EFFECTS OF LAND USE AND ASSOCIATED MANAGEMENT PRACTICES ON *CYCNIA COLLARIS*, A DISPERSAL LIMITED HABITAT SPECIALIST

By

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Abstract: Milkweed (*Asclepias* spp.) plants provide habitat for several insect species, including the unexpected cycnia (*Cycnia collaris*), a milkweed dependent moth that has limited dispersal abilities, and of which, there have been very few published studies. Land use may influence the distribution and abundance of unexpected cycnia populations, as well as parasitism on the larval stage by tachinid flies and ichneumonid wasps. The objective of this research was to evaluate the distribution and abundance of unexpected cycnia across land uses (roadsides, managed grasslands, and rangelands) and associated land management practices (mowing and prescribed fire) in north-central Oklahoma and to document parasitism rates to evaluate the potential role (sources versus sinks) of land uses for this species. I also evaluated factors influencing the distribution of unexpected cycnia throughout its range with an ecological niche model. I measured the weekly abundance of *A. viridis*, the most common milkweed species in this area, and unexpected cycnia on 5 m x 50 m transects from mid-April to early November in 2015 and 2016. I also measured milkweed characteristics along the transects. Fourth and fifth instar cycnia (having had the opportunity to be exposed to parasites in the field) were collected and reared individually in the lab to estimate parasitism rates. Annually, milkweed abundances varied among land uses but unexpected cycnia abundances did not. Timing of land management affected milkweed availability later in the growing season. Many milkweed characteristics also differed across land uses. In 2015, parasitism did not differ among land uses, but it was higher in rangelands in 2016. The dominant parasitoid varied seasonally. Parasitism by ichneumonid wasps occurred mainly in the first half of the season and then again towards the end, while tachinid fly parasitism was more common in the second half of the season. Across the entirety of its range, unexpected cycnia distribution was most influenced by annual precipitation and by land cover.

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CHAPTER I

INTRODUCTION

This study focused on the unexpected cycnia moth (*Cycnia collaris*), a milkweed dependent moth with limited dispersal abilities that is considered a species of conservation concern throughout parts of its range. The objective of my research was to evaluate the distribution and abundance of unexpected cycnia across land uses and associated land management practices in north-central Oklahoma and its distribution throughout its range. I also documented parasitism rates to evaluate the potential role (sources versus sinks) of land uses for this species. The results of this project will provide valuable life history and natural history data about a poorly studied species. These data are critical for evaluating the status of this species and identifying appropriate conservation practices. These results will also contribute to understanding the effects of land use change and land management activities on habitat specialists with limited dispersal abilities, as well as on generalist parasites and interactions between these parasites and the habitat specialists.

CHAPTER II

INFLUENCES OF LAND USE AND LAND MANAGEMENT ON *A. VIRIDIS* AND *C. COLLARIS* ABUNDANCES

INTRODUCTION

Habitat loss, fragmentation, and degradation are growing global issues as humans change land uses for urbanization, development, and agriculture. Of the world's biomes, temperate grasslands and savannas are one of the top three with the most habitat loss and also with the least protection, and therefore, are at high risk (Hoekstra et al. 2005). Over the past 50 years, the Great Plains region lost more than 70% of its grasslands to land use changes and disruption of ecological drivers, such as fire suppression and the loss of large herbivores, with less than 13% of native tallgrass prairies, 29% of mixed grass prairies and 51% of shortgrass prairies remaining today (Samson et al. 2004).

Despite this loss, remaining grasslands continue to be converted to other land uses. From 2008 to 2012, grasslands accounted for 77% (2.3 million hectares) of land in the Great Plains region converted to croplands (Lark et al. 2015). For example, in the Corn Belt region of the Midwest, over 99% of tallgrass prairies and 70% of mixed grass prairies have been lost, mainly due to conversion to row crop agriculture (Wright and Wimberly 2013). Land use changes have been modeled through 2051 based on current patterns and various natural resource policy scenarios. In these models, all scenarios resulted in loss of grassland habitat as agricultural needs increase with population growth (Lawler et al. 2014). Therefore, land use change is expected to continue to be a threat to natural ecosystems.

Alongside habitat loss, the remaining Great Plains grasslands differ from historical conditions due to fire suppression, modified fire regimes, encroachment by trees and shrubs, and the loss of large grazing herbivores, such as bison (Samson et al. 2004, Engle et al. 2008). Fragmentation from human activities, such as road and fence construction, can also lead to habitat degradation. With this continuing loss and degradation of grassland habitat, it is important to understand how native plant and insect species respond to changing land use patterns and disturbance regimes.

Effects of disturbance on plants and insects

Current disturbance regimes often differ from historical ones. Disturbances, such as fire and mowing, affect habitat quality, plant diversity and growth, and insect species distribution and abundance (Swengel 2001). Fire positively influences herbaceous plant growth and prevents encroachment by shrub and tree species (Panzer and Schwartz 2000). However prescribed fires may not occur in the same time frame as wildfires occurred historically, both in terms of frequency and season (Engle and Bidwell 2001). While many plants may positively respond to fire during any season, seasonality may influence plant community structure and composition. Dormant season spring burns can result in earlier and faster plant growth early in the growing season (Engle and Bidwell 2001). When fire occurs during the summer prior to plant senescence, it removes the above-ground portion of plants (Towne and Kemp 2008). This allows re-growth to occur later in the season and provides plant resources later in the growing season that may otherwise be unavailable (Baum and Sharber 2012, Evans et al. 2013, Baum and Mueller

2015). Additionally, fire that occurs in the summer versus the spring can increase plant community richness and diversity (Towne and Kemp 2008, Evans et al. 2013). Creating habitat heterogeneity with patches in different stages of time since fire (often referred to as “patch burning”) can be beneficial by providing habitat for species that benefit from different fire regimes (Panzer and Schwartz 2000, Fuhlendorf and Engle 2001, 2004, Engle et al. 2008). Sometimes the use of fire is restricted due to climate or social concerns. When this happens, mowing offers an alternative form of vegetation management.

Mowing involves cutting herbaceous and emergent woody vegetation to a uniform height. Timing of mowing may affect plant populations and the ability of plants to re-grow during the same season (Swengel 2001, Baum and Mueller 2015, Fischer et al. 2015). Mowing also can increase the availability of floral resources (Korosi et al. 2014). This practice can result in an immediate increase in plant species richness, but this increase may be seen for only about a year after the initial mowing. However, an increase in the relative abundance of perennial species may occur in subsequent years (Maron and Jeffries 2001). Varying the timing and frequency of mowing can be the most beneficial to plant biodiversity (Allan et al. 2014), although current practices often focus on homogeneous mowing regimes. Some mowed lands are also hayed. Haying after mowing can increase plant diversity by encouraging forbs species to establish and grow because removal of the hay allows more sunlight to reach the soil than mowing alone (Tix and Charvat 2005, Begay 2011). Burning and mowing both influence plant communities, which then have the potential to affect the insect species that rely on these plants for most or all of their life cycles.

Different insect species, even if they occur in the same habitat, have diverse requirements and will respond differently to disturbance regimes (Vogel et al. 2007). Timing of a disturbance may affect insect species in many ways. Disturbances may result in mortality of individuals if they are immobile, such as in the egg or pupal stage, or unable to escape, such as in the caterpillar/larval stage (Panzer and Schwartz 2000). Populations may be negatively impacted if individuals cannot find suitable habitat after mowing or prescribed fire or if no other populations occur nearby to recolonize the area (Panzer and Schwartz 2000, Swengel and Swengel 2007). Different management strategies may affect diversity differently, so it may be beneficial to establish areas within a site that are managed differently. For example, mowing can be used in combination with prescribed fire to create unburned areas that can act as a refugia to insects that would otherwise be removed from a site during burns (Swengel and Swengel 2007). Mowing before plants senesce may provide a benefit to insects by providing habitat (i.e., plant re-growth) later into the season than would occur with no mowing (Korosi et al. 2014, Baum and Mueller 2015, Fischer et al. 2015). Mowing multiple times per season, such as often occurs on roadsides, may result in some species failing to re-grow, as well as shorter vegetation and fewer flowering plants which makes that habitat less desirable to many insects (Saarinen et al. 2005). Fire may attract certain insect species by providing young re-growth that some species prefer to lay eggs on (Evans et al. 2013). Therefore, spatial and temporal variations in management practices can encourage heterogeneity in land units and support a variety of insect species (e.g., Swengel 2001, Engle et al. 2008, Fischer et al. 2015).

Milkweeds and their associates

Some native plants that colonize disturbed areas may be considered weedy and are targeted for removal and/or control, especially in agricultural fields (Hartzler and Buhler 2000, Hartzler 2010); however, these plants may be critical for some insect species. In the past, some milkweed species, such as common milkweed (*Asclepias syriaca*) and showy milkweed (*A. speciosa*) were considered noxious weeds in several states due to their occurrence in agricultural fields. However, milkweeds are an important resource for many insect species, including pollinators. Milkweed dependent insects include the monarch butterfly (*Danaus plexippus*), milkweed bugs, milkweed beetles, milkweed leaf-eating beetles, milkweed stem weevils (Betz et al. 1997), and the unexpected cycnia moth (*Cycnia collaris*) (Metzler and Lucas 1990). Milkweed dependent insects utilize different parts of the plant, including the leaves, stems, roots, and seed pods. Monarch and unexpected cycnia larvae feed on leaves and flowers; milkweed beetle larvae bore into the roots; milkweed stem weevil larvae develop in the stems, and small and large milkweed bug larvae feed on seed pods (Betz et al. 1997, Bess 2005). Most of these insects have aposematic orange/black coloring to warn predators that they contain cardenolides from the milkweed (with the exception of the milkweed weevils) that causes them to be distasteful and/or poisonous when ingested (Betz et al. 1997). Many other insects, such as bees and butterflies, visit milkweed flowers for nectar.

The importance of different milkweed species varies geographically and temporally. In the Great Plains, *A. syriaca* and green antelopehorn milkweed (*A. viridis*) are common and widely distributed in both natural and disturbed areas. *Asclepias syriaca* is more abundant in the upper Great Plains, while *A. viridis* is found more in the southern

Great Plains (Kartesz 2015). However, the increased use of herbicide tolerant transgenic crops, and consequently, the increased use of herbicides have decreased *A. syriaca* populations in agricultural fields and herbicide drift areas throughout the Upper Midwest region (Hartzler 2010). It has been estimated that the decline in milkweed populations in agricultural and non-agricultural lands, such as Conservation Reserve Program (CRP) lands and pastures, throughout the Midwest may be up to 58% since 1999 (Pleasants and Oberhauser 2013). Throughout all habitats in the Midwest, 40% of milkweed populations have been lost in the same time period (Pleasants 2016).

Disturbances can influence milkweed abundance and availability. If mowing or prescribed fire occur in the middle of the season, *A. viridis* has the potential to re-grow and consequently be present into the fall (Baum and Sharber 2012, Baum and Mueller 2015). *Asclepias syriaca* has a similar response to late summer mowing (Fischer et al. 2015). Management practices can mimic natural disturbances, such as wildfires, that may have occurred historically that would influence the temporal availability of milkweed for milkweed-dependent species.

