among the suitable sites identified in each WMA, sites were randomly chosen, with the number of sites relating to the amount of suitable habitat within the WMA (Figure 1).

### **Surveys**

Sites were surveyed during May, August, and September 2022. These dates were based on sightings in Hampton, Arkansas (S. Scheiman, pers. comm). For butterflies in general, the ideal time for detecting them ranges from 09:00 to 19:00, the ideal temperature varies depending on geographic location and tree cover, and the surveys are done on sunny days with mild wind (Pollard and Yates 1994, Bried and Pellet 2012, Hamm et al. 2013, Shepard et al. 2021). For Arkansas specifically, no ideal temperature

for summer surveys has been identified. Therefore, surveys commenced during the previously specified dates between the hours of 09:00 and 19:00 when wind speeds were mild, temperature notwithstanding. This excluded one survey which occurred just before 09:00. The time, general wind speed, and general cloud cover were recorded before each transect. Wind speed and cloud cover were both recorded categorically on scales of 1-3. For wind speed, a 1 indicated no wind, a 2 indicated it was slightly wind, and a 3 indicated it was very windy. For cloud cover, a 1 indicated there were no clouds, a 2 indicated it was partly cloudy or cloudy, and a 3 indicated it was overcast. Temperatures were gathered from local weather stations post hoc (Local Conditions 2022a, 2022b and Weather Underground 2022a, 2022b).

In May, surveys occurred between the 4<sup>th</sup> and 27<sup>th</sup>. I surveyed MBPNA, Casey Jones WMA, Longview Saline Natural Area WMA, Kingsland Prairie Preserve, Big Timber WMA and Warren Prairie. The sites at MBPNA and Warren Prairie were surveyed twice since no butterflies were seen in either natural area, and I suspected this was due to my first surveys being before the flight season. All of the other areas were surveyed once in May.

In August and September, surveys occurred between the 6<sup>th</sup> of August and the 2<sup>nd</sup> of September. For these surveys, I shifted my focus to MBPNA and Warren Prairie, the area where the satyr was identified, and the area where this butterfly was seen prior to this survey, respectively. For both areas, I revisited the same sites previously visited in May. At MBPNA, I mainly wanted to determine the flight season, as well as survey some other sites as time allowed. Four additional sites were surveyed in September that had not

been surveyed in May. At Warren Prairie, I wanted to determine whether or not the butterfly was present in this area.

Two to four field surveyors conducted Pollard-Yates transects at each study site. Each transect path was parallel to the road, and the distance from the road for each transect varied. Distance between transects also varied, with the minimum distance being 10 meters. In accordance with Pollard and Yates (1994), an observer walked each transect line at a slow pace and marked with a flag where all butterflies were seen within 5 meters of the transect. When a satyr was seen, their location was marked with a flag. To avoid double-counting, each observer made a mental note of where the butterfly flew to if they flew ahead of them, and only counted butterflies seen when looking forward along the transect. For each satyr spotted during the second flight season in August 2023, the GPS location was recorded. Two to three people surveyed each site, with each person walking a separate transect.

### **Vegetation surveys**

Vegetation surveys were done at every site, and at specific locations where a butterfly was identified within a site. Due to the limited area where the satyr was identified, I elected to consider the microhabitat of the satyr within the larger sites. Vegetation plots were never closer than 10 meters, and the microhabitats change fairly frequently, allowing the plots to be considered independent of one another. Sites therefore were the large areas where butterfly surveys were completed, while plots were areas within the sites where vegetation surveys were completed. At each plot, three 1 x 1-meter plots were randomly placed. I made visual estimations of the percent cover of grasses, woody plants, sedges, and forbs. Additionally, the presence or absence of

flowers was recorded. I took photographs from above for every plot to later quantify more exact percent coverages of each plant species. The heights of the four tallest plants within each plot were recorded. I also recorded average height, which was considered to be the average plant height within the plot if you removed the four tallest plants. In May, I completed one vegetation plot at every location a satyr was identified within a site (hereafter “satyr location(s)”), and if there were more than three satyrs detected, three plots were randomly chosen for vegetation samples. If multiple butterflies were clustered in one small area, it was considered to be just one location. In August, to get a better characterization of the satyr habitat, I did three vegetation plots at every satyr location within a site and averaged them together. Only three sets of plots were surveyed at one site, which were chosen randomly if more than three satyrs were detected. In August, if there were multiple satyrs in one small area, I added an additional vegetation plot, totaling four. This happened for three separate locations.

Canopy cover was also recorded at every plot in August using a convex spherical densiometer. A minimum of three readings were recorded at each plot in random locations and then averaged together post hoc. For the satyr locations, three canopy cover measurements were also recorded and averaged together *post hoc*. Canopy cover was assumed to be the same between May and August, thus the May sites that were revisited in August received the canopy cover recorded in August.

## **Data analysis**

### *Butterfly presence*

Data were recorded in a binomial fashion, with (1) denoting detection and (0) denoting non-detection. Detection was considered as identifying at least one satyr on a

transect, and non-detection was considered as not identifying any satyrs on a transect. I developed multiple logistic regression models to estimate the probability of a satyr being present, and I used Akaike's Information Criteria adjusted for a small sample size (AICc) to rank the models (Szcodronski et al. 2018). The model with the lowest AICc value, along with any models within 2 AICc, was/were considered the most supported model(s) (Burnham and Anderson 2004). The explanatory variables used in the models included temperature, wind speed, cloud cover, and vegetation metrics. The vegetation metrics included percent sedges, percent grasses, percent woody vegetation, percent forbs, presence or absence of blooming flowers, years since last burned (burn) and canopy cover. Burns were divided into two categories, 1-4 years (considered a frequent burn interval) and 5+ years (considered an infrequent burn interval). These two categories were used due to data constraints, as they allowed the models to converge. Exact burn regime dates were also gathered for each site as this could influence the survival of the satyr in different areas. Canopy cover data were missing from nine sites, and the corresponding plots were removed, leaving 84 plots to be considered in the analysis. Bare ground, average plant height, and average tallest plants were excluded due to the lack of biological relevance, and due to strong correlations between variables, all of the continuous variables were centered. R Studio (R Core Team 2022) was used to model presence/absence for this butterfly using multiple logistic regression.

#### *Habitat suitability*

Maximum entropy (Maxent) was used to identify habitat suitability, as this modeling technique can use either presence/absence data or presence-only data, which allows for flexibility in sampling (Phillips et al. 2006, Phillips et al. n.d.). Additionally,

this technique can use both categorical and continuous data, and in some cases, this technique requires only a few locations to create a useful model (Baldwin 2009). The model created also allows for specific interpretation of each environmental variable included (Phillips et al. 2006). Due to the scarcity of this butterfly and the general lack of knowledge of its exact locations, this model was a promising choice due to its flexibility in terms of the data requirements. Moreover, Maxent, in comparison to a more commonly used program like Genetic Algorithm for Rule-Set Prediction (GARP), has been shown to make more fine-grained predictions (Phillip et al. 2006) which should provide more aid in the identification of the butterfly's potential range.

The variables included in the Maxent model were based on those used by Westwood et al. (2020) along with the inclusion of annual precipitation due to the drought that occurred in the summer of 2022 and the subsequent drop in satyr numbers. Diverging from Westwood et al. (2020), level IV ecoregions were used in place of land cover. Ecoregions have been shown to be useful for analyzing land-use dynamics, and correspond to land cover patterns as well as urban settlement, and agricultural variables (Gallant et al. 2004). The variables used in the model included level IV ecological regions (EPA 2014), dominant soil drainage condition (USDA NRCS 2014), distance from water, calculated from AR rivers (ADEQ 2020), elevation, and annual precipitation, downloaded from WorldClim (2022), which has monthly climate data from 1970-2000 (Table 1). Two additional occurrences from the past 10 years were sourced from GBIF.org (2023) and added to the model. In accordance with Groff et al (2014), I used linear, quadratic, and hinge features to generate each model. Within the settings, replicates was increased to 10 and maximum iterations was increased to 5000. A bias file

was created to account for the spatial bias towards areas that were better surveyed (Kramer-Schadt et al. 2013). Bootstrapping was used as the resampling method due to the small size of the sample. Jackknifing was used to assess the relative importance of each explanatory variable included in the models. To better visualize the Maxent model predictions and calculate the amount of suitable habitat in the state, the habitat suitability was divided into four categories (unsuitable, low suitability, medium suitability, high suitability) within ArcGIS Pro using the Jenks Natural Breaks classification method. This method was taken from Groff et al. 2014.

### III. Results

I identified the satyr in only the MBPNA and along a roadside patch roughly 20.6 kilometers to the north from the nearest MBPNA site (Figure 2). Over fourteen days I completed 104 surveys. Forty-eight surveys were completed in May across eight days, and 56 were completed in the fall across six days. Three surveys were done at Big Pine WMA, two at Casey Jones WMA, one at Kingsland Prairie Preserve, six at Longview Saline Natural Area WMA, 52 at Moro Big Pine WMA, four at the roadside patch, and 36 at Warren Prairie. In total, 114 Georgia satyr butterflies were identified during surveys. The satyrs were identified at 10 different sites within MBPNA. Due to the site revisits that occurred in the Fall surveys, I expect that this number most likely included duplicates. Because the longevity of adult satyrs is unknown, the most conservative estimate was determined by assuming adults lived the entire Fall flight season and thus only counting one trip. When counting only the trip with the highest butterfly count in the Fall, I estimated that 88 unique butterflies were seen in total. Sixty-four of these were seen in May, and 24 were seen in August. Additionally, two of the butterflies seen in May and seven of the butterflies seen in August were along the roadside while the rest were all within MBPNA.

In May, the satyrs were seen as early as May 16<sup>th</sup>. However, I believe that the satyrs were out the week before, May 8-14, but due to scheduling constraints, I was unable to survey that week. I did survey the prior week on the 4<sup>th</sup>, 5<sup>th</sup>, and 6<sup>th</sup> of May, and I did not see the satyr. Sites were not revisited in May, and the satyr was not seen at any other sites, so I am unsure how long this first flight season is.



During the presumed second flight season, I revisited the sites where the satyr was observed in May as well as the sites in Warren Prairie, the recent historical site. Every site in these two areas were revisited multiple times, excluding the four additional sites surveyed once in September. In August, the satyr was identified on the 6<sup>th</sup>, albeit in very low numbers. The last sighting during this flight season was made on the 2<sup>nd</sup> of September. I observed the highest number of the satyrs on September 2<sup>nd</sup>. Based on the relatively high numbers for that flight season seen during that visit, it is likely that that flight season continued for at least another week. Due to time constraints, I was unable to make any additional trips to confirm this.

A notable difference between the known historic site, Warren Prairie, and MBPNA was the burn regimes. According to the obtained burn records, the MBPNA sites were either burned in early March or early December. In contrast, the Warren Prairie sites were burned in late March, early April, or early October.

### **Butterfly presence**

The best logistic regression model identified grasses, flowers, forbs, sedges, canopy cover and burn history as the important vegetation and habitat metrics for estimating the probability of presence of the satyr ( $\omega = 0.38$ ; Table 2). The next best model also included woody vegetation ( $\Delta AICc = 1.79$ ,  $\omega = 0.16$ ; Table 2). Due to the woody vegetation estimate of the second-best model having a confidence interval that includes zero ( $\beta = -0.027 \pm 0.033$ ; Table 2) as well as this model being more complex than the first model (Table 1), only the first model was considered. The probability of a satyr being present increased with more grasses ( $\beta = 0.086 \pm 0.032$ ; Table 3, Figures 3 and 4), more sedges ( $\beta = 0.226 \pm 0.116$ ; Table 3, Figures 5 and 6), infrequent burns ( $\beta =$

2.178 ± 0.946; Table 3, Figures 7 and 8), the absence of flowers ( $\beta = -2.262 \pm 0.891$ , Table 3, Figures 9 and 10), less forbs ( $\beta = 0.110 \pm 0.043$ ; Table 3, Figures 11 and 12), and less canopy cover ( $\beta = -0.050 \pm 0.023$ ; Table 3, Figures 13 and 14).

For environmental variables, the best model identified cloud cover as the important variable for detecting the satyr ( $\omega = 0.57$ ; Table 4). The next best model also included temperature ( $\Delta AICc = 1.62$ ,  $\omega = 0.25$ ; Table 4). Due to the temperature estimate of the second-best model having a confidence interval that includes zero ( $\beta = -0.038 \pm 0.050$ ) as well as this model being more complex than the first model (Table 4), only the first model was considered. The probability of a satyr being detected decreased with more cloud cover (clouds2 =  $-2.726 \pm 1.075$ , clouds3 =  $-2.606 \pm 1.109$ ; Table 5, Figures 15 and 16).