Study species – Cycnia collaris

While moths account for over 90% of Lepidopteran species, many moths are poorly studied, such as the unexpected cycnia moth (*Cycnia collaris*, Family: Erebidae), especially when compared to butterflies (New 2004). The unexpected cycnia moth was previously classified as *Cycnia inopinatus*, but in 2015 it was determined to be synonymous with *C. collaris* and *C. tenerosa*. *Cycnia collaris* was the first of these species to be described and therefore, the three species have been combined under that name (Lafontaine and Schmidt 2015). The unexpected cycnia emerges as an adult in the early spring and produces two to three generations each year (Covell 1984, Bess 2005). Adults from overwintered pupae emerge in April, while the second generation overwinters as pupae in leaf litter. Cream/yellow colored, spherical eggs are laid singly or in clusters on milkweed leaves and stems. Caterpillars are bright orange with bright orange to dark gray/brown tufts of hair and feed on milkweed leaves. They drop off the plant when disturbed. The unexpected cycnia is most easily identified as caterpillars because adults appear identical to the delicate cycnia (*C. tenera*) and the Oregon cycnia (*C. oregonesis*), all three of which have overlapping ranges to some extent. Unexpected cycnia caterpillars and adults sequester cardenolides from milkweeds. When raised on sandhill milkweed (*A. humistrata*), cardenolide concentrations stored in the caterpillar exceeded those of the host plant (Nishio 1980).

Unexpected cycnia are associated with dry prairies and oak barren habitats throughout the Great Plains, east to the Atlantic coast, and south to Florida (Covell 1984, Bess 2005), as well as into New Mexico and Arizona. The unexpected cycnia moth is highly localized in distribution (Bess 2005), and is thought to have limited dispersal abilities. Maximum dispersal distances are estimated from a few hundred meters to less than 800 m, suggesting unexpected cycnia moths can only disperse when large continuous areas of habitat are present, although specific habitat requirements are not known (or at least not published) (Bess 2005). At the state level, the unexpected cycnia is considered endangered in Ohio and threatened in Massachusetts, with habitat loss and fragmentation and fire suppression identified as the main threats (Metzler and Lucas 1990, NHESP 2012). Other threats include invasive plants, insecticides, parasitoids, and light pollution (NHESP 2012). These factors are likely common throughout the entirety of its range.

Despite its consideration as a species of conservation concern, few studies have been published on the unexpected cycnia. The goal of my research is to evaluate the distribution and abundance of unexpected cycnia across land uses and associated management practices in north central Oklahoma. I hypothesize that unexpected cycnia abundance will vary among land uses with higher abundances in natural land uses with patchy disturbance regimes (i.e., patch burn rangelands), which will prevent disturbances from affecting the entire population.

METHODOLOGY

Study sites

To evaluate the distribution and abundance of milkweed and unexpected cycnia across land uses, I identified three replicate sites of each of three land uses, which included managed grasslands, roadsides, and rangelands. Managed grasslands and roadsides were mowed and rangelands were burned (Table 1). These land uses and management practices are present in grasslands throughout the Great Plains. Selected sites all had known populations of *A. viridis* (the most common milkweed species in the study region) and unexpected cycnia. Many of these sites were previously monitored for monarch use for research in the Baum Lab (Baum and Sharber 2012, Mueller 2013, Mueller and Baum 2014, Andreoli 2015, Baum and Mueller 2015).

Roadsides and managed grasslands were located within a 20-km radius of Stillwater, OK in Payne and Noble Counties and were mowed at different intervals. Managed grasslands were mowed, and sometimes hayed, once a year. Four managed grasslands were identified (versus three replicates for the other land uses) to account for management activities outside of our control. Managed grasslands were composed of native grasses and forbs. The first site is located north of Boomer Lake at the southwest corner of Kameoka Trail and E. Rogers Dr. with an area of 0.0675 km^2. This site was mowed in both 2015 and 2016. OSU's Cross Country field was the second site, located north of campus and has an area of 0.189 km^2. The Cross Country field was mowed in 2015 but not 2016. The third site is at the southeast corner of N. Perkins Rd. and Airport Rd. and has an area of 0.10 km^2. This site was mowed and hayed once in 2015 and twice in 2016. The fourth site, located at the northwest corner of N. Perkins Rd. and E. Richmond Rd, has an area of 0.02 km^2. This site was mowed and hayed in 2016 but not 2015.

Roadsides were mowed several times a year. Roadside sites included Highway 177, Highway 51, and North Perkins Road. The two highways are managed by the Oklahoma Department of Transportation (ODOT). Surveyed areas for Highway 177 were in the 10.1 km between the turnpike and Highway 64. Highway 51 was surveyed between Range Rd. and Coyle Rd., a distance of 7 km. Surveys along Perkins Rd. occurred in the 3.2 km between Richmond Rd. and Yost Rd. Survey sites were limited to areas that had a shoulder or turnoff to safely pull off the road. In 2016, ODOT changed roadside management practices to be more beneficial for monarch and pollinator habitat. In doing so, they switched from mowing multiple times per year to once in mid-summer (ODOT 2016) and a fall clean-up mow. Safety zones and operational zones continued to be mowed multiple times a year. Vegetation in safety zones is kept at a height of less than 30 centimeters to ensure visibility for motorists (Montgomery et al. 2010).

Safety/operational zones may extend from three to nine meters from the edge of the road. These zones are managed multiple times a year to maintain “desirable” grasses while reducing the amount of weeds present, including herbicide applications (Montgomery et al. 2010).

Rangeland sites were located at OSU’s Stillwater Research Range, which is located about 20 km southwest of Stillwater, OK on Coyle Rd. The Stillwater Research Range includes three patch burned pastures, with areas spanning from 0.48 to 0.7 km^2. In these patch burned pastures, one-sixth of the site is burned every spring and one-sixth is burned every summer for an overall three-year fire return interval. Three subplots at each site were chosen to assess different times since burn and season of burn and included those burned the spring prior to sampling, the same spring, and the same summer. For 2015, these sites included the subplots burned Spring 2014, Spring 2015, and Summer 2015. The subplots in 2016 were those burned Spring 2015, Spring 2016, and Summer 2016; therefore, the Spring 2015 subplot was used both years.

Distribution and abundance surveys

Sampling occurred in 2015 and 2016, beginning in mid-April, corresponding to when milkweed emerged to document when the first eggs were laid and continued into the first week of November when most milkweed had senesced, with each site visited once per week. I waited two weeks after any management activity occurred to resume sampling to allow time for milkweed to re-grow. I concluded sampling at a site when I could find no milkweed for at least two consecutive weeks (at least four weeks post-management activity). During each site visit, I recorded the density of milkweed plants found on one 5 m x 50 m transect. The starting location and direction of each transect were randomly selected during each site visit to provide an overall view of milkweed availability at each site. Individual plants were defined as the set of stems emerging from the same central location. I measured the height (height above ground level in cm) and width (the diameter of the smallest circle needed to encompass the entire plant in cm) of the first thirty milkweed plants along each transect, as well as the distance to the nearest milkweed plant (length from the edge of the plant to the edge of the nearest plant). For these thirty plants, I also recorded the phenological stage and number of stems (based on aboveground separation), buds, flowers, and seed pods. Phenological stages included vegetative (green stems/leaves, but no buds, flowers, or seed pods), pre-reproductive (buds present), flowering/anthesis (flowers present and open), fruit development (seed pods present), seed shatter (seed pods dehisced), and senescing (stems/leaves starting to yellow, typically with no buds or flowers, but seed pods may be present). When multiple phenological stages were present, the plant was placed in the latest possible phenological stage. For example, a plant with buds, flowers, and seed pods would be placed in the fruit development stage. In 2015, I completed 98 transects in managed grasslands, 62 along roadsides, 62 in previous spring (Spring 2014) burn plots, 67 in same spring (Spring 2015) burn plots, and 75 in summer (Summer 2015) burn plots. In 2016, I completed 92 transects in managed grasslands, 63 along roadsides, 57 in previous spring (Spring 2015) burn plots, 58 in same spring (Spring 2016) burn plots, and 78 in summer (Summer 2016) burn plots. Differences in the number of transects completed reflect gaps in time (two weeks) following mowing or burning events when sites were not visited.

All milkweed plants on each transect were inspected for unexpected cycnia eggs and larvae. I recorded the number of eggs and larvae (including instar stage) per plant to determine the distribution, abundance, and density of unexpected cycnia. I also recorded whether eggs were located on the top or bottom of the leaf, the distance from the ground, distance from stalk, and distance along stalk; however, it was uncommon to find unexpected cycnia eggs. Instar stages for this species are determined by size and setae/hair density (setae/hairs are located in distinct clumps and the number of hairs in a clump increases with instar stage) of the caterpillar, with each subsequent instar getting increasingly larger and more hairy (Figure 1). It was uncommon to find adults; however, I recorded any adults, if present. However, it should be noted that adults are almost identical in appearance to *C. oregonesis* and *C. tenera*, which may also be found in the study area, and identifications can be difficult to confirm in the field (Bess 2005). I also recorded the presence and abundance of other milkweed associated insects on these transects.

Statistical analysis

I compared milkweed and unexpected cycnia abundances across the land uses and seasons using an analysis of variance (ANOVA) at a significance level of 0.05 using R version 3.1.2. Because insect abundances fluctuate seasonally, I used circular statistics. I converted the abundance of caterpillars per month into frequencies of corresponding angles (April: 0 radians through November: 5.5 radians) to estimate the mean vector angle, circular standard deviation, and a measure of concentration (r) (Pinheiro et al. 2002, Floss et al. 2013) using the 'circular' package in R. I used the Rayleigh test to find the signification of the concentration value (Floss et al. 2013).

To compare *A. viridis* changes throughout the growing season, I selected three different two-week time periods to compare plant characteristics during mid-May (after flowering began), in Mid-July (after senescence began, but before the summer burns), and in mid-September (before complete senescence along roadsides). Unexpected cycnia caterpillars were present during these time frames. Milkweed characteristics were compared using one-way ANOVAs. I used chi-square tests to find if there were differences in phenological stages during these periods. I used ANOVAs to test if the mean date of flowering and mean date of senescence differed among land uses based on the latest phenological stage of the plants measured along transects (Augspurger and Salk 2017). Tukey's Honestly Significant Difference (HSD) post hoc analysis was run for any significant ANOVA results. I also tested for relationships between plant characteristics using Pearson's correlations.

RESULTS

For both years, I began milkweed transects in April and continued until milkweed senesced in November. Roadsides in the spring had the most abundant milkweed; however, with multiple mowing events during the growing season and the timing of mowing activities, no milkweed was present by the end of September. Most milkweed had senesced by late August and early September in sites that had no management in the same year (i.e., previous year spring burns) as well as sites that had management near the beginning of the growing season (i.e., same year spring burns), while sites with summer management (mowing or burning) had milkweed into October and some into November. Unexpected cycnia caterpillars were found from April through October. Eggs were only found on three plants throughout all transects in both years and therefore were not included in this analysis. While unexpected cycnia densities were variable across land uses, the differences were not significant in either year (2015: $F=1.123$, $df_{(4,361)}$, $p=0.345$;

2016: F=1.999, $df_{(4,349)}$, p=0.0942) (Figure 2). In 2015, caterpillars were most abundant during July and August in all land uses except for those burned the previous spring, while in 2016, peak abundance varied more among the land uses (Table 2). For both years, caterpillar abundances were more clustered during the collection period in the same spring burn plots (2015: r=0.913; 2016: r=0.829) than other treatments, and more spread out in managed grasslands (2015: r=0.601; 2016: r=0.612) and the summer burn treatments (2015: r=0.606; 2016: r=0.554) (Table 2).

Plant height was positively correlated with plant width for all treatments for both years (p<0.001), but this correlation was stronger along roadsides (0.624) than within managed grasslands (0.42) or burned sites (0.395-0.495) in 2015 (Figure 3). In 2016, the correlation between plant height and plant width was similar among all land uses and ranged from 0.41 to 0.48 (Figure 4).

Plants began to flower toward the end of April in both years regardless of land use and management (Table 3); however, the mean date of flowering differed among land uses and management practices in both years (2015: $df_{(4,490)}$, p=0.003; 2016: $df_{(5, 557)}$, p<0.001). In 2015, average flowering dates were later in summer burn plots than roadsides (p=0.046), same spring burn sites (p=0.01), and previous spring burn sites (p=0.003). In 2016, managed grasslands had a later average flowering date than roadsides (p=0.048), previous spring burn sites (p<0.001), and same spring burn sites (p<0.001), while summer burn plots had a later average flowering date than the two other times since burn (p<0.001).

Plants began to senesce a month earlier in 2016 (June 6) than 2015 (July 5) across all land uses (Table 3). During both years, there was a difference in the mean senescence date among the plants measured in the transects (2015: $df_{(4,580),}$ $p<0.001$; 2016: $df_{(4,968),}$ $p<0.001$). In 2015, average senescence dates were later in managed grasslands and roadsides than the three burn treatments ($p \leq 0.03$) Plants in areas burned the previous spring senesced earlier than areas burned the same spring ($p=0.03$). In 2016, plants in managed grasslands senesced later in the season than all other treatments ($p \leq 0.004$). Plants along roadsides senesced earlier than those in summer burn plots ($p=0.004$) but later than those in previous spring burn plots ($p=0.004$). Senescence occurred later in summer burn plots than the other two burn sites ($p<0.001$).

Seasonal differences in A. viridis and C. collaris

In May 2015, there was a significant difference in milkweed abundance ($F=5.406$, $df_{(4,59)}$, $p=0.00145$) (Figure 5A). Milkweed was more abundant along roadsides than in the rangeland sites ($p \leq 0.032$) during this time. There was also a difference in unexpected cycnia abundances ($F=2.563$, $df_{(4,59)}$, $p=0.04$) (Figure 6A); however, the post-hoc test did not reveal where these differences occurred ($p \geq 0.07$ for all). During this time period, there were differences in plant characteristics, including plant height ($F=39.56$, $df_{(4,575)}$, $p<0.001$), plant width ($F=4.327$, $df_{(4, 575)}$, $p=0.001$), and number of stems ($F=5.703$, $df_{(4,575)}$, $p<0.001$) (Table 4). There was a difference in distance to the nearest milkweed ($F=16.6$, $df_{(4, 573)}$, $p<0.001$). Plants in managed grasslands and roadsides were closer together than those in all rangelands ($p<0.001$); however, recall that abundances were also lower in rangeland sites. There was also a difference in phenological stage between the land uses ($\chi^2=18.3725$, $df=8$, $p=0.0186$); most plants were budding or flowering in areas that were burned that same spring, while a greater proportion of plants were in the vegetative stage in the other areas.

In May 2016, there was a significant difference in milkweed abundance (F=4.184, $df_{(4,59)}$, p=0.00475) (Figure 5B). Milkweed was more abundant along roadsides than in the areas burned the previous spring (p=0.008). There was no difference in unexpected cycnia abundances (F=0.54, $df_{(4,59)}$, p=0.707) (Figure 6B). During mid-May, there were differences in height (F=7.058, $df_{(4,859)}$, p<0.001), width (F=5.26, $df_{(4, 859)}$, p<0.001), and number of stems (F=8.188, $df_{(4,859)}$, p<0.001) (Table 4). There was also a difference in distance to the nearest milkweed (F=6.206, $df_{(4,859)}$, p<0.001). Managed grasslands and roadside plants were closer to one another than those in plots burned the previous spring (p<0.002), while plants in areas burned in the previous spring were farther apart than those in plots that would be burned later that summer (p=0.02). Phenological stage was independent of land use during this time period (χ^2=20.7838, df=12, p=0.053).

In July 2015, there was no difference in milkweed abundance (F=1.168, $df_{(4,59)}$, p=0.334) (Figure 5A) or in unexpected cycnia abundances (F=1.035, $df_{(4,59)}$, p=0.396) (Figure 6A). During mid-July (after senescence began), there were significant differences in plant height (F=94.01, $df_{(4, 649)}$, p<0.001), width (F=19.98, $df_{(4,649)}$, p<0.001), number of stems (F=3.72, $df_{(4,649)}$, p=0.005), and number of seedpods (F=4.048, $df_{(4, 649)}$, p=0.003) (Table 4). Phenological stage was dependent on land use (χ^2= 85.93, df=12, p<0.001). A majority of plants along roadsides (83%) were in the vegetative stage, while a quarter of plants in areas that would soon be burned in the summer had begun to senesce.

In July 2016, there was no difference in milkweed abundance (F=1.63, $df_{(4,59)}$, p= 0.179) (Figure 5B) or in unexpected cycnia abundances (F=1.826, $df_{(4,59)}$, p=0.136) (Figure 6B). In 2016, plant senescence began earlier, and some of the managed grasslands had already been mowed before July. Plant height ($F=42.88$, $df_{(4,657)}$, $p<0.001$), width ($F=13.36$, $df_{(4,657)}$, $p<0.001$), and number of stems ($F=4.836$, $df_{(4, 657)}$, $p<0.001$) were all significantly different (Table 4). There was a difference in the distance to the nearest milkweed ($F=3.916$, $df_{(4, 657)}$, $p=0.003$). Plants in managed grasslands and same spring burn areas were closer than in areas burned the prior spring ($p<0.04$). Phenological stage was dependent on land use ($\chi^2=190.47$, $df=16$, $p<0.001$). Almost half of plants along roadsides were in the vegetative stage, while over 70% of plants in areas that had not been burned in 2016 were senescing.

In September 2015, there was not a significant difference in milkweed abundance ($F=1.237$, $df_{(4,37)}$, $p= 0.302$) (Figure 5A) or in unexpected cycnia abundances ($F=0.67$, $df_{(4,37)}$, $p=0.518$) (Figure 6A). Towards the end of September, plants were only found in managed grasslands, roadsides, and sites burned that summer. In 2015, plant height was the only plant characteristic that differed during this time period ($F=5.867$, $df_{(2,151)}$, $p=0.0035$) (Table 4). There was a difference in distance to the nearest milkweed ($F=13.62$, $df_{(2,144)}$, $p<0.001$). Plants in mowed sites were closer together than in summer burn plots ($p<0.01$). Phenological stage was dependent on land use ($\chi^2= 19.7519$, $df=4$, $p<0.001$). Most plants in managed grasslands (68%) were in the vegetative stage while almost half of plants along roadsides were senescing.

In September 2016, there was a significant difference in milkweed abundance ($F=8.064$, $df_{(4,32)}$, $p= 0.00146$) (Figure 5B). Milkweed was more abundant in the summer burn plots than the mowed sites ($p\leq0.04$). There was not a difference in unexpected cycnia abundances ($F=1.004$, $df_{(4,32)}$, $p=0.378$) (Figure 6B). Plant height was also the only plant characteristic that differed among the three land uses that had milkweed ($F=13.01$, df$_{(2, 123)}$, $p<0.001$) (Table 4). There was a difference in distance to the nearest milkweed ($F=24.78$, df$_{(2, 120)}$, $p<0.001$), with plants in managed grasslands and summer burn areas being closer together than plants along roadsides ($p<0.001$). Phenological stage was independent of land use during this time period ($\chi^2=5.8864$, df=3, $p=0.1173$); this comparison was only between managed grasslands and summer burn plots because of low milkweed numbers along roadsides.

DISCUSSION

Annually, unexpected cycnia abundances did not differ across land uses (Table 5), even though milkweed availability did vary across land uses, which could influence unexpected cycnia distributions (Stoner and Joern 2004). Land uses with mowing as the management practice had more milkweed than those that were burned, regardless of the time since fire. However, that does not necessarily mean that mowing promotes milkweed recruitment more than prescribed fire, and additional data are needed to evaluate this possibility.

Regardless of land use, milkweed abundance was highest in the spring and decreased in summer and fall during each year. Mowing or burning in the mid- to late summer allows milkweed to re-grow and therefore be available to milkweed dependent herbivores later in the fall. The timing of both practices also influences milkweed availability and the amount of time that individual plants have to re-grow, and plants that have senesced before management occurs may not re-grow the same season (Baum and Sharber 2012, Baum and Mueller 2015). In 2016, managed grasslands were mowed two months earlier at some sites. Milkweed was available later in the season when mowing practices were later in the summer. Distances between plants increased as milkweed abundance decreased over the growing season. It is unknown how far unexpected cycnia caterpillars can travel to find milkweed. In 2016, a few unexpected cycnia caterpillars were found on the ground several hundred meters from any milkweed; however, it is unknown if these caterpillars would have made it to another milkweed plant. It is also unknown if there are any effects on the plants the year after they re-grow.

Milkweed plant characteristics varied seasonally, and may have been influenced by temperature and precipitation. Overall, average temperatures in 2016 were generally warmer than 2015 (Mesonet). In 2015, rainfall was below average in months following summer management practices (Figure 7A), whereas in 2016, rainfall was above average in the months following summer management practices (Figure 7B). This could explain why milkweed was available longer into the season in 2016; milkweed was found into mid-November. According to reports on Journey North (learner.org/jnorth/monarch/), the first milkweed appeared in Stillwater around the same time both years at the end of March/early April. The timing of management practices varied annually, which could have also influenced milkweed characteristics.

Roadsides milkweed plants were smaller than those in managed grasslands during all time periods except for in the fall, which is after milkweeds in both of these land uses had experienced mowing and/or haying. More frequent mowing leads to shorter vegetation than less frequent mowing practices (Saarinen et al. 2005). Plant height is a frequently used plant trait for measuring plant response to land management, and it is an important trait for competition with surrounding plant species; however, using a combination of traits may be more useful for quantifying a plant’s response to a management event (Klimesova et al. 2008). In the spring and summer, plants in spring burn sites were shorter than other rangeland sites and managed grasslands. In the fall, plants in summer burn sites were shorter than other treatments. However, this does not mean that these plants were necessarily smaller. Many of these plants were also wider than in other treatments. After burning, milkweeds may not grow as tall because the burned areas are more open and there is less surrounding vegetation for them to compete with. Plants along roadsides had more stems per plant than other management practices early in the growing season; however this pattern was not observed later in the season. Mowing multiple times in the same growing season also resulted in fewer plants reaching the later phenological stages (dehiscence and senescence).

The correlation between plant height and plant width was strongest along roadsides in 2015, but plants in areas without any management that year (e.g., previous spring burn sites) had the highest allometric constant (slope of the regression line) (Figure 3); however, this did not continue into 2016 when slopes for regression lines were fairly similar (Figure 4). This could be due in part to ODOT's change in the mowing schedule in 2016, which delayed mowing until early August and limited the number of mowing events so that the two ODOT managed roadsides in this study were mowed less frequently than in the past. Future studies should look at the influence of surrounding vegetation and the timing of land management practices on the sizes and phenology of milkweed plants and milkweed recruitment.

Unexpected cycnia abundances were lowest in the spring when milkweed was most abundant and more available throughout the landscape; although, the high availability of milkweed could also allow the caterpillars to more widely disperse across an area, especially if a greater percent of the landscape contains milkweed in the spring.