### **Habitat suitability**

The current known distribution of the satyr includes only Calhoun County in Arkansas. (Figure 2). The Maxent model predicted that Ouachita, Union, Bradley, Drew, and Ashley County possess the most suitable habitats for the satyr (Figure 18). Five additional counties were predicted to have moderately suitable habitats, and four additional counties were predicted to have low suitable habitats (Figure 18). The jackknife test of the Maxent model identified the most important factor for predicting the satyr's range as dominant soil drainage condition (Figure 17). Dominant soil drainage condition had an 83.1 percent contribution, with the next highest percent contribution to be elevation with 6.7 percent (Table 6).

## IV. Discussion

### Vegetation relationships

The only vegetation characteristics that had a positive relationship with the satyr's presence were grasses and sedges. This relationship supports the notion of grasses and/or sedges being the most likely host plant for this butterfly. According to BAMONA (2022a, 2023b, 2023h, 2023j-1.) there are two butterflies within the Satyrinae subfamily that use grasses and sedges as their host plant, and four additional butterflies with grasses and sedges as probable host plants. Moreover, for Satyrinae species that occur in Arkansas, all are recorded as having grasses as their host plant (BAMONA 2023a, 2023c-g), excluding one, which has bamboo switch cane (BAMONA 2023i). This could suggest that sedges are less likely to be a host plant for Satyrinae species in Arkansas, or it could suggest that the satyr is able to take advantage of an underutilized niche in Arkansas.

The Satyrinae subfamily is understudied in North America, with only about 30% of the species having host plants listed or even theorized (BAMONA n.d.). With all of this information in mind, as well as the report from the Florida Native Plant Society (2018), I believe that sedges are the only host plant. This would explain the positive relationship found in this study. Moreover, sedges as the only host plant would explain why I found this species in the same locations as the Carolina satyr (*Hermeuptychia sosybius*) and little wood satyr (*Megisto cymela*), which both utilize species of grasses as host plants (BAMONA 2023a, 2023f). By utilizing an unused plant group as its host plant, the satyr would limit interspecific competition among the caterpillars, explaining the cohabitation (Dhondt 2011). The positive association with grasses, could be explained by the habitat characteristics as well as being potentially related to their adult food

sources. Most of the sites that they occurred in had areas of shade and sun, with the shade supporting sedges and the sun supporting grasses, and hence, even though they do not need the grass for food, they do need the sunny areas to help regulate their temperature (Kemp and Krockenberger 2002).

The reported adult foods in the Satyrinae subfamily include flower nectar, rotting fruits, sap, bird droppings, carrion, fungi, and aphid honeydew (BAMONA n.d.). The two species identified in the same area, the Carolina satyr and the little wood satyr, consume sap, aphid honeydew, rotting fruit, and rarely flower nectar (BAMONA 2023a, 2023f). Following my previous thoughts on interspecific competition and what I surveyed in this study, I expected this butterfly's presence to be associated with flowers, but my analysis proved otherwise. My results suggest that flower nectar is not an adult food source for the satyr. However, I only examined flower presence rather than abundance. Thus, it is possible that with fewer flowers, there is a positive association that was overlooked. This would suggest that they consume nectar from flowers rarely, like the little wood satyr (BAMONA 2023f). Additional observational studies should be conducted to determine whether flowers are a rare adult food source or simply not a food source. Much like host plant determination, additional observational studies will need to be completed to determine what exactly this butterfly feeds on as an adult, if they feed at all. If the adult does not use flowers as food, then it could potentially consume sap, aphid honeydew, and/or fungi, especially considering the positive relationship with grasses. Sap is produced by the trees in their preferred habitat, and since both species of butterflies, the little wood satyr and Carolina satyr observed in the same areas also consume sap (BAMONA 2023a, 2023f), it is likely that sap is a plentiful resource in their preferred

habitat. Aphids also consume grass (Lewis 1992), and then produce their sugary “honeydew” waste (Townsend 2000) which could be another food source. A fungus can also grow on this waste (Townsend 2000). Mushrooms were also spotted within the habitat, making fungi a potential food source.

### **Habitat and Satyrs**

The satyr was not found in Warren Prairie, a site the species was previously known from. The habitat characteristics are similar at Warren Prairie and MBPNA, with MBPNA being where the butterfly was found in substantial numbers this year. Both areas have an abundance of both grasses and sedges, and various other potential adult food sources. As stated previously, the one notable difference between the two areas seems to be the burning regimes. Based on the observations of this butterfly the 3<sup>rd</sup> week of May, the satyr is likely in the highly vulnerable caterpillar stage throughout the end of March and into April. Since eight of the ten sites that were examined in Warren Prairie were burned during this time, it is possible that the prescribed burns decimated the satyr caterpillars. However, it is also possible that this species is prepared for such hot conditions. *Eumaeus atala* caterpillars will burrow into the soil to pupate, which allows them to survive even as the area they inhabit is burned (Thom et al. 2015). Buried chrysalis of the satyr have not been observed, but, within the Satyrinae subfamily, the *Neominois ridingsii* has underground pupae (Scott 1992). The *N. ridingsii* butterfly, however, is not found in similar areas or habitats to the satyr, with the *N. ridingsii* being found in the western half of the United States in intermountain areas, short-grass prairies, and grasslands (BAMONA 2022b). This phenomenon does not appear to be well studied, likely due to the difficulty of finding the buried chrysalises or knowing whether to even

look for them. The previously mentioned *E. atala* butterfly can exhibit chrysalis burial, however they will also pupate in leaf litter or at the base of their host plant (Thom et al. 2015). Because the pupating behaviors of the satyr are currently unknown, chrysalis burial cannot be ruled out for this species with absolute certainty.

Nonetheless, if I assume that this butterfly does not have the capabilities to pupate underground and protect itself from fires, then fires are the most likely culprit for the local extinction of the Warren Prairie population. Thus, changing the prescribed burning regimen could allow for reintroduction into Warren Prairie. While halting burns for the short-term could aid in their reintroduction, establishing a proper regimen would help the population more in the long-term. This has been seen with a metapopulation of *Callophrys irus* butterflies, which resided in longleaf pine forests, and had been shown to initially dramatically decline after burns and then exhibited the highest population numbers three years after the burns (Jue et al. 2022). Specific suggestions for the burn regimen in Warren Prairie are discussed in Management Implications.

### **Maxent and Metapopulations**

Dominant soil drainage type was the most influential variable when building the Maxent model. This further supports the theory that sedges are the sole host plant of the satyr, as sedges grow best in soil that is moist and well-drained (Mercer 2022). Elevation, the next most influential variable, most likely had little importance for the model due to the similarity in elevation of southern Arkansas. While the northern and western parts of the states have mountainous areas over 460 m, most of the state is below 300 m above sea level (NWS 2022). This variable thus acted largely to exclude the mountainous areas in the state. Annual precipitation could work to further narrow down the areas in southern

Arkansas where the satyr could be found. Across southern Arkansas, average annual precipitation differs by up to 400 mm between general areas, with areas in the center tending to have greater annual averages (NWS 2022). However, these differences may also be too minimal for differentiating, which would explain the low variable influence.

The Maxent model identifies the roadside area as low suitability. In addition, the immediate surrounding area consists of unsuitable habitat interspersed with additional low suitability areas. This would suggest that the roadside location is a small isolated population, or potentially a sink population within the MBPNA metapopulation.

Metapopulations exist when species occupy small and often fragmented habitat patches within a larger landscape, which creates a temporal web across many connected habitat patches (Dallas et al. 2020), which was observed in MBPNA. To be a metapopulation, dispersal must be possible between the patches. The patches at MBPNA are between 1-6 km apart, which would make dispersal or movement between patches feasible. The roadside patch is at least 20 km from the nearest occupied patch within MBPNA that I observed. If MBPNA serves as a source population for other local populations in the area, then that would mean the satyr can travel much greater distances than I would expect based on field observations of this butterfly flying, as well as the flight capabilities of other satyr butterflies. *Neonympha mitchellii*, a sedentary satyr butterfly, has minimum home ranges of only 0.0022 to 0.007 km<sup>2</sup> (Barton and Bach 2005). The *Neonympha mitchellii francisci*, another sedentary satyr butterfly, has been observed traversing up to 15 km (Kuefler et al. 2008). Due to the 20 km distance between MBPNA and the roadside location, it seems more likely that there is a single isolated population at the roadside location.

Based on the number of individual satyrs counted at the roadside site, which was identified by the Maxent model to be low suitability, this could be evidence of the imperfection of this model. To determine the suitability of a given grid cell in a landscape, Maxent uses the presence-only data along with a group of environmental predictors to estimate the probability of a species occurring in each grid cell (Merow et al. 2013). The imperfection in my Maxent model is likely due to the inability to include direct estimates of sedges, the currently presumed host plant. Unfortunately, while physiologically or ecologically specific variables to a species can produce more accurate models (Low et al. 2021), such data are often unavailable. Instead, more standard environmental variables are often used to reflect more broad biological factors like energy and water availability (Xu and Hutchinson 2012). However, due to the relatively small size of the roadside patch, the broad biological factors likely did not capture the uniqueness of this area compared to its surroundings. Thus, in accordance with the Maxent model and this fact, I would suggest that the areas identified as low suitability be considered as important for surveying as areas identified as areas of medium or high in suitability.

### **Management implications**

The Maxent model identified additional areas within MBPNA, Casey Jones WMA, and Warren Prairie that were considered to be of high suitability that could be surveyed for the satyr. When equating all levels of suitability, Beryl Anthony Lower Ouachita WMA, Crossett Experimental Forest WMA, Hall Creek Barrens Natural Area WMA, Freddie Black Choctaw Island WMA, Kingsland Prairie Natural Area WMA, Longview Saline WMA, and Two Bayou Creek WMA all contains area identified as



suitable for the satyr and should also be surveyed. Within these areas, I suggest looking for the habitat characteristics defined by the logistic regression model. Burn regime data would identify which of these areas are infrequently burned, and preliminary field-based surveys could be done to help narrow down the identified areas. Ideal areas would have more grass cover than forb cover, adequate sedge cover, minimal flowers, and less than 50% canopy cover.

The area within Warren Prairie that has been identified as highly suitable was not surveyed during this study. One of the areas identified as highly suitable in Casey Jones WMA was surveyed during the study and no satyrs were detected there. This could mean that I missed the satyr when surveying, or it could offer another potential area for a translocation. If I missed the butterfly while surveying, the butterfly most likely was present in very low numbers there. The site I surveyed was about 9.5 km south of the area I surveyed in Warren Prairie, which was a known historical area. This could be a travelable distance for the satyr. However, before establishing any populations at greater distances than about 6 km, a mark-recapture study should be completed to determine the movement capabilities of this non-migratory butterfly.

To help support organisms in isolated, fragmented habitats, corridors can be created. Corridors help to facilitate movement between otherwise isolated patches, increasing gene flow and thus reducing the risk of extinction for small populations (Brown and Kodric-Brown 1977). While corridors need to facilitate movement, they do not necessarily need to be made up of high-quality habitat. This is especially true when neither reproduction nor establishment within the corridor are necessary (Haddad and Tewksbury 2005). Habitat quality has also been shown to be less important in recently

colonized areas (Kalarus and Nowicki 2015). However, it has also been shown that for some butterfly species, corridor quality is important and effects movement rates. Corridor quality is often linked to edge habitat as well as specific plants' abundance. Important plants include the host plant as well as nectar sources (Haddad and Tewksbury 2005, Kalarus and Nowicki 2015). While corridors could be effective for the satyr, before considering their creation, the host plant needs to be confirmed as well as the adult food sources, if there are any. Once this information is ascertained, the map created with the Maxent model could be used to determine potential corridor locations.

To allow for reintroduction of the satyr into Warren Prairie, I would suggest either halting prescribed burnings to allow the satyr to establish a proper metapopulation. For the monarch butterfly (*Danaus plexippus*), habitats are burned in small patches to allow for recolonization following the fire and when the butterflies are absent from the habitat (MacDougall 2020). For this non-migratory butterfly, fires could be prescribed when the satyrs are adults and able to evade the fire. The current dates for the burns in MBPNA show that the areas were burned when this species was in a state of dormancy. This suggests that the burning schedule and pattern in MBPNA allows for survival of the metapopulation. The burn records for MBPNA show that the sites were burned over a three-year period with closer sites being burned at least a year apart. This burning regimen likely kills some small subpopulations of the satyr in the short-term, but in turn creates better quality habitat in the long-term, allowing the metapopulation to thrive. By altering the MBPNA dates to May-June and August-September, this should allow for the greatest long-term benefits for the habitat and smallest short-term population declines.