Also, sites without summer land management practices had little to no milkweed available in the fall, so there may be fewer overwintering pupa in these sites since they cannot support caterpillars in the fall. Sometimes unexpected cycnia were present at a site but were not present on the 5 m by 50 m transect. These presences were not included in the abundance results, so that abundances can be interpreted on a per milkweed or per unit area basis. Unexpected cycnia abundances were higher in 2016 than 2015 in mowed sites and summer burn sites. Mowed sites consistently have management each year (in that the same area is mowed each year, with a few exceptions), whereas in the patch burn sites, the same area is burned once every three years, so that each subplot has a three year fire return interval (Table 1).

For both years, the number of unexpected cycnia per milkweed was higher in the fall, when milkweed densities were lowest, than in the spring or summer. For example, in the plots burned in the same summer in 2015, there was approximately one caterpillar per 52 plants in the summer, but post burn, there was one caterpillar per 13 plants. This trend continued in 2016 with same summer burn plots containing one caterpillar per 10 plants in the summer and one caterpillar per 3 plants in the fall. During these periods, unexpected cycnia abundances were similar pre- and post- burn in the 2015 and higher post-burn in 2016 (Figure 6). This suggests that other factors, such as climate, may be at play in unexpected cycnia abundances, in addition to the influences that milkweed abundance may have on unexpected cycnia populations. It is unknown what minimum threshold of milkweed abundance that unexpected cycnia require to persist in an area.

However, the opposite was found in sites without summer management activities (i.e., spring burn plots). Milkweed senesced by late August and early September in sites with no management (i.e., previous spring burns); therefore, if any moths emerged in these sites in that time period, they would have to move to another location to find milkweed. After pupation, the unexpected cycnia emerges as an adult in approximately two and a half weeks unless it enters into diapause. Sixty percent of the unexpected cycnia that I collected and that pupated from mid-July through October entered diapause and overwintered as pupae. These individuals will not emerge as adults until the next spring; therefore, a portion of the local population will not require milkweed resources until the next spring. Milkweed is still required for moths that do emerge later in the same season and produce another generation, and one female can produce over 200 eggs (Kersten, pers. obs.). It is unknown what environmental factors promote caterpillars that pupate in the summer and fall to diapause for upwards of nearly a year (Figure 8). Future research could consider the importance of these later season generations to unexpected cycnia populations as well as the factors that cause them to enter diapause.

Unexpected cycnia pupate in leaf litter, which may make them more or less susceptible to different land management practices as pupae. For example, mowing likely negatively impacts caterpillars more than pupae, although I have found caterpillars in recently mowed (within a few days) sites. At one roadside site, 96 unexpected cycnia caterpillars, mostly third instars, were found prior to a mowing event (and several stripped milkweed from their feeding). This site was mowed several days later, and a few days after the mowing event, nine caterpillars were found feeding on the clipped milkweed. Summer burns would likely kill any unexpected cycnia caterpillars or pupae; however, depending on the intensity of the burn and location of the pupae, it is possible that 100% mortality would not occur (Swengel 2001).

Similarly, spring burns would likely result in the death of any pupae overwintering in the leaf litter (Bess 2005); therefore, having a mosaic of burn treatments, such as occur in patch burn sites could benefit unexpected cycnia by providing habitat throughout the growing season and refugia for the pupae so that local populations may persist. It is unknown if the unexpected cycnia has any adaptations to fire since it is common in fire dependent ecosystems, such as burrowing into the ground. In 2015 and 2016, seasonal burn treatments were adjacent to each other and ranged in size from 0.48 to 0.7 km^2, and it is unknown if results may have differed had the treatments been farther apart or if plot sizes had been larger. Unexpected cycnia moths are thought to be able to disperse up to 0.8 km (Bess 2005); therefore, it is possible that they could disperse within these pastures to other subplots to find milkweed resources. Since milkweed was not available in the spring burn sites in the fall, or any other subplots in the patch burn pastures (i.e., 5/6 of each pasture), it is possible that adults from surrounding areas moved into the summer burn plots to take advantage of its milkweed availability.

Monarchs and other milkweed associates

Monarch butterfly caterpillars and other milkweed associated insects were also found at these sites. Sometimes these caterpillars occupied the same plants as the unexpected cycnia, but more often they were found on separate plants. Previous studies found that monarch densities per unit area are also lower in the spring than in the fall; similarly, more monarch caterpillars were found per plant in the fall than in the spring (Andreoli 2015). However, given the milkweed available throughout the landscape in the spring, it may be difficult to accurately estimate milkweed associated insect densities in the spring. In the spring, milkweed may not be a limiting factor for milkweed associated insects, and the higher milkweed densities could allow them to be more widely distributed throughout the landscape as opposed to being concentrated in the fewer locations that contain milkweed, also at lower densities, in the fall. It is unknown whether interspecific competition might occur between these two species (or other species using milkweed as a food source), but given that fewer milkweeds were available in the fall, that would be when interactions would be expected to occur.

Other milkweed associates, such as milkweed stem weevils (*Rhyssomatus lineaticollis*), large milkweed bugs (*Oncopeltus fasciatus*), small milkweed bugs (*Lygaeus kalmii*), milkweed longhorn beetles (*Tetraopes* spp.), and mouse-colored lichen moth caterpillars (*Pagara simplex*) were present throughout the growing season, and herbivory by some species may reduce plant availability for others. For example, herbivory by milkweed stem weevils causes increased stem mortality in common milkweed (Agrawal and Van Zandt 2003). Monarch caterpillars and leaf beetle larvae (*Labidomera clivollis*) have been found to be less likely to occur on common milkweed damaged by weevils (Van Zandt and Agrawal 2004). Future research should look at the dynamics between the suite of milkweed associates that use *A. viridis* throughout the season to see what interspecific effects may exist and consider the effects of milkweed stem weevils on other milkweed associated insects.

Conservation efforts for the monarch butterfly have the potential to positively influence the unexpected cycnia and other milkweed associates by increasing the availability of milkweed. However, there are differences in conservation needs. In north central Oklahoma, unexpected cycnia and other milkweed associates require resources throughout the growing season, while conservation efforts for the monarch butterfly focus on the spring and fall, when they are present in the area. Management practices are necessary during the summer if milkweed resources are to be available into the late summer and fall. Providing a mosaic of management strategies, such as occurs in patch burning, may benefit unexpected cycnia populations by providing milkweed for caterpillars that diapause both earlier and later in the season, and by not affecting all pupae once they have entered diapause. Future studies should evaluate the importance of fall generations to the overall population and should also consider potential differences throughout the geographic range of the unexpected cycnia and how unexpected cycnia utilize habitat at different spatial scales.

CHAPTER III

EFFECTS OF LAND MANAGEMENT ON PARASITISM OF *C. COLLARIS* CATERPILLARS

INTRODUCTION

Tritrophic interactions occur between herbivores, their host plants, and their parasites, and each level may be affected by the others. Phytophagous insect populations may be affected from bottom up (host plants) and top down (predators and parasites) influences (Sait et al. 1997, De Moraes et al. 2000, Stoepler et al. 2011). Parasitoids can also be impacted directly and indirectly by host plants. Plant chemistry may directly impact a parasitoid's ability to grow and survive through the host's ability to sequester plant toxins, while indirect effects include impacting the growth of the parasitoid's herbivorous host (Stoepler et al. 2011). The size of the caterpillar may vary based on host plant quality, and the biomass and development of the parasitoid is linked to that of its host (Stoepler et al. 2011).

Parasitoids, such as tachinid flies and ichneumonid wasps, can regulate host populations and community structures (Stireman et al. 2006). Both host species and parasitoids can experience local extinction at a site. High parasitism rates can cause local extinction of the host species, which can then lead to local parasitoid extinction; however, since the parasitoid is at a higher trophic level, it is more at risk of local extinction than its host (Cronin and Reeve 2005). Often times, different parasitoid species will also compete with one another for a common host, which can lead to near extinction to the less competitive species, and additionally, those with higher reproductive potential and physiological tolerances comparable to the host will have better success (Force 1974).

Parasitoids must locate their hosts in the landscape using many different cues. Some plants produce chemical cues (plant volatiles) in response to herbivory, which attract parasitoids to the caterpillars consuming them (Turlings et al. 1995, De Moraes et al. 1998). Other parasitoids detect hosts using caterpillar body odors, frass and other excretions, or through simply seeing the host (Stireman et al. 2006). Many tachinid flies and ichneumonid wasps are generalists and kionobionts, meaning that they develop inside the host while the host continues to grow.

The Tachinidae family is quite large and diverse, containing thousands of species, all of which parasitize insects, mostly lepidopterans, and other arthropod species (Stireman et al. 2006); they only attack the larval stage of their hosts (Stireman and Singer 2003a). Some tachinids are specialists and target only specific hosts, while others are generalists (Stireman et al. 2006). Tachinid fly eggs can be oviposited either on the host or on the host plant, with larvae burrowing into the host after hatching (Stireman and Singer 2003a). Tachinid larval development typically occurs within one to three weeks with many emerging after the host pupates, although some tachinid species overwinter in their host (Stireman et al. 2006). Tachinid flies are also influenced by host characteristics, such as host-plant specificity and abundance, and tachinid species richness can be explained by host abundance and host plant range (Stireman and Singer 2003a).

The Ichneumonidae family contains over 60,000 species, and may infect the egg, larval, or pupal stage of their insect hosts, which include lepidopterans, dipterans, and even other hymenopterans (Price 1973). They will often inject their hosts with eggs/larvae. Ichneumonid wasps are also capable of overwintering in the host. The presence and activity of ichneumonid wasps can be greatly influenced by weather. Ichneumonid and braconid wasps can be affected by temperature, relative humidity, wind speed, and light intensity (Juillet 1964). Another study found that wasps are more likely to be active when it is sunny and calm (Jervis et al. 1993).

Various factors may play a role in the abundance of parasitoids and amount of parasitism in an area. Parasitoids may compete with one another (Force 1974), and host availability, including abundance and accessibility, will impact parasitoid populations (Price 1973). More abundant hosts may also decrease parasitoid success as higher abundances may lead to higher predation (Price 1973). Some species may have better success parasitizing specific caterpillar instars. For some caterpillars of the Limacodiae family, wasps are more likely to target earlier instars, while flies infect later (fourth and fifth) instars; therefore, parasitism rates by tachinid flies may be reduced if they are unable to find suitable hosts (Stoepler et al. 2011). However, wasps that infect earlier instars may be less likely to survive to adulthood (Harvey et al. 1994). Hairy caterpillars are more likely to be parasitized by tachinid flies, while caterpillars with aposematic coloring tend to have a less diverse suite of tachinid species that utilize them as hosts (Stireman and Singer 2003b). Both characteristics deter predators and therefore increase the likelihood of parasitoid success (Price 1973, Stireman and Singer 2003b). Seasonal and annual variations in host populations will also affect their parasitoids (Price 1973);

however, ichneumonid wasps and tachinid flies that compete for the same hosts may reduce this competition by being active in different seasons (Stoepler et al. 2011).

Land use influences on parasitism

Habitat requirements for parasitoid wasps include a host population, nectar food sources for adults, and shelter sites (Shaw 2006). The sugars provided in nectar allow adult parasitoids to survive and reproduce (Jervis et al. 1993, Lee and Heimpel 2002, Shaw 2006, Al-Dobai et al. 2012); the importance of these resources to adult tachinid flies is unknown (Stireman et al. 2006). Land management practices can alter plant communities and the availability of flowering plants for adult parasitoids, as well as adult hosts.