Although my study was limited due to the rarity of the satyr, my results provide essential information that can be used to locate the satyr in other areas of Arkansas as well as manage its habitat to promote long-term success. Overall, further research regarding the desired habitat characteristics for the satyr is necessary to provide managers with the proper tools for managing this species. Through additional research and more targeted management, the satyr could experience great increases in both range and abundance throughout Arkansas.

TABLE 1. Covariates used in Maxent modelling of the Georgia satyr (*Neonympha areolatus*) in southern Arkansas.

Layer	Description	Number of categories	Data year	Resolution
Ecological Region	Level IV ecoregions	32	2014	0.86 km <sup>2</sup>
Dominant Soil Drainage Type	Frequency and duration of wet periods	7	2012	0.86 km <sup>2</sup>
Distance from Water	Distance from nearest river	Continuous	2015	0.86 km <sup>2</sup>
Elevation	Elevation above sea level	Continuous	1970-2000	0.86 km <sup>2</sup>
Annual Precipitation	Sum of rainfall and water equivalent of snowfall in a year	Continuous	1970-2000	0.86 km <sup>2</sup>

TABLE 2. Candidate model sets developed to estimate the probability of presence of the Georgia satyr (*Neonympha areolatus*) in southern Arkansas, in 2022, based on habitat metrics. Grasses, forbs, sedges, and woody all denote for the percent of each vegetation type at each plot. Flowers denotes the presence or absence of blooming flowers at each site. Canopy cover denotes the canopy cover of each plot. Burn denotes the frequency of burning for each plot, which were identical for the larger sites.

Rank	Model	K	$\Delta AICc$	$w_i AICc$
1	Grasses + Flowers + Forbs + Sedges + Canopy + Burn	7	0.00	0.38
2	Grasses + Woody + Flowers + Forbs + Sedges + Canopy + Burn	8	1.79	0.16
3	Grasses + Flowers + Forbs + Canopy + Burn	6	2.07	0.13
4	Grasses + Flowers + Forbs + Sedges + Burn	6	3.22	0.08
5	Grasses + Woody + Flowers + Forbs + Canopy + Burn	7	3.33	0.07
6	Woody + Flowers + Forbs + Sedges + Canopy + Burn	7	4.42	0.04
7	Grasses + Woody + Flowers + Forbs + Sedges + Canopy	7	5.05	0.03
8	Grasses + Woody + Flowers + Forbs + Sedges + Burn	7	5.57	0.02
9	Grasses + Flowers + Sedges + Canopy + Burn	6	5.80	0.02
10	Grasses + Forbs + Sedges + Canopy + Burn	6	5.93	0.02
11	Flowers + Forbs + Sedges + Canopy + Burn	6	6.01	0.02
12	Grasses + Woody + Forbs + Sedges + Canopy + Burn	7	6.62	0.01
13	Grasses + Woody + Flowers + Sedges + Canopy + Burn	7	8.18	0.01
14	NULL	1	44.49	0.00

TABLE 3. Summary outputs for the best logistic regression model for presence, identified in Table 1.

Effect	Estimate	Standard error
Intercept	1.114	0.741
Grasses	0.086	0.032
Flowers1	-2.262	0.891
Forbs	-0.110	0.043
Sedges	0.226	0.116
Canopy	-0.050	0.023
Burn5	2.178	0.946

TABLE 4. Candidate model sets developed to estimate the probability of detecting the Georgia satyr (*Neonympha areolatus*) in southern Arkansas, in 2022, based on environmental metrics. Clouds and wind each denote the amount of wind or cloud cover during the survey, recorded categorically from 1-3. Temperature denotes the temperature during each survey, which was gathered post hoc from the closest weather station.

Rank	Model	K	$\Delta AIC_c$	$w_i AIC_c$
1	Clouds	3	0.00	0.56
2	Clouds + Temperature	4	1.62	0.25
3	Clouds + Wind	5	3.37	0.10
4	Clouds + Wind + Temperature	6	4.28	0.07
5	NULL	1	8.01	0.01
6	Temperature	2	9.02	0.01
7	Wind	3	10.12	0.00
8	Wind + Temperature	4	11.01	0.00

TABLE 5. Summary outputs for the best logistic regression model for detecting the satyr, identified in Table 3.

Effect	Estimate	Standard error
Intercept	2.773	1.031
Clouds2	-2.726	1.075
Clouds3	-2.606	1.109



TABLE 6. Percent contribution of all the environmental variables used to generate the Maxent model. Dominant soil drainage condition was utilized by Maxent substantially more than the other variables.

Variable	Percent contribution
drain_output	83.1
elev_output	6.7
anprec_output	4.7
water_output	4.2
eco_output	1.4

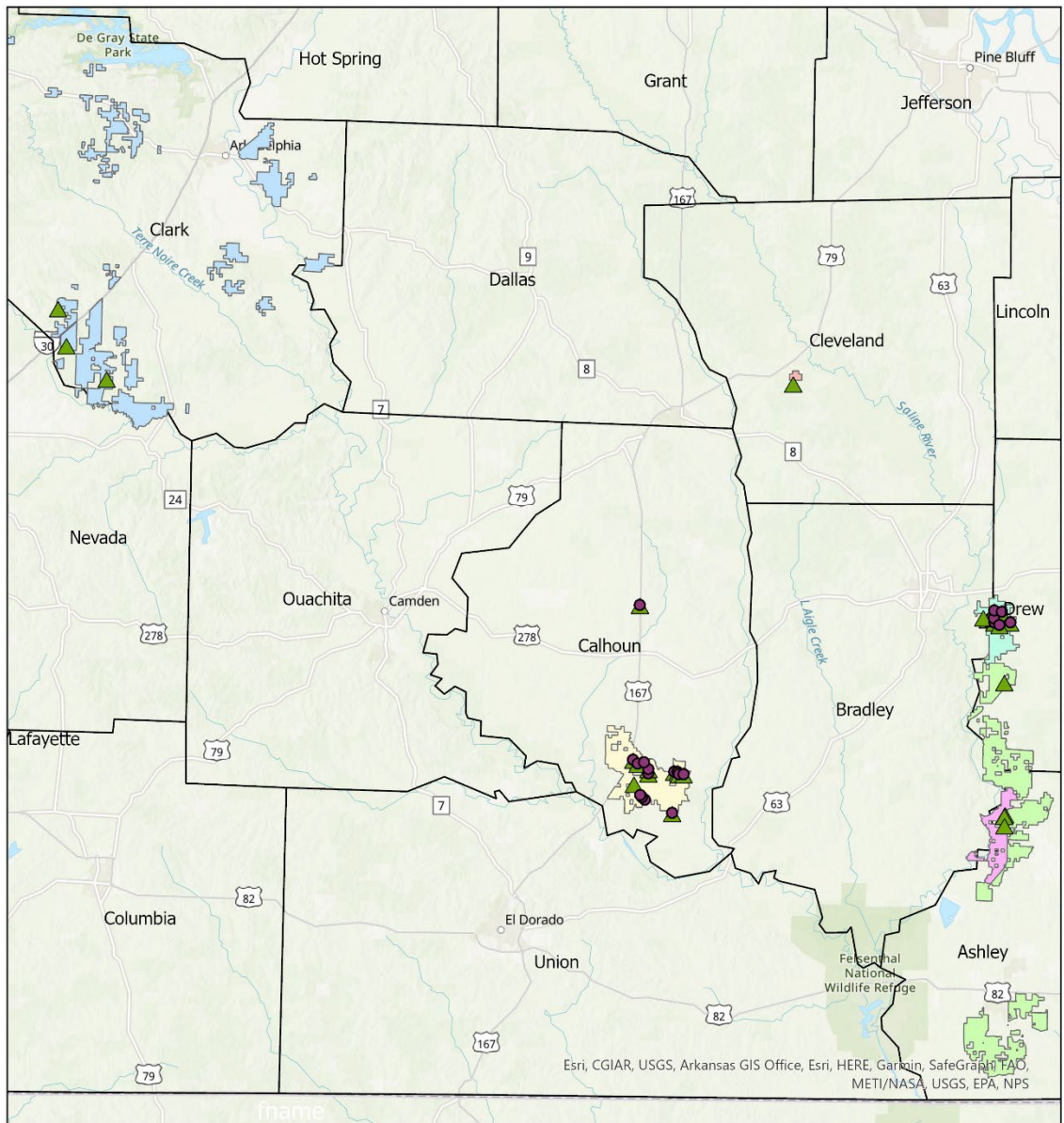


FIGURE 1. Sites surveyed in May and August-September of 2022. The August sites also include the sites done one day in September.

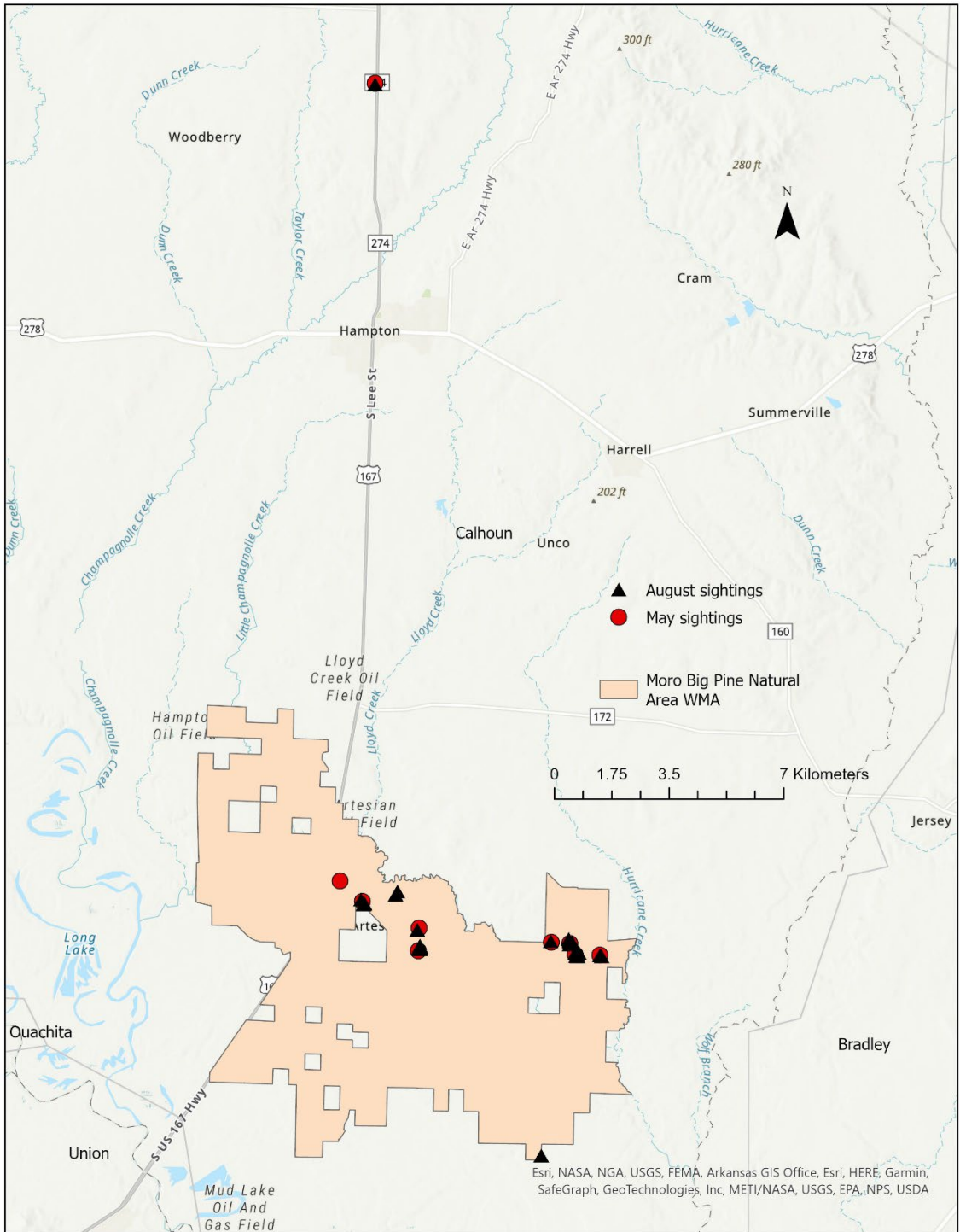


FIGURE 2. Sites where the Georgia satyr was identified in May and August of 2022. The August sites also include the sites done one day in September.

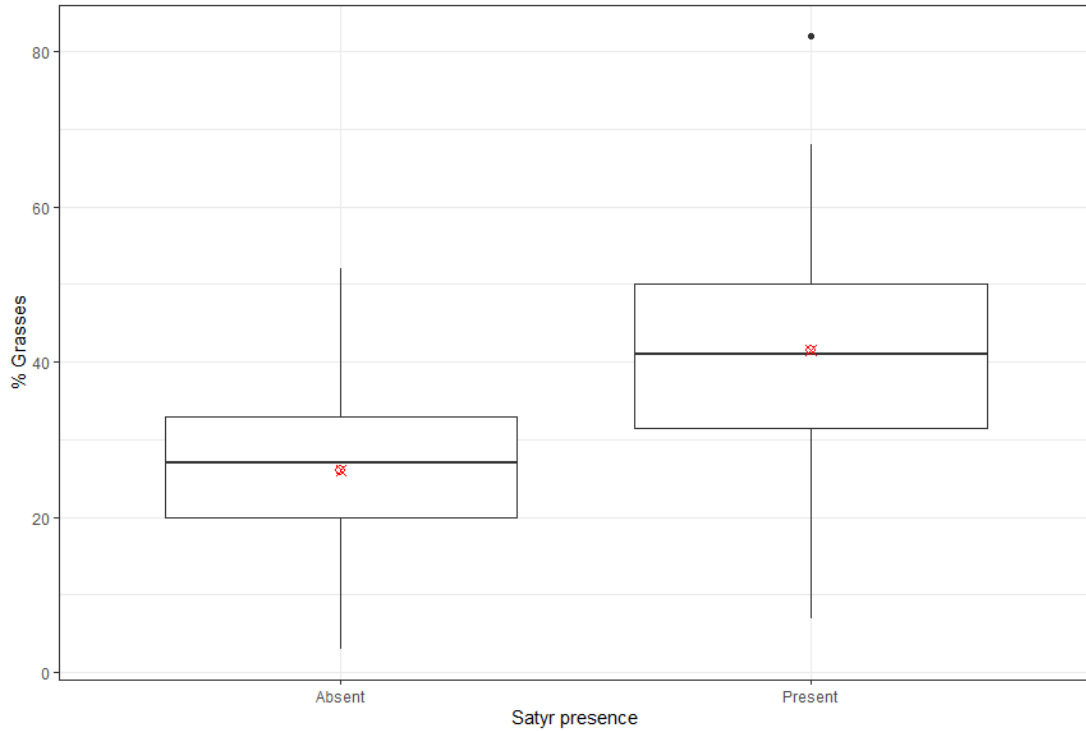


FIGURE 3. Percent of grasses at plots based on whether the satyr was present. The red symbol indicates the mean percentage of grasses, which was 26 when the satyr was absent, and 42 when the satyr was present.

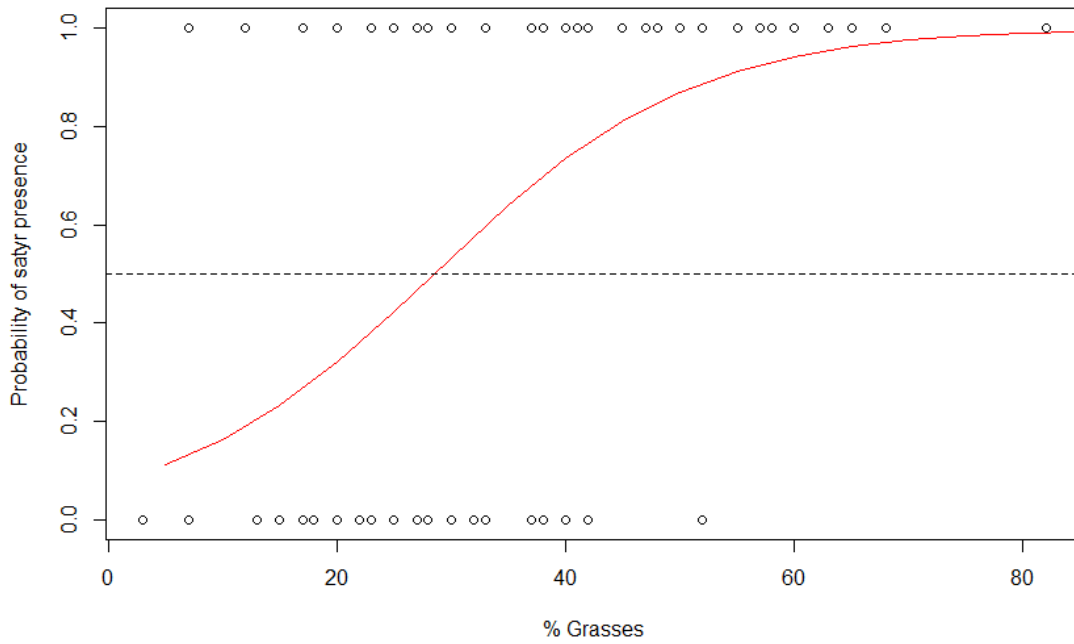


FIGURE 4. The probability of the satyr being present based on grass cover. The probability of the satyr being present was greater than 50% when the percent of grasses at a plot was greater than 30%.

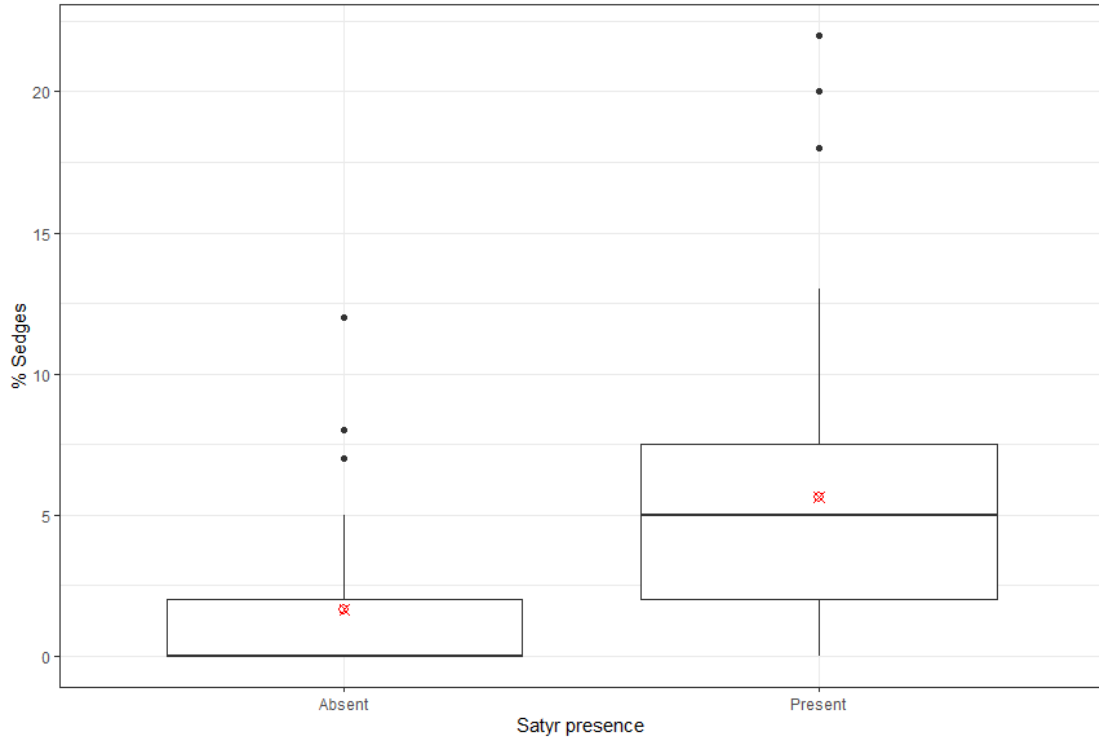


FIGURE 5. Percent of sedges at plots based on whether the satyr was present. The red symbol indicates the mean percentage of sedges, which was 1.64 when the satyr was absent, and 5.65 when the satyr was present.

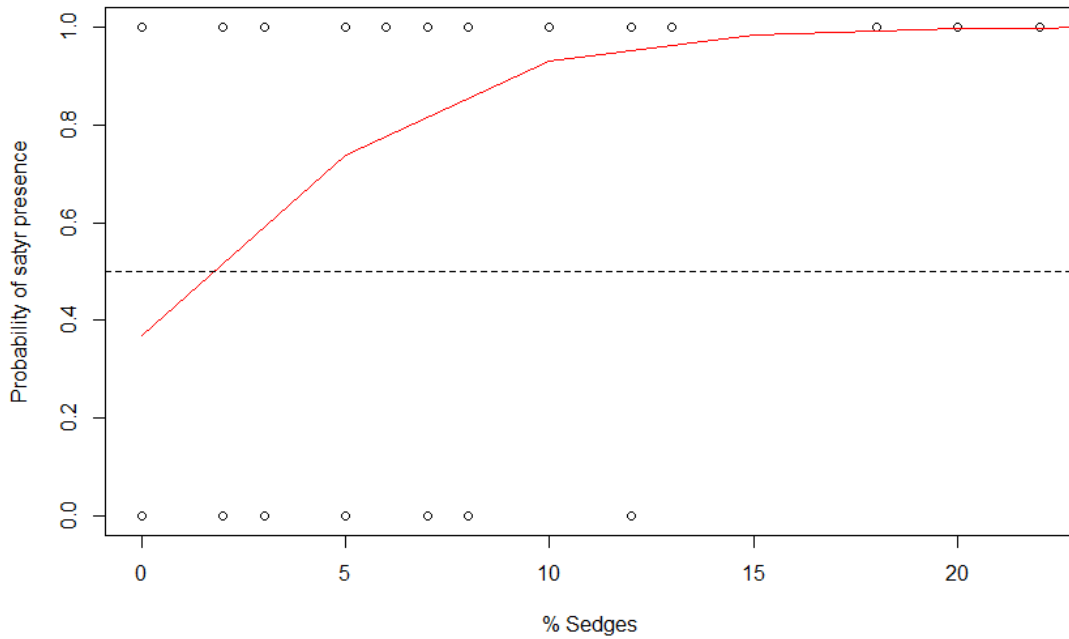


FIGURE 6. The probability of the satyr being present based on sedge cover. The probability of the satyr being present was greater than 50% when the percent of sedges at a plot was greater than 2.5%.

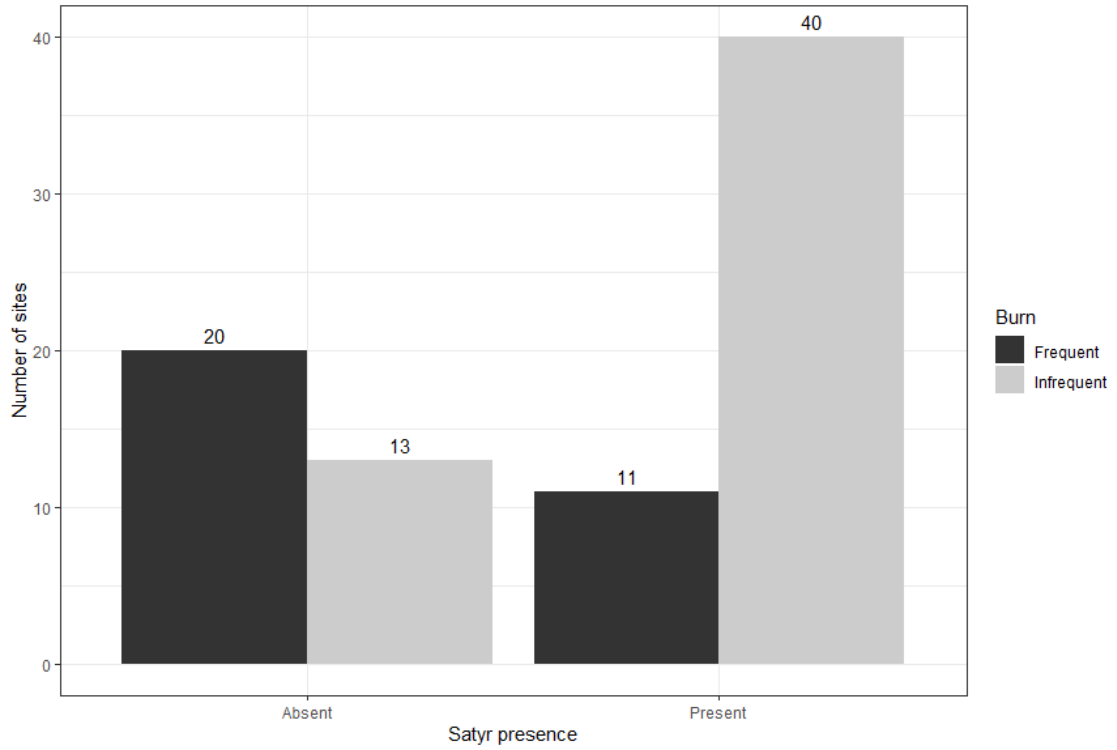


FIGURE 7. Number of survey plots for each burn type based on whether the satyr was present or absent.