Parasitoid populations may be influenced by habitat fragmentation and habitat availability across the landscape. Land management practices may impact the quality of resources and their availability for parasitoid species. In fragmented landscapes, the arrangement of fragments is most important when there is less habitat available (Tscharntke et al. 2002). As the higher trophic level, parasitoids may be affected by those below, such as their host and host plant populations, both of which may be impacted by land use and land management practices. For example, mowing can lead to increased parasitism rates because this activity can lead to less dense vegetation that can increase parasitoid success even if host and parasitoid populations are lower (Herbst et al. 2013). Land management may alter some cues that parasitoids rely on to find hosts. Increased plant height and density may make it more difficult for parasitoids to find hosts (Herbst et al. 2013). In the Great Plains, grasslands are often burned or mowed. Additionally, rangelands often have grazers, such as cattle, present. Grasshoppers are more likely to be parasitized by flies in lands that are grazed as opposed to lands that are ungrazed (70-80% parasitism in grazed watersheds), although burning interval did not influence parasitism (Laws and Joern 2012). Grasshopper parasitism was also not affected by the annual abundance of grasshoppers. Land management practices may affect nectar resource availability for parasitoids as adults. More forbs are found in these grazed watersheds, which provides more nectar resources for adults parasitoids (Laws and Joern 2012).

Monarch caterpillars (*Danaus plexippus*) are parasitized by the tachinid species *Lespesia archippivora* in north central Oklahoma, but they can also be parasitized by six other tachinid species throughout their range (MLMP 2016). In natural areas, parasitism of monarch caterpillars by tachinid flies varies between land uses. Parasitism by tachinid flies on monarch caterpillars does not differ between managed grasslands and roadsides (Mueller and Baum 2014), but was higher in burned rangelands than mowed sites during one year (Andreoli 2015). Parasitism may also vary from year to year and spatially (Oberhauser et al. 2007, Oberhauser 2012). For example, tachinid flies parasitized an average of 13% of monarch butterflies overall, but some locations experienced parasitism rates as high as 90% (Oberhauser et al. 2007). However, other host species in the same locations may be affected differently by parasitism based on numerous factors, such as whether they are residents or migratory and their movement abilities. Host populations that are dispersal limited may experience distance-dependent parasitism with some patches of host populations being more greatly affected by parasitoids than those that are at a farther distance from this main source of parasitoids (Maron and Harrison 1997).

Study system

The unexpected cycnia (*Cycnia collaris*) is a dispersal limited moth that is dependent upon milkweed (*Asclepias* spp.) as a host plant (Bess 2005). It is thought to be capable of dispersal only when large patches of habitat or corridors between patches are present (Bess 2005). Tachinid flies and ichneumonid wasps are known to utilize the unexpected cycnia caterpillar as a host (Schaffner and Griswald 1934, Arnaud 1978). Known tachinid species that parasitize the unexpected cycnia include *Hyphantrophaga euchaetiae* and *H. hyphantriae* (previously documented as *Zenilla ceratomiae*) (Arnaud 1978). Unexpected cycnia collections from New York, New Jersey, and Pennsylvania in the 1930s assessing parasitism found that unexpected cycnia were also infected by three Hymenopteran (Family: Ichneumonidae) species: *Therion morio, T. sassacus,* and *T. waccagum*, all of which have the ability to overwinter in the host pupa (Schaffner and Griswald 1934). A solitary fly or wasp will emerge from the infected host pupa (Schaffner and Griswald 1934). Parasitism rates on the unexpected cycnia are unknown, as are the potential effects of parasitism on unexpected cycnia populations.

I collected unexpected cycnia caterpillars to document parasitism rates for this species across land uses and to evaluate the potential role (source vs. sink) of these land uses for this species. I hypothesized that parasitism rates will vary among land uses, with higher rates in land areas that are frequently burned, which creates a mosaic of habitat for parasitoids and their hosts. Additionally, I report basic life history information about the unexpected cycnia to help fill existing data gaps.

METHODOLOGY

Study sites

To evaluate the parasitism rates of the unexpected cycnia across land uses, I selected three land use types, including managed grasslands, roadsides, and rangelands. I identified three replicate sites of each of these three land uses. Managed grasslands and roadsides were mowed and rangelands were burned (Table 1), and these land uses and management practices are present in grasslands throughout the Great Plains. Selected sites all had known populations of *A. viridis* (the most common milkweed species in the study region) and unexpected cycnia. Many of these sites were previously monitored for monarch use for research in the Baum Lab (Baum and Sharber 2012, Mueller 2013, Mueller and Baum 2014, Andreoli 2015, Baum and Mueller 2015).

Roadsides and managed grasslands were located within a 20-km radius of Stillwater, OK in Payne and Noble Counties and were mowed at different intervals. Managed grasslands were mowed, and sometimes hayed, once a year. Four managed grasslands were identified (versus three replicates for the other land uses) to account for management activities outside of our control. Managed grasslands were composed of native grasses and forbs. The first site is located north of Boomer Lake at the southwest corner of Kameoka Trail and E. Rogers Dr. with an area of 0.0675 km^2. This site was mowed in both 2015 and 2016. OSU’s Cross Country field was the second site, located north of campus and has an area of 0.189 km^2. The Cross Country field was mowed in 2015 but not 2016. The third site is at the southeast corner of N. Perkins Rd. and Airport Rd. and has an area of 0.10 km^2. This site was mowed and hayed once in 2015 and twice in 2016. The fourth site, located at the northwest corner of N. Perkins Rd.

and E. Richmond Rd, has an area of 0.02 km^2.This site was mowed and hayed in 2016 but not 2015.

Roadsides were mowed several times a year. Roadside sites included Highway 177, Highway 51, and North Perkins Road. The two highways are managed by the Oklahoma Department of Transportation (ODOT). Surveyed areas for Highway 177 were in the 10.1 km between the turnpike and Highway 64. Highway 51 was surveyed between Range Rd. and Coyle Rd., a distance of 7 km. Surveys along Perkins Rd. occurred in the 3.2 km between Richmond Rd. and Yost Rd. Survey sites were limited to areas that had a shoulder or turnoff to safely pull off the road. In 2016, ODOT changed roadside management practices to be more beneficial for monarch and pollinator habitat. In doing so, they switched from mowing multiple times per year to once in mid-summer (ODOT 2016) and a fall clean-up mow. Safety zones and operational zones continued to be mowed multiple times a year. Herbicide is also applied in these areas. Vegetation in safety zones are kept at a height of less than 30 centimeters and are implemented to provide visibility (Montgomery et al. 2010). Operational zones may extend from three to nine meters from the edge of the road. These zones are managed multiple times a year to maintain “desirable” grasses while reducing the amount of weeds present (Montgomery et al. 2010).

Rangeland sites were located at OSU’s Stillwater Research Range, which is located about 20 km southwest of Stillwater, OK on Coyle Rd. The Stillwater Research Range includes three patch burned pastures, with areas spanning from 0.48 to 0.7 km^2. In these patch burned pastures, one-sixth of the site is burned every spring and one-sixth is burned every summer for an overall three-year fire return interval. Three subplots at each site were chosen to assess different times since burn and season of burn and included those burned the spring prior to sampling, the same spring, and the same summer. For 2015, these sites included the subplots burned spring 2014, spring 2015, and summer 2015. The subplots in 2016 were those burned spring 2015, spring 2016, and summer 2016; therefore, the spring 2015 subplot was used both years.

Field data collection

To estimate parasitism from tachinid flies and ichneumonid wasps, I collected fourth and fifth instar unexpected cycnia from these sites and individually reared them in the lab. Caterpillar collection occurred from mid-April through late-October of 2015 and 2016, coinciding with milkweed transects and surveys. Late instars were used because they had time to be exposed to parasites in the field. Based on the developmental time of each instar, it is possible that fourth instars collected one week may have still been present the next sampling period as fifth instars; however, this would only cause issues if parasitoids targeted the fifth instar stage. I collected caterpillars found on weekly 5 x 50 m transects to determine population densities. Additionally, I spent 20 minutes searching milkweed throughout the site for more caterpillars.

Laboratory data collection

Each caterpillar was kept individually in a 1-liter translucent container with a ventilated lid covered with netting and marked with the capture date and location. They were checked daily and fed *A. viridis* leaves as needed until pupation. *Asclepias viridis* was collected from the field, sterilized with a 10% bleach solution, and kept covered with a bag in the refrigerator until use (Altizer and Oberhauser 1999). Unexpected cycnia collected late in the year (September and October) often did not emerge until the following spring or summer, but could still be successfully reared in the lab. Overwintering pupae in the lab were monitored weekly, increasing to twice a week in March and April when emergence was expected. After pupae had been in the lab for at least one year, I dissected overwintering pupae to evaluate for moth or parasitoid presence.

For all collected caterpillars, I recorded molt date (if relevant), pupation date, moth emergence date and sex. When parasites emerged, the date and parasitoid family were recorded. Parasites were kept and preserved for future identification to species. Because the unexpected cycnia is a species of conservation concern in some states and has limited dispersal abilities, adult moths that emerged in the lab were released at the location of original capture. Rearing these specimens in the lab also allowed me to collect basic life history data that are currently not available for unexpected cycnia, including sex ratios, emergence timing of males and females, and developmental periods.

Statistical analysis

I compared parasitism rates among land uses using a chi-square test using R version 3.1.2. I combined wasps and flies into a single category (“parasitized”) because otherwise expected values were too low for the test to be valid. Rangeland sites were also combined for the same reason. In addition to looking at overall parasitism, I compared parasitoids that emerged during the same season and parasitoids that overwintered in the host pupae. I also compared parasitism between fourth and fifth instar caterpillars.

RESULTS

In 2015, a total of 356 unexpected cycnia caterpillars were collected across sites, with the first caterpillar collected on May 11, 2015 and the last on October 29, 2015 (Table 6). A majority (71%) of these caterpillars were collected in July and August. The

Spring 2014 and 2015 burn sites were not checked for caterpillars after August due to no milkweed availability; therefore, no caterpillars were collected from these sites after August. Caterpillars were collected from summer 2015 burn sites until mid-October. Most of these caterpillars emerged as moths (40%), and ichneumonid wasps were the most prevalent parasitoid (Table 6). Two braconid wasps emerged from caterpillars collected from rangeland sites. No flies emerged from caterpillars collected from managed grasslands or plots burned the previous spring. A majority of caterpillars died in the caterpillar (18.8%) and pupal stage (28.1%) from unknown causes. Those in the pupal stage had an unsuccessful diapause, and the pupae were empty inside when dissected one year after the caterpillar pupated.

I collected 462 caterpillars from April 29 to October 27, 2016 (Table 6). Once again, a majority (56%) of caterpillars were collected in July and August. The last caterpillar was collected from Spring 2015 burn sites at the end of July and from Spring 2016 burn sites at the beginning of August. These sites were not checked for caterpillars after mid-August because all milkweed had senesced. As of April 25, 2017, around 35 % of the caterpillars had emerged as moths and there were similar proportions of parasitism by ichneumonid wasps and tachinid flies (Table 6). Two braconid wasps emerged from caterpillars collected from rangeland sites. One caterpillar was infected with a gregarious eulophid wasp, of which 39 emerged. Twenty-four (5%) died in the caterpillar stage and 72 were unsuccessful as pupa. Thirty percent remain in their pupa.