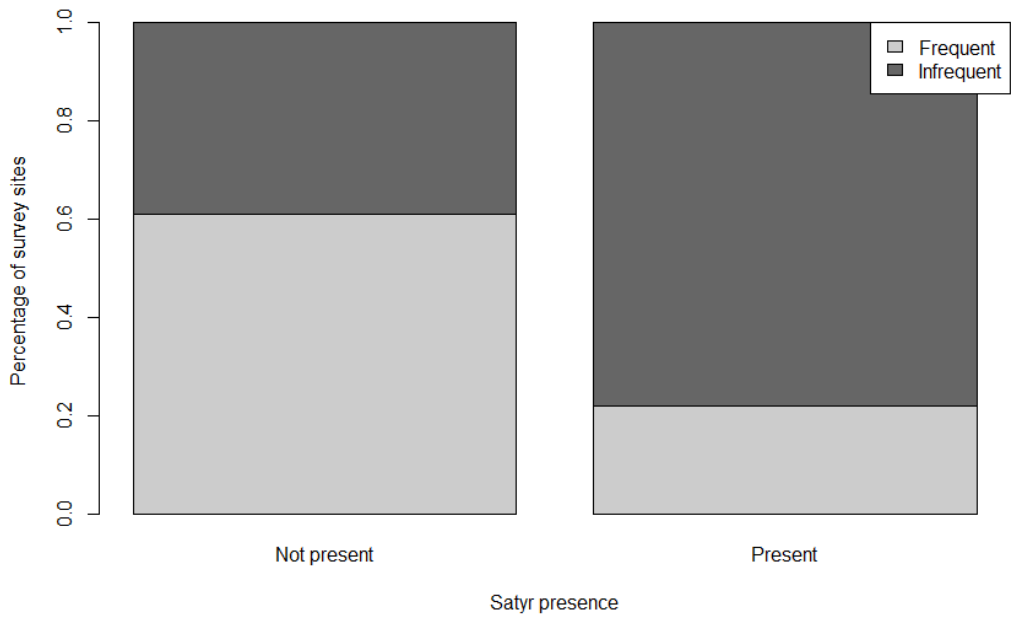


FIGURE 8. Burn frequency at survey plots where the satyr was present or not present. Plots where the butterfly was present had a higher percentage of infrequent burns than plots where the butterfly was not present.

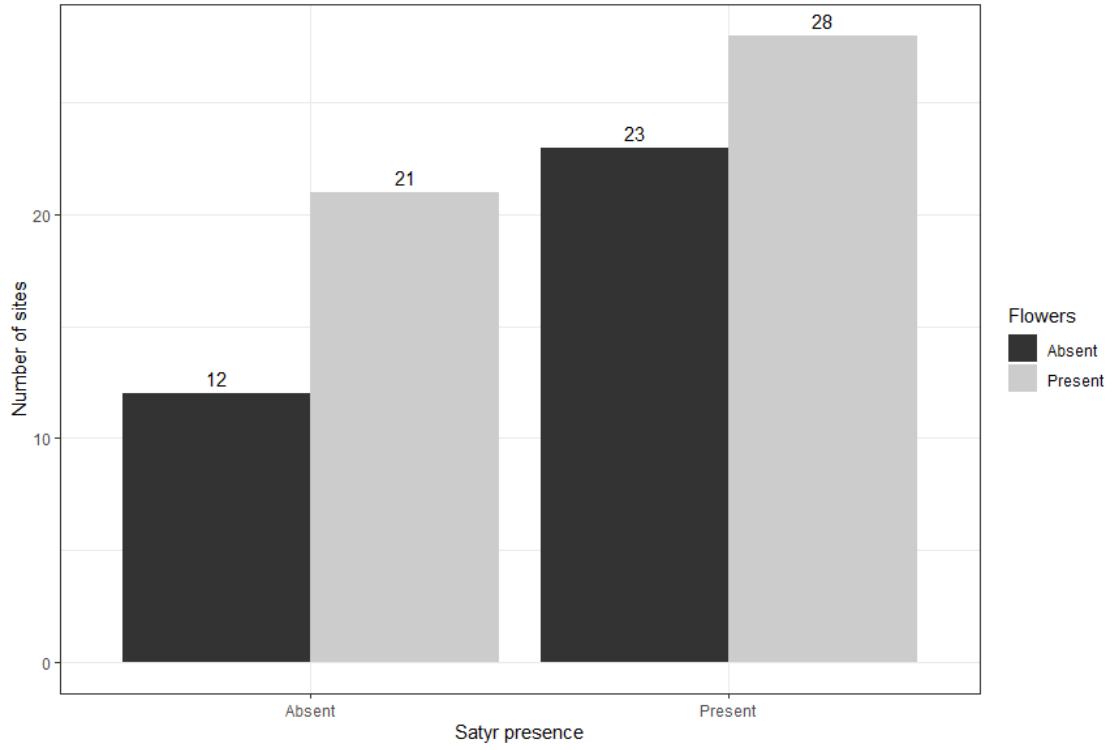


FIGURE 9. Number of survey plots based on whether flowers were present and whether the satyr was present.

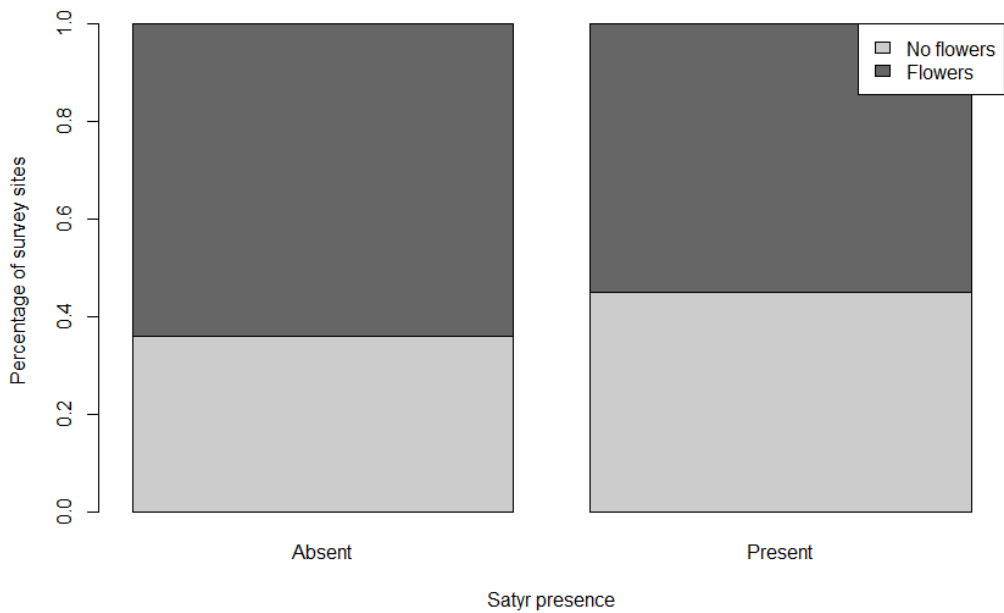


FIGURE 10. Presence of flowers at survey plots where the satyr was present or not present. A higher percentage of plots where the butterfly was present had no flowers than plots without the butterfly present.

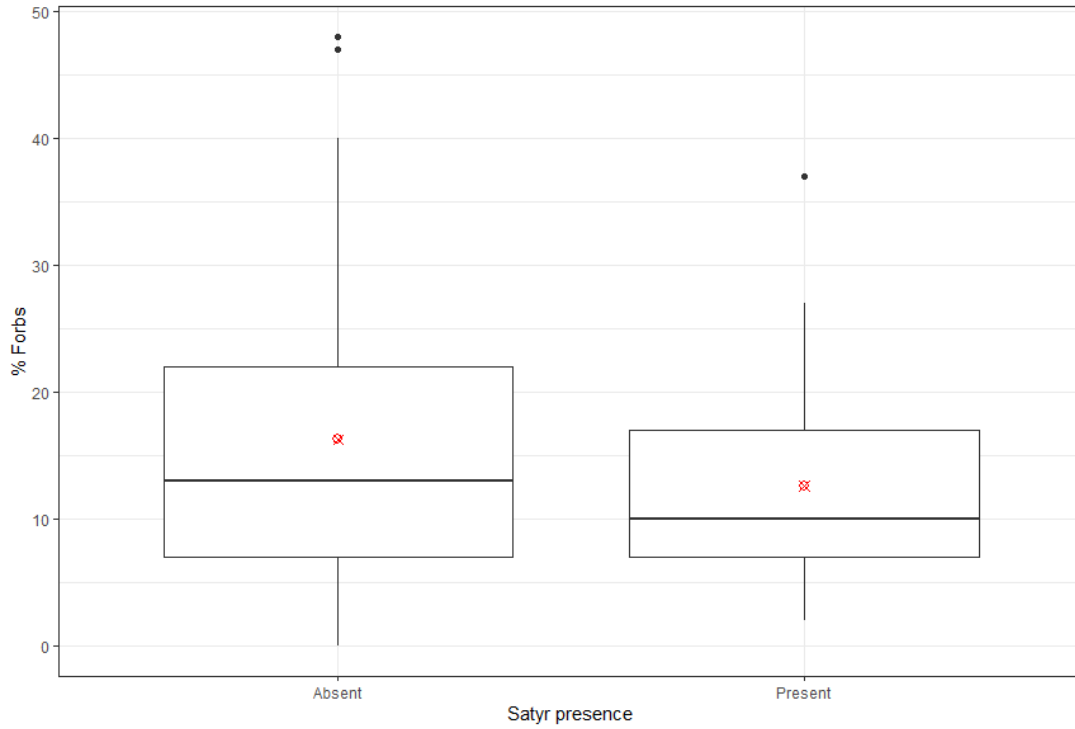


FIGURE 11. Percent of forbs at plots based on whether the satyr was present. The red symbol indicates the mean percentage of forbs, which was 16 when the satyr was absent, and 13 when the satyr was present.

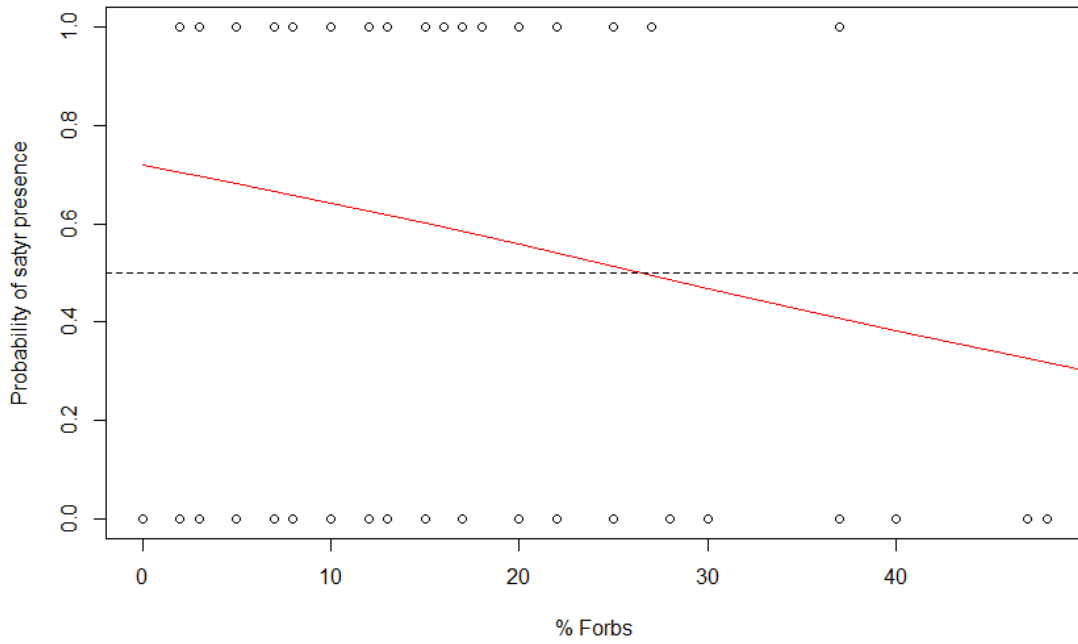


FIGURE 12. The probability of the satyr being present based on forb cover. The probability of the satyr being present was greater than 50% when the percent of forbs at a plot was less than 27%.

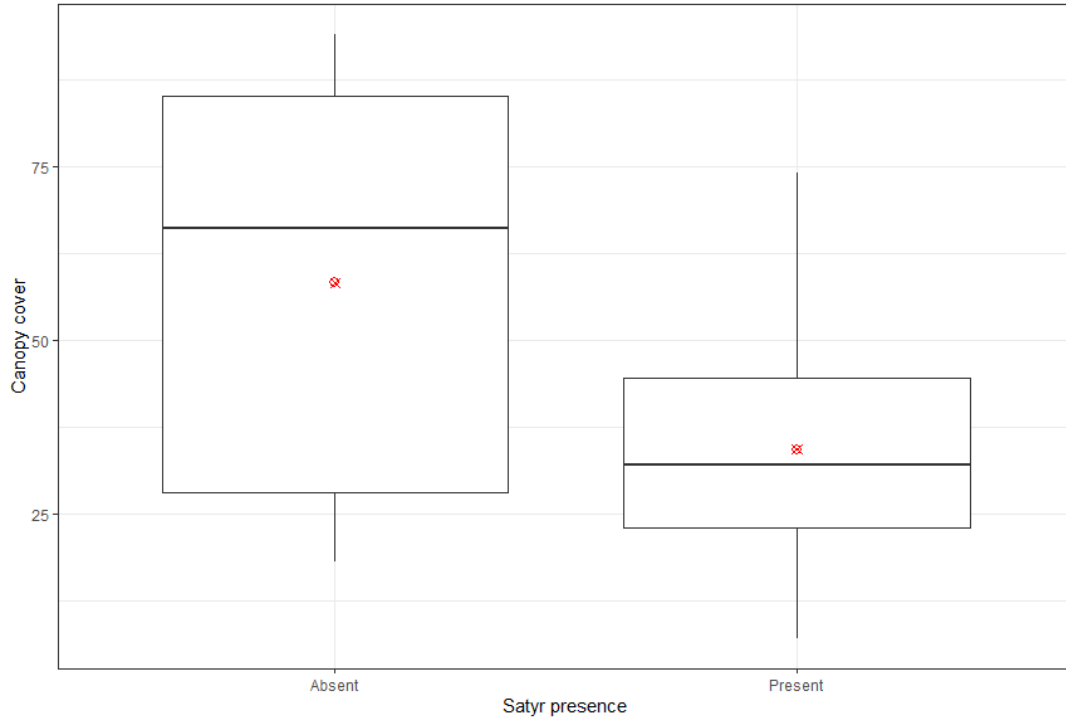


FIGURE 13. Canopy cover at plots based on whether the satyr was present. The red symbol indicates the mean canopy cover, which was 58 when the satyr was absent, and 34 when the satyr was present.

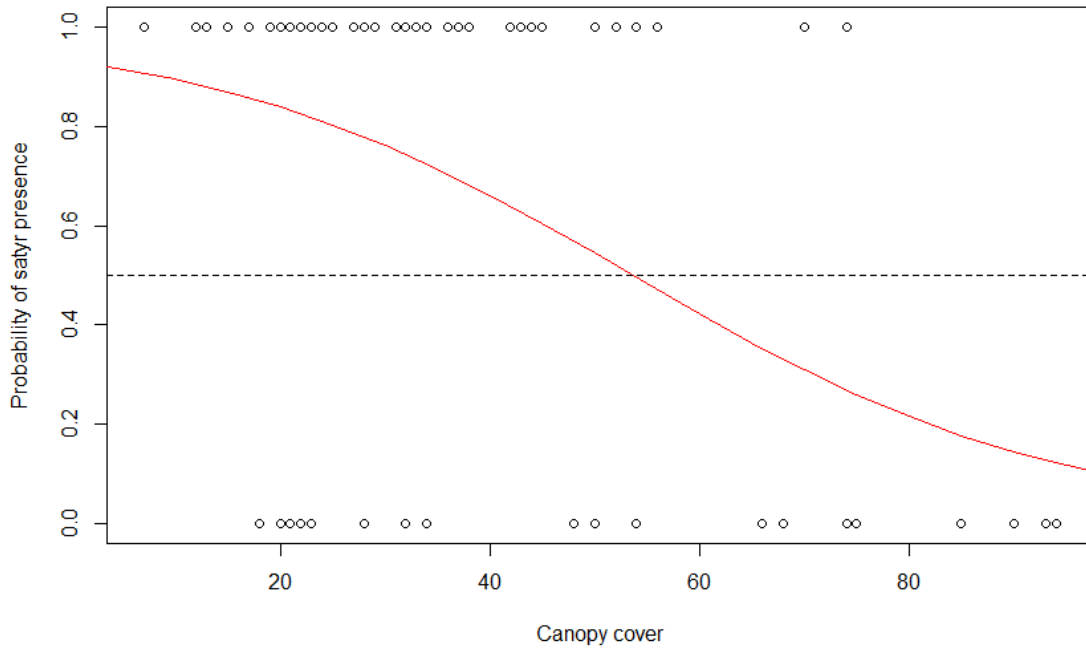


FIGURE 14. The probability of the satyr being present based on canopy cover. The probability of the satyr being present was greater than 50% when the canopy cover at a plot was less than 53.

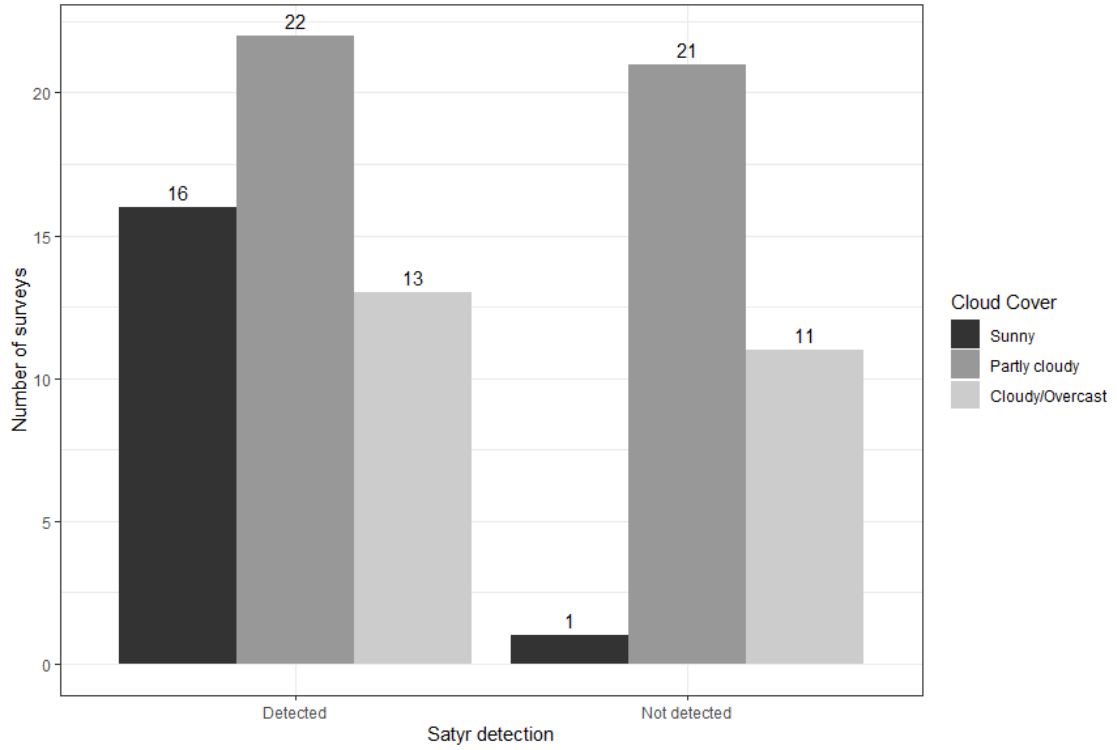


FIGURE 15. Number of surveys based on cloud cover and satyr detection.



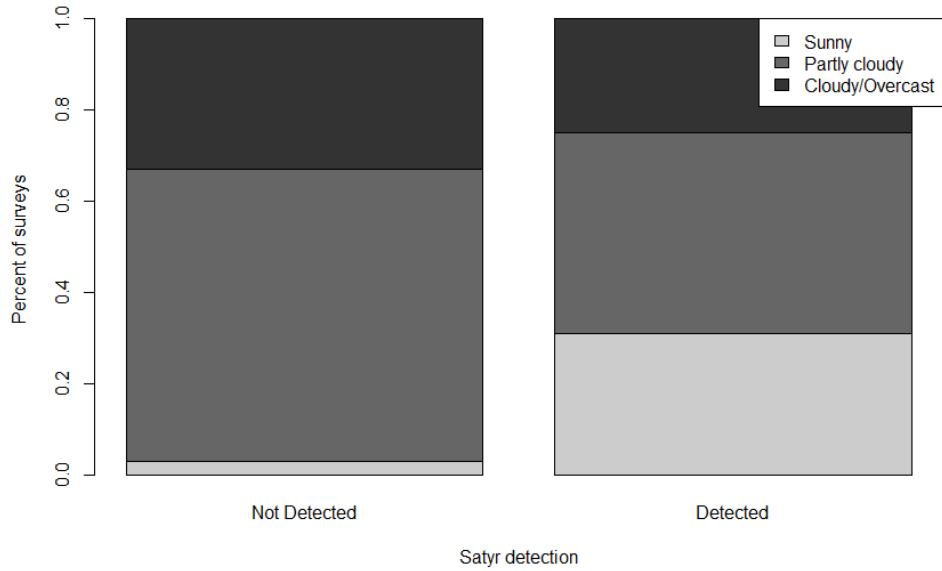


FIGURE 16. Cloudiness during surveys where the satyr was detected or not detected.

When it was cloudy/overcast or partly cloudy, the satyr was more likely to not be detected.