In 2015, parasitism was independent of land use (χ^2= 3.2045, df=2, p=0.2014) (Figure 9A). No tachinid flies emerged from caterpillars collected from managed grasslands. Parasitism was independent of land use for those that emerged during the same season (χ^2=2.9735, df=2, p=0.2261) (Figure 10A). For those that were collected in 2015 and overwintered in the host pupae and emerged in 2016, there was a difference in parasitism (χ^2=9.888, df=2, p=0.007) (Figure 11A). Parasitism was highest in managed grasslands (41%) and lowest along roadsides (5%). Tachinid flies only emerged from overwintering pupae of caterpillars collected from rangeland sites. I also compared the three different times since burn. In 2015, parasitism did not differ across burn periods (χ^2=2.2293, df=2, p=0.328).

Some sites did not have any parasitism by tachinid flies in 2015 but did in 2016. For 2016 (as of April 25, 2017), parasitism was dependent on land use (χ^2=11.556, df=2, p=0.0003) (Figure 9B). Parasitism was highest in rangeland sites (17%). No flies emerged from caterpillars collected in the spring (before June 20). Parasitism was dependent on land use for parasitoids that emerged during the same season (χ^2=14.0638, df=2, p=0.00088) (Figure 10B). Parasitism was highest in rangeland sites (48%) and lowest in managed grasslands (17%). Data for overwintering pupae have not been finalized yet as more than half remain in their pupa; however as of April 25, 2017, parasitism was dependent on land use in overwintering pupae (χ^2=6.2413, df=2, p=0.04413) (Figure 11B). In 2016, parasitism did differ among the burn subplots and was highest in the summer burn plots (23%) (χ^2=6.6907, df=2, p=0.035).

Ichneumonid wasps, braconid wasps, and tachinid flies emerged from fourth and fifth instars. Parasitism did not vary between fourth (21%) and fifth instars (28%) (χ^2=1.1487, df=1, p=0.2838). During both years, ichneumonid wasps were more common during the first half of the season, while tachinid flies emerged from caterpillars collected during the second half of the growing season (Figure 12). The two parasitoids overlapped during about two months in the middle of the growing seasons. Ichneumonid wasps also emerged from caterpillars collected in October. Ichneumonid wasps that overwintered in the host pupa emerged from March through July of the following year (Figure 8).

Developmental periods

Developmental periods varied seasonally for moths and parasitoids. Caterpillars collected through mid-June all emerged in the same season, and some caterpillars (19%) from the rest of the collection period also emerged in the same season. For those that did emerge the same season, tachinid flies averaged 29.5 days in the cycnia pupa, while ichneumonid wasps had the longest development time with an average of 42.3 days in the cycnia pupa. Braconid wasps averaged 18.8 days in the cycnia pupa. Female moths spent an average of 16.8 days in pupa, and males averaged 18 days in pupa (Figure 13). In 2016, 39 eulophid wasps emerged from one cycnia ten days after pupation. This caterpillar was collected from a managed grassland site (the field north of Boomer Lake). These wasps emerged from pupae from inside the cycnia pupa. Overall, only two tachinid larvae emerged from the caterpillar stage; these two emerged from two dead caterpillars, pupated in the bottom of the rearing container, and emerged as adults. All other tachinid flies emerged from the cycnia pupa as tachinid adults, so the tachinid pupal stage occurred within the cycnia pupa. Most (60%) of the caterpillars collected from mid-June through the end of the collection period overwintered as pupa (or did not survive).

For the pupa that entered diapause, tachinid flies spend the least amount of time as pupa at an average of 137.6 days, ichneumonid wasps emerged after an average of 214 days, females moths emerged after an average of 225.1 days, and male moths emerged after an average of 239.8 days (Figure 14). In the spring, male and female moths begin to emerge around the same time (Figure 8). Caterpillars collected in 2015 were more male dominated (67 males to 59 females). More females overwintered (22 females versus 15 males); therefore, more males emerged during the same season. Sexes were more balanced for moths that emerged during the same season in 2016 with nearly equal numbers of males to females (37 to 36).

DISCUSSION

Parasitism of unexpected cycnia caterpillars varied annually. Unexpected cycnia caterpillars were more abundant in 2016 than 2015 and also found for a longer period of time in 2016. Overall, there was no relationship between land management and parasitism in 2015, but there was in 2016 when parasitism was highest in the rangeland sites. Most of the rangeland parasitism occurred in the time following the burns when vegetation was shorter, which could have increased parasitoid success in finding hosts (Herbst et al. 2013). More parasitoids overwintered in pupae in 2015 in managed grasslands. Between years and seasonally, the dominant parasitoid varied. Overall, parasitism by tachinid flies more than doubled in 2016 when compared to 2015 (2.3% in 2015 vs. 5.6% in 2016); however, most of these occurred later in the season after the summer burn. In Spring 2015, 37% of caterpillars collected were parasitized by ichneumonid wasps, but in Spring 2016, only 24% parasitized by ichneumonid wasps.

Even though we did not return parasitoids to the field, it does not seem likely that collections would have impacted parasitoid populations for the next year since not all caterpillars were collected from a site (only a portion of the site was searched each week). The lower number of ichneumonid wasps later in 2016 could reflect the lower parasitism rates earlier that same year, compared to the same time period in 2015; however, it is also possible that they are still overwintering in the host pupae. Only four braconid wasps were collected; all of which came from caterpillars collected from rangeland sites (one from prior spring burn, and three from same spring burn sites). Parasitism also varied among caterpillars collected from the same plant. In Spring 2015, four caterpillars collected from one *A. viridis* plant in the rangeland were all infected by ichneumonid wasps, while in Spring 2016, two caterpillars were collected from the same plant and one was infected by an ichneumonid wasp and the other was uninfected. However, we do not know which instar stages the wasps attack and how far caterpillars move, and it is possible that the two caterpillars were not on the same plant during the time of infection.

Temporal differences in parasitism could be related to seasonal differences in milkweed and host abundance. Milkweed is more abundant across the landscape in the spring, which may make it more difficult for parasitoids to locate their hosts. In the fall, milkweed densities are lower so there are fewer plants for parasitoids to search for hosts; however, the distance between these plants is also greater. The search abilities and dispersal distances of these parasitoid species are unknown. Unexpected cycnia abundances are also higher in the summer and fall than in the spring. Milkweeds are only present in the fall in areas where activities that remove the aboveground portion of the plant have occurred, such as mowing or burning (Baum and Sharber 2012, Baum and Mueller 2015), and therefore there are fewer locations for cycnia to occur.

During both years, parasitism was highest in the spring and fall, but sample sizes were also much lower in the spring. Climate can also influence the tritrophic interaction. Parasitism was lower in the summer when temperatures are higher. Increasing temperatures increase caterpillar sizes as a result of increased herbivory; however, parasitism rates may decrease with increasing temperatures (de Sassi and Tylianakis 2012).

All three *Therion* spp. that infect the unexpected cycnia undergo one or two generations a year (Schaffner and Griswald 1934) and have alternate hosts available in north-central Oklahoma. *Therion morio* has three other known Lepidopteran hosts, two of which are also present in this part of Oklahoma: Virginia tiger moth (*Spilosomoa virginica*) and salt marsh moth (*Estigemene acrea*). *Therion sassacus* also uses the fall webworm moth (*Hyphantria cunea*). *Therion waccagum* also infects the delicate cycnia moth (*Cycnia tenera*). All three of these ichneumonid species hibernate in the host pupa (Schaffner and Griswald 1934); therefore, these parasitoids need to infect hosts in the summer and fall to overwinter in the pupa. In both years, parasitism by ichneumonid wasps was highest in caterpillars at the beginning and the end of the growing season, in caterpillars collected in May, June, and October. Ichneumonid wasps have longer developmental periods than unexpected cycnia moths and their other parasitoids (braconid wasps and tachinid flies). Because of this, ichneumonid wasps would need to infect caterpillars earlier in the growing season if they are going to have two generations per season, while also timing it so that they can find hosts to overwinter. Ichneumonid wasps that successfully overwintered emerged from March through July of the next year in the lab setting.

Many of the caterpillars that went into a diapause did not successfully overwinter. Since they pupate in leaf litter, it may be possible that we missed some necessary components of microhabitat needed for them to complete their diapause successfully. All caterpillars were kept in separate containers at lab temperature. Therefore, they did not experience changing temperatures, which may have influenced developmental times and caused some of the overwintering pupa to emerge early or some to not emerge at all. Covell (1984) suggests rearing pupa in the conditions they would experience in nature, as many species that overwinter as pupa are not successfully reared indoors. Other studies with insects that diapause simulate a winter period for several months and then gradually warm the pupa to break the diapause (Nelson and Forbes 2014). A few moths and parasitoids did successfully survive the diapause, but it is unknown how many more may have been successful had more suitable conditions been provided and how many more parasitoids may have emerged from the unsuccessful pupae. Future studies on the unexpected cycnia should consider what overwintering conditions are required for pupae.

Since unexpected cycnia are non-migratory and present in the same locations throughout the growing season, they share food resources with other milkweed associates, such as the monarch butterfly and the mouse-colored lichen moth (*Pagara simplex*). The mouse-colored lichen moth is also parasitized by tachinid flies (Kersten, pers. obs.). Caterpillars of these three species have different parasitoids, and the tachinid flies that target each are different species. Having multiple herbivores feeding on leaves and in the same vicinity may affect plant volatiles being produced that may influence parasitoid success. Parasitoids that overwinter in the host pupa would face the same risks as pupa. For example, because they pupate on the ground in leaf litter, these pupae would likely not survive a fire event.

We looked at fourth and fifth instar caterpillars; therefore, it is still unknown if the unexpected cycnia is parasitized at the egg or pupal stages, and if the different stages experience different infection rates. It also may be possible that hyperparasitism occurs.

Ichneumonid, braconid, and tachinid parasitoids can all experience hyperparasitism, which can then impact parasitoid populations in the same manner that parasitoid populations may affect their hosts. Hyperparasitism of tachinid flies occurs occasionally in monarch butterflies (Oberhauser et al. 2007), and it may be possible that the unexpected cycnia's tachinid flies also experience it.

Other factors, such as shape, size, surrounding habitats, and arrangement of host plants within the habitat may influence parasitism. Because the unexpected cycnia are localized in distribution, they might have less opportunity to recolonize an area if parasitism was high enough to lead to local population extinction, which could also negatively affect parasitoid populations. Roadsides are linear; however, we did not consider adjacent habitat, which would likely have different management strategies and insects may move between the adjacent habitats. Mowing practices in managed grasslands are often homogenous throughout the entire unit. The mosaic formed in the rangelands led to habitat/milkweed availability throughout the growing season, but it also may have provided high quality habitat for parasitoids. Having this patchy landscape may result in a more complex landscape and more nectar resources to support a diverse herbivore and parasitoid community (Thies et al. 2003).

Parasitism varied from year to year, and it is unknown what factors may have contributed to this variation. The survival rate of unexpected cycnia caterpillars from egg to moth also remains unknown as they experience predation in addition to parasitism. Future research could also evaluate what factors might influence parasitism of this species and other dispersal limited species, such as the influences of patch sizes and habitat use by both the host and their parasitoids. The effects of surrounding habitats on parasitism, habitat connectivity, and habitat fragmentation on these species could also be investigated.

CHAPTER IV

POTENTIAL INFLUENCES ON THE DISTRIBUTION OF *C. COLLARIS*

INTRODUCTION

Habitat loss and fragmentation have been identified as important factors contributing to the decline of most species of conservation concern. Therefore, it is important to identify factors that influence the geographic distribution of a species, especially those of conservation concern. Some habitats are being lost more rapidly than others. For example, prairies are considered one of the most threatened biomes in the world (Hoekstra et al. 2005). In the Great Plains region of the United States, less than 30% of historical grasslands remain (Samson et al. 2004), and those that do remain continue to be converted to other uses (Lark et al. 2015).

In addition to habitat loss, some native plant species that colonize disturbed areas may be considered weedy and targeted for removal or control, especially in agricultural fields (Hartzler and Buhler 2000, Hartzler 2010); however, these plants may be critical for some insect species of conservation concern. Milkweeds (*Asclepias* spp.) are one such example. Milkweeds are present throughout the United States (Woodson 1954), but the importance of different milkweed species varies both temporally and spatially. Several insect species are dependent upon milkweeds for part of their life cycle, such as the monarch butterfly (*Danaus plexippus*), large milkweed bugs (*Oncopeltus fasciatus*), small milkweed bugs (*Lygaeus kalmii*), milkweed longhorn beetles (*Tetraopes* spp.) (Betz et al. 1997) and the unexpected cycnia moth (*Cycnia collaris*) (Metzler and Lucas 1990), and other insects use milkweed as a nectar source.

The unexpected cycnia is a milkweed dependent species that not much is known about. The unexpected cycnia was previously classified as *Cycnia inopinatus*, but in 2015 it was determined to be synonymous with *C. collaris* and *C. tenerosa* and that only geographic distributions differed between these three species (Lafontaine and Schmidt 2015). *Cycnia collaris* was the first of these species to be described and therefore, the three species have been combined under that name (Lafontaine and Schmidt 2015). While exact habitat requirements are unknown, *C. inopinatus* was associated with dry prairies and oak barren habitats throughout the Great Plains, east to the Atlantic coast, and south to Florida (Covell 1984, Bess 2005) while *C. collaris* extended into New Mexico and Arizona. Not much information is available about the distribution of *C. tenerosa*; however, it was described from a specimen collected in Mexico (Dyer 1913).

The unexpected cycnia moth is highly localized in distribution (Bess 2005), and is thought to have limited dispersal abilities. Maximum dispersal distances are estimated anywhere from a few hundred meters to less than 800 m, suggesting unexpected cycnia moths can only disperse when large continuous areas of habitat are present, although specific habitat requirements are not known, or at least not published (Bess 2005). Several states list *C. inopinatus* as a species of conservation concern. At the state level, it is considered critically imperiled to vulnerable in Virginia (Robel 2013), while it is considered imperiled to vulnerable in North Carolina (Ratcliffe et al. 2016). It is endangered in Ohio and threatened in Massachusetts, with habitat loss and fire suppression identified as the main threats (Metzler and Lucas 1990, Program 2012). These factors are likely common throughout the entirety of its range. Other threats include invasive plants, insecticides, parasitoids, and light pollution (Program 2012).

Range-wide surveys have not been conducted for this species, and it is possible that more populations exist than previously thought, especially in the central United States (Bess 2005). By identifying where potential habitat exists and the potential range of this species, actions can be taken to find new populations and to conserve, protect, and enhance existing habitat. I hypothesized that the potential habitat for unexpected cycnia throughout its range (as assessed with ecological niche modeling) will vary with dominant land uses.

METHODOLOGY

Study area

The study area was delineated based upon the known range of the unexpected cycnia from the Great Plains to the East Coast and south to Florida (Covell 1984, Bess 2005) as well as Arizona and New Mexico. Because distribution data is very limited for *C. collaris* and *C. tenerosa*, I also included the rest of the continental Unites States to see if other locations may exist based on environmental conditions. *Cycnia tenerosa* may expand south into Mexico; however, due to a lack of availability of current occurrence data, I did not include Mexico in my analysis.

Occurrence data and environmental layers

I used data collected by citizen scientists and from scientific repositories to assess large-scale distribution patterns of unexpected cycnia. To gather these data, I contacted Native Plant Societies and Master Gardener programs throughout the known range of *Cycnia inopinatus* to request observations from their members (Table 7). I developed newsletter materials on the unexpected cycnia, including identification of the egg and larval stages, along with photographs and descriptions of instars. This newsletter was distributed by the Monarch Larva Monitoring Project (MLMP, Director: Dr. Karen Oberhauser, University of Minnesota). MLMP volunteers monitor milkweed weekly for monarch larvae and collect site data; therefore, they may encounter unexpected cycnia during their surveys. Working with citizen science groups allows researchers to gather data on a much larger scale, in this case range wide, which would not be possible otherwise (Tulloch et al. 2013).

Additionally, I created a project through iNaturalist (iNaturalist.org), a website which allows anyone to upload observations. Users often attach pictures so identifications can be requested and/or confirmed. Identification confirmations result in the observation being deemed “research grade”. I also retrieved unexpected cycnia occurrence points from the Butterflies and Moths of North America website (www.butterfliesandmoths.org/species/Cycnia-inopinatus). This website did not contain any recent observations under *C. collaris* or *C. tenerosa*. Members of this website can report sightings of lepidopteran species along with descriptions and photographs.

Geographic coordinates are not directly available on this website; however, aerial imagery is provided for each point. Using this imagery and matching it to aerial imagery on Google Earth, location data can be found for these points. Finally, I searched Flickr (www.flickr.com) and BugGuide (www.bugguide.org) for unexpected cycnia photos that were geotagged or provided geographic coordinates. I also used coordinates from a moth survey in Tennessee (Brown 2003). Additionally, I used presence data from moth surveys conducted on The Nature Conservancy (TNC) preserves in Oklahoma provided by John Fisher. Each state maintains county lists; however, these data lack geographic coordinates and only account for presence/absence at a county scale; therefore, I was unable to use them in my analysis. I limited observations to those that occurred from 2000 to present. Because overfitting of the model occurred when occurrence points were located too close together and concentrated in areas in Oklahoma and Kansas, I rarefied the occurrence data by 20 km using the feature in SDMToolbox (www.sdmtoolbox.org). Overfitting continued to occur with 20 km, so I rarefied the data to 50 km. This left me with 62 occurrence points.

I downloaded BIOCLIM climatic layers from WorldClim (www.worldclim.org/bioclim). BIOCLIM current conditions represent 1950-2000 at a 1 km (30 arc-seconds) resolution. I found elevation layers at the same 1 km scale resolution through GTOPO30 (earthexplorer.usgs.gov). The continental United States is found in the following entity IDs: GT30W100N40, GT30W100N90, GT30W140N40, and GT30W140N90. I combined these layers using the Mosaic to New Raster tool in ArcMap. Categorical land cover data came from the 2002 North American Land Cover Characteristics at a 1 km resolution available from the USGS (https://nationalmap.gov/small_scale/mld/landcvi.html). I resampled the land cover raster to the same cell size (1 km) as the BIOCLIM and elevation layers. I calculated correlation coefficients for climatic variables using SDMToolbox to reduce collinearity, which occurs when at least two variables are linearly related and provide the same information (Dormann et al. 2013). Using variables with strong collinearity can influence the model results as these variables might be evaluated with more importance than they would without the other strongly correlated variable (Baldwin 2009). Beginning with an ecologically important climate variable (e.g. maximum temperature), I did a sequential regression to remove variables that have a correlation coefficient greater than 0.7 with the first variable (Dormann et al. 2013). For BIOCLIM layers, I began with BIO5 and BIO6 (maximum temperature of the warmest month and minimum temperature of the coldest month, respectively). Following the sequential regression, I was left with BIO2 (mean diurnal range), BIO8 (mean temperature of the wettest quarter) and BIO12 (annual precipitation). Climate and elevation environmental layers were continuous, while land use environmental layers were categorical. All environmental layers were masked to the same extent of the study area using the Spatial Analyst extension in ArcMap. All shapefiles and rasters were projected to WGS 1984.

Maxent

Because I had presence-only data, I used Maxent, Version 3.3.3K which finds the maximum entropy distribution based upon presence data by creating pseudo-absences to account for a lack of absence data (Elith et al. 2010, Franklin 2010, Jimenez-Valverde et al. 2010). I used Maxent's default settings (logistic output format, 10000 background points, 500 maximum iterations). Because the unexpected cycnia had a small sample size with a low number of occurrence points (<70), I cross-validated with ten replicates. Cross validation uses different subsets of training and testing occurrences to generate and test replicate models and averages the results for the final model (Franklin 2010). For all models, I ran a jackknife to measure the importance of each environmental variable, which assesses the variable's importance when used alone and with the other variables. The gain of a variable when used alone shows which variable has the most useful information when used alone, while the gain when omitted shows which variable has the most unique information. Additionally, Maxent creates a receiver operating characteristic (ROC) curve for training and testing data which plots the false-positive error rate on the x-axis and the true positive rate on the y-axis (Franklin 2010). Maxent also calculates the area under the curve (AUC) for the ROC. AUC values closer to 1 show a stronger prediction while values close to 0.5 indicate that the prediction is completely random. Omission rates show the known presences that are predicted absent. AUC is considered a threshold-independent measure while omission error rates are threshold-dependent (Jimenez-Valverde 2014). Omission errors occur when a species is predicted absent in an area of known presence or the prediction of unsuitable habitat where it is actually suitable. I ran one model with climate variables and elevation only and a second model with climate variables, elevation, and land use to increase the AUC and decrease omission rates.

Model post-processing

Maxent models were produced in ASCII format and converted to raster format (ESRI Grid) using Arc Map 10.2. The logistic output creates a continuous output, so I applied the minimum presence threshold to create a binary map of suitable (1; greater than threshold value) and unsuitable (0; less than threshold value) habitats.

RESULTS

After applying the minimum training threshold, both models had similar results in the potential suitable habitat for this species (Figure 15, Figure 16); however, including land cover reduced the area considered suitable. According to the climate and elevation model, conditions exist that should be suitable for the unexpected cycnia from Texas to North Dakota and east to the East Coast. Additionally, there are areas in eastern New Mexico and Arizona, all of which follow the known range of the unexpected cycnia. However, there may also be suitable habitat in other parts of the western United States based on the models.

For both models, annual precipitation (BIO 12) had the greatest effect on habitat suitability (Table 8). When included, land cover had the second highest contribution (30%). For the training data of the climate model, the jackknife results showed that annual precipitation (BIO 12) had the highest gain when used in isolation, while the minimum temperature of the coldest month (BIO 6) decreased the gain most when omitted. For the training data of the climate and land use model, the jackknife results showed that annual precipitation still had the highest gain when used alone, while land cover decreased the gain most when omitted. Both models resulted in AUCs above 0.7. The climate and elevation model had a training AUC of 0.8573 and a testing AUC of 0.8220, while the climate, elevation, and land cover model resulted in a training AUC of 0.8838 and testing AUC of 0.8351. Both results included all occurrences used in the testing in the suitable habitat.

Most observations came from Oklahoma, Kansas, and Missouri. Unexpected cycnia caterpillars were reported as feeding on fifteen different milkweed species (Table 9). A majority of observations used in the models (points remaining after being rarefied by 50 km) were found in dryland cropland and pasture, cropland/grassland mosaic, and deciduous broadleaf forest land covers. In the land cover model, most of the suitable habitat occurred in dryland cropland and pasture, cropland/grassland mosaic, grassland, shrubland, and deciduous broadleaf forest (Figure 17).