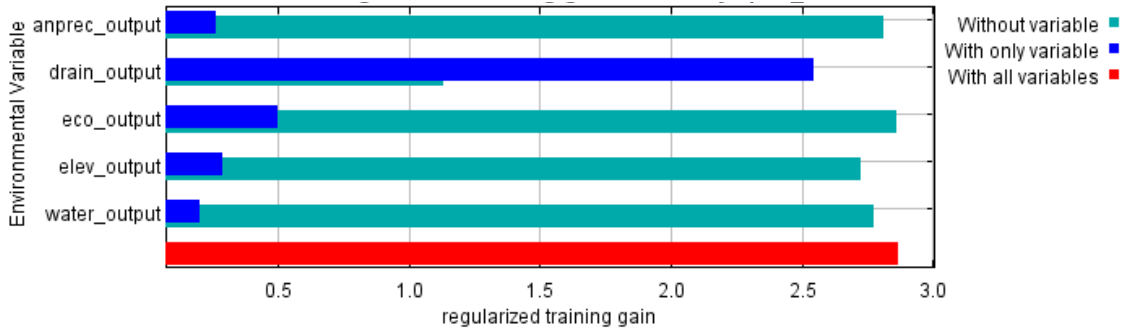
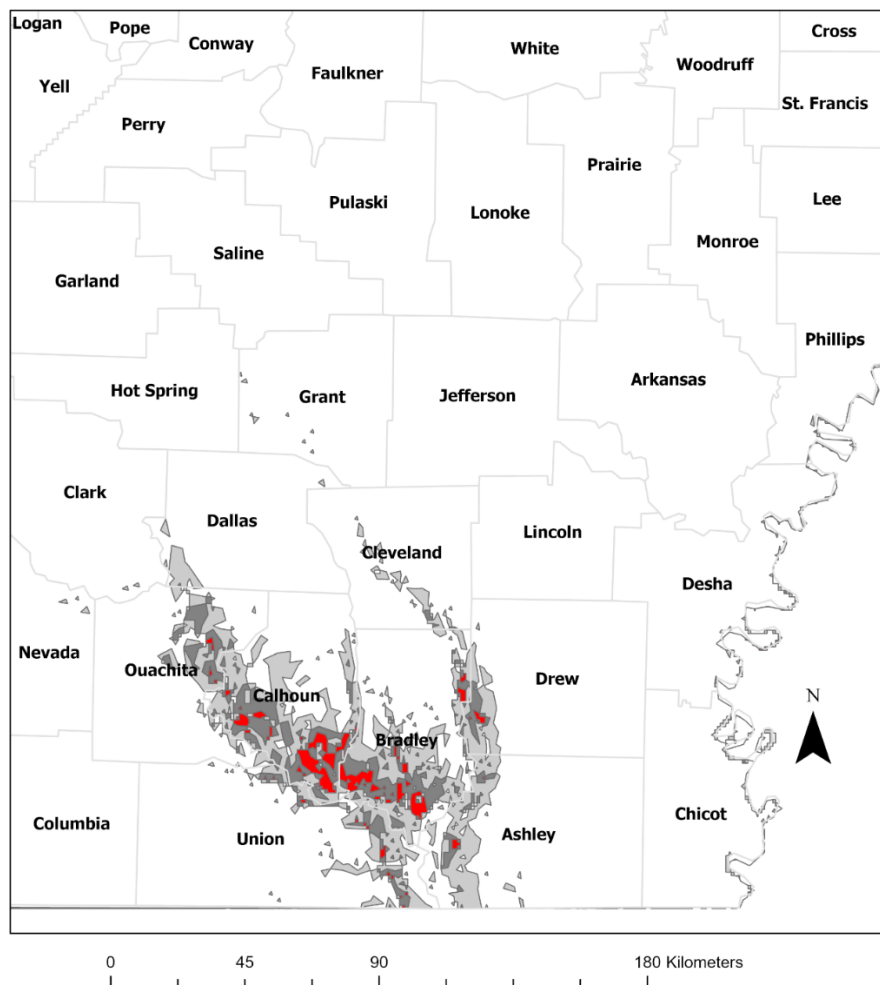


FIGURE 17. Regularized training gain of all the environmental variables used to generate the Maxent model. The blue bars represent the univariate model gain for each individual variable. The light blue bars represent the multivariate model gain when every variable except that individual variable is used in the model generation. The red bar at the bottom represents the multivariate model gain when all variables are utilized. Anprec\_output denotes annual precipitation, drain\_output denotes dominant soil drainage condition, eco\_output denotes ecological region, elev\_output denotes elevation, and water\_output denotes distance from water. As shown by the light blue and dark blue bars for dominant soil drainage condition is the only variable with a substantial amount of valuable information not provided by the other variables.



**Suitability**  
 ■ High suitability  
 ■ Low suitability  
 ■ Medium suitability  
 □ Unsuitable

Suitability	Precent_Area
Unsuitable	97.787259
Low suitability	1.491033
Medium suitability	0.55728
High suitability	0.164422

Figure 18. Estimate of the potential distribution of the satyr across southern Arkansas, produced by a Maxent model. Ouachita, Calhoun, Union, Bradley, Drew, and Ashley County possess areas identified as having high suitability. The previously listed counties, along with Phillips, Desha, Chicot, Cleveland, and Dallas County, possess areas identified as having medium suitability. Moreover, additional habitats in Nevada, Clark, Hot Springs, and Grant were identified as having low suitability.

## References

- Arkansas Department of Environmental Quality (ADEQ). 2020. DEQ water base layer. Retrieved from <<https://gis.arkansas.gov/product/adeq-water-base-layer/>>. Accessed 15 Feb 2023.
- Arkansas lepidoptera survey. 2018. Retrieved from <<http://arkansaslepidopterasurvey.net/checklist/>>. Accessed 21 Sept 2021.
- Baldwin, R. A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* 11:854-866.
- Barton, B. J., and C. E. Bach. 2005. Habitat use by the federally endangered Mitchell's satyr butterfly (*Neonympha mitchellii mitchellii*) in a Michigan prairie fen. *The American Midland Naturalist*, 153:41-51.
- Bergman, K. O. 2001. Population dynamics and the importance of habitat management for conservation of the butterfly *Lopinga achine*. *Journal of Applied Ecology* 38:1303-1313.
- Bragg, D. C., R. O'Neill, W. Holimon, J. Fox, G. Thornton, and R. Mangham. 2014. Moro Big Pine: conservation and collaboration in the pine flatwoods of Arkansas. *Journal of Forestry* 112:446-456.
- Bried, J. T., and J. Pellet. 2012. Optimal design of butterfly occupancy surveys and testing if occupancy converts to abundance for sparse populations. *Journal of Insect Conservation* 16:489-499.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261-304.

Butterflies and Moths of North America project [BAMONA]. 2021. Georgia satyr page. <<https://www.butterfliesandmoths.org/species/Neonympha-areolatus>>. Accessed 21 Sept 2021.

Butterflies and Moths of North America project [BAMONA]. 2022a. Magdalena alpine page. <<https://www.butterfliesandmoths.org/species/Erebia-magdalena>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2022b. Ridings' satyr page. <<https://www.butterfliesandmoths.org/species/Neominois-ridingsii>>. Accessed 23 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023a. Carolina satyr page. <<https://www.butterfliesandmoths.org/species/Hermeuptychia-sosybius>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023b. Colorado alpine page. <<https://www.butterfliesandmoths.org/species/Erebia-callias>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023c. Common wood-nymph page. <<https://www.butterfliesandmoths.org/species/Cercyonis-pegala>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023d. Creole pearly-eye page. <<https://www.butterfliesandmoths.org/species/Enodia-creola>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023e. Gemmed satyr page. <<https://www.butterfliesandmoths.org/species/Cyllopsis-gemma>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023f. Little wood-satyr page. <<https://www.butterfliesandmoths.org/species/Megisto-cymela>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023g. Northern pearly-eye page. <<https://www.butterfliesandmoths.org/species/Enodia-anthedon>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023h. Polixenes arctic page. <<https://www.butterfliesandmoths.org/species/Oeneis-polixenes>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023i. Southern pearly-eye page. <<https://www.butterfliesandmoths.org/species/Enodia-portlandia>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023j. Uhler's arctic page. <<https://www.butterfliesandmoths.org/species/Oeneis-uhleri>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023k. White-veined arctic page. <<https://www.butterfliesandmoths.org/species/Oeneis-bore>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. 2023l. Yellow-dotted alpine page. <<https://www.butterfliesandmoths.org/species/Erebia-pawlowskii>>. Accessed 1 May 2023.

Butterflies and Moths of North America project [BAMONA]. N.d. Family *Nymphalidae* (brush-footed butterflies) page. <<https://www.butterfliesandmoths.org/taxonomy/Nymphalidae>>. Accessed 1 May 2023.

Butterfly Conservation. N.d. Why butterflies matter. <<https://butterfly-conservation.org/butterflies/why-butterflies-matter>>. Accessed 21 Sept 2021.

Choudhary, N. L., and N. Chishty. 2020. Effect of habitat loss and anthropogenic activities on butterflies' survival: A review. *International Journal of Entomology*.

Dallas, T. A., M. Saastamoinen, T. Schulz, and O. Ovaskainen. 2020. The relative importance of local and regional processes to metapopulation dynamics. *Journal of Animal Ecology* 89:884-896.

Dennis, R. L. 2004. Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. *Ecological Entomology* 29:744-752.

Dennis, R. L., L. Dapporto, T. H. Sparks, S. R. Williams, J. N. Greatorex-Davies, J. Asher, and D. B. Roy. 2010. Turnover and trends in butterfly communities on two

- British tidal islands: stochastic influences and deterministic factors. *Journal of Biogeography* 37:2291-2304.
- Dhondt, A.A. 2011. *Interspecific competition in birds*. Oxford University Press, Oxford, United Kingdom.
- Dodds, J. S. 2022. *Carex cumulate*.  
<<https://www.nj.gov/dep/parksandforests/natural/heritage/docs/carex-cumulata-profile-clustered-sedge.pdf>>. Accessed 9 Feb 2023.
- Drechsler, M., F. V. Eppink, and F. Wätzold. 2011. Does proactive biodiversity conservation save costs?. *Biodiversity and Conservation* 20:1045-1055.
- Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival: ecological archives e066-008. *Ecology* 66:1762-1768.
- Ferrer-Paris, J. R., A. Sanchez-Mercado, A. L. Vilorio, and J. Donaldson. 2013. Congruence and diversity of butterfly-host plant associations at higher taxonomic levels. *PLoS ONE* 8.
- Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16:265-280.
- Florida Native Plant Society. 2018. *Native host plants for scarce south Florida butterflies 2018* edited by Broward Butterfly & Native Plant Chapters.  
<<https://broward.fnpschapters.org/data/uploads/downloads/host-plants-for-scarce-sf-butterflies-fnps-2018.xlsx.pdf>>. Accessed 21 Sept 2021.
- Forister, M. L., A. C. McCall, N. J. Sanders, J. A. Fordyce, J. H. Thorne, J. O'Brien, D. P. Waetjen, and A. M. Shapiro. 2010. Compounded effects of climate change and



- habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences* 107:2088-2092.
- Frankham, R. 1998. Inbreeding and extinction: island populations. *Conservation Biology* 12:665-675.
- Gallant, A. L., T. R. Loveland, T. L. Sohl, and D. E. Napton. 2004. Using an ecoregion framework to analyze land-cover and land-use dynamics. *Environmental Management* 34:S89-S110.
- GBIF.org. 2023. GBIF occurrence download. <<https://doi.org/10.15468/dl.ecqzx7>>. Accessed 4 March 2023.
- Ghazanfar, M., M. F. Malik, M. Hussain, R. Iqbal, and M. Younas. 2016. Butterflies and their contribution in ecosystem: A review. *Journal of Entomology and Zoology Studies* 4:115-118.
- Gompert, Z., L. K. Lucas, C. A. Buerkle, M. L. Forister, J. A. Fordyce, and C. C. Nice. 2014. Admixture and the organization of genetic diversity in a butterfly species complex revealed through common and rare genetic variants. *Molecular Ecology* 23:4555-4573.
- Groff, L. A., S. B. Marks, and M. P. Hayes. 2014. Using ecological niche models to direct rare amphibian surveys: a case study using the Oregon spotted frog (*Rana pretiosa*). *Herpetological Conservation and Biology* 9:354-368.
- Grundel, R., and N. B. Pavlovic. 2007. Resource availability, matrix quality, microclimate, and spatial pattern as predictors of patch use by the Karner blue butterfly. *Biological Conservation* 135:135-144.

- Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9:623-633.
- Haddad, N. M., and J. J. Tewksbury. 2005. Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications* 15:250-257.
- Hamm, C. A., B. L. Williams, and D. A. Landis. 2013. Natural history and conservation status of the endangered Mitchell's satyr butterfly: synthesis and expansion of our knowledge regarding *Neonympha mitchellii mitchellii* French 1889. *The Journal of the Lepidopterists' Society* 67:15-28.
- Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology* 10:578-590.
- Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239-251.
- Hanski, I. A., and O. E. Gaggiotti, editor. 2004. *Ecology, genetics and evolution of metapopulations*. Academic Press, Cambridge, Massachusetts, USA.
- Hare M. L., X. W. Xu, Y. D. Wang, and A. E. Gedda. 2021. Do woody tree thinning and season have effect on grass species' composition and biomass in a semi-arid savanna? The case of a semi-arid savanna, southern Ethiopia. *Frontiers in Environmental Science* 9:692239.
- Inchausti, P., and J. Halley. 2003. On the relation between temporal variability and persistence time in animal populations. *Journal of Animal Ecology* 72:899-908.

- Janz, N., S. Nylin, and N. Wahlberg. 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evolutionary Biology* 6:1-10.
- Jue, D. K., A. C. Merwin, S. S. Jue, D. McElveen, and B. D. Inouye. 2022. Effects of frequency and season of fire on a metapopulation of an imperiled butterfly in a longleaf pine forest. *Conservation Science and Practice* 4:e12739.
- Kalarus, K., and P. Nowicki. 2015. How do landscape structure, management and habitat quality drive the colonization of habitat patches by the dryad butterfly (Lepidoptera: Satyrinae) in fragmented grassland?. *PloS ONE* 10:e0138557.
- Kemp, D. J., and A. K. Krockenberger. 2002. A novel method of behavioural thermoregulation in butterflies. *Journal of Evolutionary Biology* 15:922-929.
- Kerr, J. T., and I. Deguise. 2004. Habitat loss and the limits to endangered species recovery. *Ecology Letters* 7:1163-1169.
- Kral, K. C., R. F. Limb, J. P. Harmon, and T. J. Hovick. 2017. Arthropods and fire: previous research shaping future conservation. *Rangeland Ecology & Management* 70:589-598.
- Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, M. Stillfried, I. Heckmann, A. K. Scharf, D. M. Augeri, and S. M. Cheyne. 2013. The importance of correcting for sampling bias in Maxent species distribution models. *Diversity and Distributions* 19:1366-1379.
- Krauss, J., I. Steffan-Dewenter, and T. Tschardt. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. *Biological Conservation* 120:355-361.

- Krebs, C. J. 1972. The experimental analysis of distribution and abundance. Harper and Row. New York, USA.
- Kuefler, D., N. M. Haddad, S. Hall, B. Hudgens, B., Bartel, and E. Hoffman. 2008. Distribution, population structure and habitat use of the endangered Saint Francis satyr butterfly, *Neonympha mitchellii francisci*. The American Midland Naturalist 159:298-320.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. American Entomologist 15:237-240.
- Lewis, D. 1992. Greenbug aphid damage to lawns apparent now. Iowa State University Extension and Outreach: Horticulture and Home Pest News: 125.
- Local Conditions. 2022a. Jersey, AR past weather.  
<<https://www.localconditions.com/weather-jersey-arkansas/71651/past.php>>.  
Assessed 30 May 2022.
- Local Conditions. 2022b. Warren, AR past weather.  
<<https://www.localconditions.com/weather-warren-arkansas/71671/past.php>>.  
Assessed 30 May 2022.
- Lovely, E. C., and J. K. Ettman. 2013. Arkansas lepidoptera survey: a preliminary check list of Arkansas species. Journal of the Arkansas Academy of Science 67:180-196.
- Low, B. W., Y. Zeng, H. H. Tan, and D. C. Yeo. 2021. Predictor complexity and feature selection affect Maxent model transferability: evidence from global freshwater invasive species. Diversity and Distributions 27:497-511.

- MacDougall, S. 2020. More than monarchs: effects of wildfire on monarch butterfly habitat. <<https://monarchjointventure.org/blog/more-than-monarchs-effects-of-wildfire-on-monarch-butterfly-habitat>>. Accessed 14 April 2023.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theoretical Population Biology* 21:269-288.
- Melnechuk, M., B. Holimon, and R. O'Neill. 2008. Implementation of the Warren Prairie conservation area plan: woodland, savanna, and prairie habitat restoration and ecological monitoring. <<https://www.wildlifekansas.com/proposals/2008Preproposals/Warren%20Prairie%20restoration%20and%20monitoring.pdf>>. Accessed 9 Feb 2023.
- Mercer, J. 2022. Sedge grass care. <<https://plantaddicts.com/sedge-grass-care/>>. Accessed 26 May 2023.
- Merow, C., M. J. Smith, and J. A. Silander Jr. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058-1069.
- Milko, L. V., N. M. Haddad, and S. L. Lance. 2012. Dispersal via stream corridors structures populations of the endangered St. Francis' satyr butterfly (*Neonympha mitchellii francisci*). *Journal of Insect Conservation* 16:263-273.
- Multi-Resolution Land Characteristic Consortium [MRLC]. 2015. North American land change monitoring system. Retrieved from <<https://www.mrlc.gov/data?f%5B0%5D=region%3Anorth%20america>>. Accessed 10 Nov 2022.

- Nieminen, M., M. C. Singer, W. Fortelius, K. Schöps, and I. Hanski. 2001. Experimental confirmation that inbreeding depression increases extinction risk in butterfly populations. *The American Naturalist* 157:237-244.
- Nowicki, P., J. Settele, P. Y. Henry, and M. Woyciechowski. 2008. Butterfly monitoring methods: the ideal and the real world. *Israel Journal of Ecology and Evolution* 54:69-88.
- Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology* 194:5-16.
- Phillips, S. J., M. Dudík, and R. E. Schapire. N.d. Maxent software for modeling species niches and distributions (Version 3.4.1). Retrieved from [http://biodiversityinformatics.amnh.org/open\\_source/maxent/](http://biodiversityinformatics.amnh.org/open_source/maxent/). Accessed 15 Oct 2022.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Pollard, E., and T. J. Yates. 1994. *Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme*. Springer Science & Business Media.
- Polus, E., S. Vandewoestijne, J. Choutt, and M. Baguette. 2007. Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodiversity and Conservation* 16:3423-3436.
- R Core Team. 2022. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

- Raney, H. 2017. Butterflies of Arkansas homepage. <<http://www.hrna.com/RNA/Bfly%20pages/Checklist%20foodplant%20page%20.htm>>.  
Accessed 21 Sept 2021.
- Robinson, G. S., P. R. Ackery, I. J. Kitching, G. W. Beccaloni and L. M. Hernández, 2010. HOSTS - A database of the world's lepidopteran hostplants. Natural History Museum, London. <<http://www.nhm.ac.uk/hosts>>. Accessed 21 Sept 2021.
- Rouse, E. 1968. Satyrs and wood nymphs of Arkansas. *Journal of the Arkansas Academy of Science* 22:29-32.
- Schulz, T., J. Vanhatalo, and M. Saastamoinen. 2020. Long-term demographic surveys reveal a consistent relationship between average occupancy and abundance within local populations of a butterfly metapopulation. *Ecography* 43:306-317.
- Scott, J. A. 1992. Hostplant records for butterflies and skippers (mostly from Colorado) 1959-1992, with new life histories and notes on oviposition, immatures, and ecology (Doctoral dissertation, Colorado State University. Libraries).
- Severns, P. M. 2003. The effects of a fall prescribed burn on *Hemileuca eglanterina* Boisduval (Saturniidae). *Journal of the Lepidopterists Society* 57:137-143.
- Sharma, A., D. K. Brethauer, J. McKeithen, K. K. Bohn, and J. G. Vogel. 2020. Prescribed burn effects on natural regeneration in pine flatwoods: implications for uneven-aged stand conversion from a Florida study. *Forests* 11:328.
- Shepard, C. A., L. C. Crenshaw, E. M. Baldwin, K. Sammon, K. M. Holman, D. A. Gazaway, N. E. Phelan, W. H. Baltosser, M. Lombardi, M. D. Moran, and M. R. McClung. 2021. Distribution and habitat preferences of a frosted elfin subspecies

- (*Callophrys Irus hadros*, Lycaenidae) in Arkansas. The Journal of the Lepidopterists' Society 75:104–112.
- Singer, M. C., and B. Wee. 2005. Spatial pattern in checkerspot butterfly—host plant association at local, metapopulation and regional scales. *Annales Zoologici Fennici* 42:347–361.
- Singer, M. C., and C. D. Thomas. 1996. Evolutionary responses of a butterfly metapopulation to human-and climate-caused environmental variation. *The American Naturalist* 148:S9-S39.
- Swengel, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. *Biological Conservation* 76:73-85.
- Szcodronski, K. E., D. M. Debinski, and R. W. Klaver. 2018. Occupancy modeling of *Parnassius clodius* butterfly populations in Grand Teton National Park, Wyoming. *Journal of Insect Conservation* 22:267-276.
- The Nature Conservancy & Arkansas Natural Heritage Commission. 2009. Restoration of woodland habitats at the Moro-Big Pine and Blackland Prairie and woodland conservation areas and measuring progress towards desired ecological conditions. <<https://www.wildlifearkansas.com/materials/ProjectReports/T26-05%20Moro-%20big%20Pine%20and%20Blackland%20prairie%20and%20woodland%20conservation%20FINAL.pdf>>. Accessed 21 Sept 2021.
- Thom, M. D., J. C. Daniels, L. N. Kobziar, and J. R. Colburn. 2015. Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida. *PLoS ONE* 10:e0126755.



- Tian, Q., L. Yang, P. Ma, H. Zhou, N. Liu, W. Bai, H. Wang, L. Ren, P. Lu, W. Han, P. A. Schultz, J. D. Bever, F. H. Zhang, H. Lambers, and W. H. Zhang. 2020. Below-ground-mediated and phase-dependent processes drive nitrogen-evoked community changes in grasslands. *Journal of Ecology* 108:1874-1887.
- Townsend, L, Extension Entomologist University of Kentucky College of Agriculture. 2000. Aphids. <<https://entomology.ca.uky.edu/files/efpdf1/ef103.pdf>>. Accessed 1 May 2023.
- United States Department of Agriculture, Natural Resources Conservation Service, National soil survey center (USDA NRCS national soil survey center). 2014. gSSURGO Muaggat FY 2013. Retrieved from <<https://gis.arkansas.gov/product/gssurgo-muaggat-fy-2013/>>. Accessed 15 Feb 2023.
- United States Department of Commerce, National Ocean and Atmospheric Administration, National Weather Service [NWS]. 2022. NWS Little Rock, AR - new elevation based zones in the Little Rock county warning Area. <<https://www.weather.gov/lzk/newzones.htm>>. Accessed 26 May 26, 2023.
- United States Environmental Protection Agency (EPA). 2014. Ecoregions level III and IV 2004 (polygon). Retrieved from <<https://gis.arkansas.gov/product/ecoregions-level-iii-and-iv-2004-polygon/>>. Accessed 15 Oct 2022.
- Vogel, J. A., R. R. Koford, and D. M. Debinski. 2010. Direct and indirect responses of tallgrass prairie butterflies to prescribed burning. *Journal of Insect Conservation* 14:663-677.

- Wallisdevries, M. F., C. A. Van Swaay, and C. L. Plate. 2012. Changes in nectar supply: a possible cause of widespread butterfly decline. *Current Zoology* 58:384-391.
- Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. *Forest Ecology and Management* 47:195-210.
- Waltz, A. E. M., and W. W. Covington. 2004. Ecological restoration treatments increase butterfly richness and abundance: mechanisms of response. *Restoration Ecology* 12:85-96.
- Warchola, N., E. E. Crone, and C. B. Schultz. 2018. Balancing ecological costs and benefits of fire for population viability of disturbance-dependent butterflies. *Journal of Applied Ecology* 55:800-809.
- Warren, M. S. 1985. The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white *Leptidea sinapis*. *Biological Conservation* 33:147-164.
- Weather Underground. 2022a. El Dorado, AR weather history. <<https://www.wunderground.com/history/daily/us/ar/warren/KELD/date/2020-5-16>>. Assessed 3 Sept 2022.
- Weather Underground. 2022b. Hot Springs, AR weather history. <<https://www.wunderground.com/history/daily/us/ar/hot-springs/KHOT/date/2022-5-27>>. Assessed 3 Sept 2022.
- Wells, C. N., R. S. Williams, G. L. Walker, and N. M. Haddad. 2009. Effects of corridors on genetics of a butterfly in a landscape experiment. *Southeastern Naturalist* 8:709-722.

- Westwood, R., A. R. Westwood, M. Hooshmandi, K. Pearson, K. LaFrance, and C. Murray. 2020. A field-validated species distribution model to support management of the critically endangered Poweshiek skipperling (*Oarisma poweshiek*) butterfly in Canada. *Conservation Science and Practice* 2:e163.
- WorldClim. 2020. Historical climate data. Retrieved from <https://worldclim.org/data/worldclim21.html>. Accessed 10 Oct 2022.
- Woś, B., M. Pająk, and M. Pietrzykowski. 2022. Soil organic carbon pools and associated soil chemical properties under two pine species (*Pinus sylvestris* L. and *Pinus nigra* Arn.) introduced on reclaimed sandy soils. *Forests* 13:328.
- Xu, T., and M. F. Hutchinson. 2013. New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. *Environmental Modelling & Software* 40:267-279.
- Zhang, R., A. A. Degen, Y. Bai, T. Zhang, X. Wang, X. Zhao, and Z. Shang. 2020. The forb, *Ajania tenuifolia*, uses soil nitrogen efficiently, allowing it to be dominant over sedges and Graminae in extremely degraded grasslands: implications for grassland restoration and development on the Tibetan Plateau. *Land Degradation & Development* 31:1265-1276.
- Zhang, Y., Q. Zheng, Q., X. Gao, Y. Ma, K. Liang, H. Yue, X. Huang, K. Wu and X. Wang. 2022. Land degradation changes the role of above-and below-ground competition in regulating plant biomass allocation in an alpine meadow. *Frontiers in Plant Science* 13:3.