DISCUSSION

Precipitation was a driving factor in the unexpected cycnia's distribution in both models, which would also have an impact on its milkweed host plants. In the climate and elevation model, the mean temperature of the wettest quarter had the second highest influence. However, when land cover was included, it replaced the contribution of mean temperature of the wettest quarter, which was then third highest and similar in contribution to minimum temperature of the coldest month. Mean temperature could influence development times of the unexpected cycnia, with warmer climates producing more generations in one year than cooler climates (Bess 2005). Since the unexpected cycnia is mainly associated with prairies and oak barrens, their distribution may be more limited by their specific habitat needs than climate.

Land covers considered most suitable for habitat included dryland cropland/pasture and cropland/grassland mosaics. Nineteen observations were associated with deciduous forests. Several of these observations were associated with *A. tuberosa*. I checked aerial imagery, and many were located in open areas surrounded by forests. Therefore, this finding could be due more to the scale of the land cover layer and these small openings being surrounded by forests were classified as forests as opposed to this species occurring in forested areas.

All land cover would only be suitable if milkweed is present, and in many of these areas milkweed may be targeted for removal. Despite the growing recognition by the public of the need for milkweed for the monarch butterfly, milkweed may still be considered a weedy/pest species in some areas. For example, some sources suggest landowners eradicate milkweed from their pastures to prevent poisoning of cattle and horses (e.g., Turner et al. 2010, Rizza 2013); however, it is unlikely that cattle and horses would eat milkweed if better and more suitable food choices are readily available. Despite being native to North America, seven milkweed species are listed as weedy/noxious in the USDA plants database according to county and state weed lists.

Models do not account for milkweed availability. The unexpected cycnia uses more milkweed species that previously stated, and the extent of their use of each species is still not known. It is likely that the unexpected cycnia utilizes different milkweed species spatially and even temporally, depending on what it available. It is also possible that the unexpected cycnia may use additional species than documented in this project throughout its range.

Land use plays a large role in milkweed occurrence and subsequently milkweed dependent insect populations. It has been reported that the unexpected cycnia may use at least fifteen different milkweeds for host plants (Table 9) (Nishio 1980, Bess 2005, Delaney et al. 2008). Milkweeds have different habitat requirements, and different species are present in and more plentiful in different parts of their range. Some milkweeds require more high quality habitats, while others thrive in disturbed habitats

(Wilbur 1976). In north central Oklahoma, where *Asclepias viridis* is the most abundant plant species, the unexpected cycnia is commonly found on this species. However, when other milkweeds, such as *Asclepias tuberosa*, were present, caterpillars used them as well. The phenology of different milkweed species may also influence their suitability as hosts. Some studies suggest that some insects are rare because their host plant habitats are rare (Hopkins et al. 2002), and while most milkweeds are not necessarily considered rare, because of land use changes, their habitat is in decline.

Habitat loss is a significant problem and will likely continue to be an issue for this species, especially in the Great Plains where more than 70% of grasslands have been lost due to land use changes and disruption of ecological drivers (Samson et al. 2004). Land use change is a major conservation issue that would have an immediate impact on this species' distribution. Many potentially suitable habitats may not actually be habitat that is available to the unexpected cycnia. Grasslands and pastures continue to be converted to croplands continue to be created across the United States, with conversions highest in western Oklahoma, Texas, and Kansas (Lark et al. 2015). This trend continues in the Cornbelt region and throughout the Upper Midwest, where large amounts of Conservation Reserve Program (CRP) lands that may have provided habitat as grasslands are being converted to more intensely managed crops that would likely not have the milkweed to support this species (Wright and Wimberly 2013, Morefield et al. 2016). In the Midwest, milkweed populations have decreased by 40% when using Iowa as a model (Pleasants 2016). Additionally, roadsides may contain suitable habitat for this species. According to Pleasants, 2016, roadsides have the second highest milkweed availability in the Midwest. The most abundant milkweed species along roadsides may vary regionally.

In the Midwest, *A. syriaca* is the most common milkweed species along roadsides; however, its density varies across the landscape (Kasten et al. 2016). Roadsides can provide additional habitat for insects, but the timing of management activities may influence whether these habitat are sources or sinks for different insect species (Hopwood 2013). Roadside efforts to increase habitat for pollinators may also benefit the unexpected cycnia.

Throughout the unexpected cycnia's range, there has been widespread habitat loss, degradation, and fragmentation due to development, urbanization, and introduction of exotic species. These factors have resulted in the unexpected cycnia being listed as a species of conservation concern in several states along the East Coast (listed under *C. inopinatus*). However, the unexpected cycnia seems to be more abundant in Oklahoma, Kansas, and Missouri. It appears that multiple populations occur in these states which contradicts previous thoughts that states in its range each contain one or few populations (Bess 2005). It is possible that grasslands provide more preferable habitats than those that occur through the East Coast. Additionally, several observations from the central United States came from gardens, and some people welcomed their presence while others regarded them as a pest as these caterpillars can defoliate milkweed plants, especially when multiple unexpected cycnia caterpillars occur on the same plant.

The lack of knowledge of specific habitat requirements for the unexpected cycnia makes it difficult to conclude the accuracy of the high suitability habitat. Including other variables, such as those that might take into account possible patch size of milkweeds present, could assist in finding new populations of the unexpected cycnia. Patch size can have a significant effect on the abundance of herbivorous insects present (Bach 1988).

Because the unexpected cycnia has limited dispersal abilities, patch size and corridors between patches could play a large role in the unexpected cycnia's ability to react to disturbances. In order for potential conservation efforts to be successful, we still need more information about the unexpected cycnia's range and population statuses throughout its range. Conservation efforts for other milkweed associates that share the same habitat, such as the monarch butterfly, have the potential benefit the unexpected cycnia as well.

CHAPTER V

CONCLUSIONS

The results of this study show that the studied land uses do not influence abundances of this dispersal limited habitat specialist. Unexpected cycnia populations appear to have similar responses to mowing and prescribed fire in north central Oklahoma. Unexpected cycnia caterpillars are mainly parasitized by tachinid flies and ichneumonid wasps. Occasionally, braconid wasps and eulophid wasps use unexpected cycnia caterpillars as hosts. The range of the unexpected cycnia appears to be driven primarily by annual precipitation. More research should be done to evaluate milkweed species preferences, minimum patch size requirements, and milkweed-cycnia-parasite interactions. It is likely that more populations exist due to lack of reporting of presences of this species. Efforts should be made to document new populations, when found, to continue to build data about this species.

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APPENDICES

Table 1. Sites and dates of management practices for 2015 and 2016. Some mowing dates are approximate as sites were visited after the mowing occurred, and mowing times were outside of our control. Managed grasslands were also hayed, with the exception of the one located North of Boomer Lake. Prescribed fire dates include the plots used for each field season: previous spring burn, same spring burn, and same summer burn.

Land Use	Management Practice	Location	Management Date(s):
Managed Grassland	Mowed and hayed	North of Boomer Lake (Southwest corner of Kameoka Trail and E Rogers Dr.)	2015: 9/4/15 2016: 6/13/16
		OSU Cross Country Field	2015: 8/6/15 2016: None
		Southeast corner of N Perkins Rd and Airport Rd	2015: 8/21/15 2016: 6/15/16, 8/15/16
		Northwest corner of N Perkins Rd and E Richmond	2015: None 2016: 8/10/16
Roadsides	Mowed	Hwy 177	2015: 7/10/15, 9/18/15 2016: 6/13/16, 7/7/16, 8/17/16, 9/6/16
		Hwy 51	2015: 6/16/15, 6/29/15, 8/25/15, 9/4/15, 10/11/15 2016: 8/22/16
		N Perkins Rd	2015: 6/19/15, 6/25/15, 8/21/15, 9/15/15, 10/16/15 2016: 4/28/16,6/24/16, 8/24/16, 9/30/16
Rangeland	Prescribed fire	Pasture 9	2015: 4/1/14, 3/11/15, 7/23/15 2016: 3/11/16, 2/22/16, 7/21/16
		Pasture 17	2015: 2/13/14, 3/26/15, 8/23/15 2016: 3/26/15, 3/16/16. 8/16/16
		SE Pasture	2015: 3/9/14, 2/9/15, 7/24/15 2016: 2/9/15, 3/14/16, 7/22/16

Table 2. Mean vector angles and standard deviations of unexpected cycnia caterpillar (*Cycnia collaris*) abundances. Each month of the collection period was divided into radians starting with April at 0 radians and ending in November at 5.5 radians. The length of the vector is a measure of concentration that ranges from 0-1 with values closer to 1 being more abundant during one month. The significance of the mean angle was found using the Rayleigh test.

Year	Land Use	Mean Vector Angle (radians)	Circular Standard Deviation	Month(s) Corresponding to Mean Vector	Length of the vector (r)	p-value
2015	Managed Grasslands	2.678	1.00955	July-August	0.601	<0.001
	Roadsides	2.95	0.5598	July-August	0.855	<0.001
	Rangeland - Previous Spring Burn	1.401	0.8666	May-June	0.689	<0.001
	Rangeland - Same Spring Burn	2.91	0.463	July-August	0.913	<0.001
	Rangeland – Summer Burn	2.861	1.0014	July-August	0.606	0.0041
2016	Managed Grasslands	3.02	0.9909	July-August	0.612	<0.001
	Roadsides	2.33	7945	July	0.729	<0.001
	Rangeland - Previous Spring Burn	1.68	0.70497	June	0.78	<0.001
	Rangeland - Same Spring Burn	1.85	0.61337	June-July	0.829	<0.001
	Rangeland – Summer Burn	3.2	1.0869	August-September	0.554	<0.001

Table 3. Ranges of dates of flowering and senescing for *Asclepias viridis* for each land use. Date ranges of phenological stages may include breaks if management activities occurred and allowed plants to re-grow. Areas with summer mowing or prescribed fire had multiple periods of flowering. These calculations come from plants measured during transects through the entirety of each sampling period.

		2015		2016	
Land Use		Flowering	Senescing	Flowering	Senescing
Managed grasslands	Range(s)	May 1 – Jul. 8; Sept. 17 – Sept. 29	Jul. 17-Sept. 4; Oct.1 – Nov. 8	Apr. 26-Aug 9; Aug. 24-Oct. 5	Jun. 6-Nov. 9
	Mean	May 26	Aug. 9	May 30	Aug. 5
Roadsides	Range(s)	Apr. 29 – Jun. 12; Jul 25 – Aug. 12	Jul. 8 – Sept. 18	Apr. 24-Jun. 15; Ju1. 18 – Jul. 28, Sept. 21	Jun. 6 – Aug. 24
	Mean	May 23	Aug. 16	May 20	Jul. 17
Rangeland – Previous Spring Burn	Range(s)	Apr 30 – Jun. 29	Jul. 5 – Sept. 1	Apr. 24 – Jun. 5	Jun. 8 – Aug. 2
	Mean	May. 19	Jul. 25	May 12	Jul. 6
Rangeland-Same Spring Burn	Range(s)	Apr. 30 – Jun. 28	Jul. 10 – Aug. 30	Apr. 24-Jun. 8	Jun. 5 – Aug. 14
	Mean	May 21	Aug. 2	May 13	Jun. 10
Rangeland – Summer Burn	Range(s)	Apr. 30 – Jun. 29; Aug. 17- Oct. 11	Jul. 5 – Oct. 17	Apr. 24-Jun 14; Aug. 13 – Oct. 3	Jun. 5 – Aug. 3 Sept. 12 – Nov. 14
	Mean	Jun. 3	Jul. 30	May 29	Jul. 26

Table 4. *Asclepias viridis* characteristics (mean ± SE) during two week periods in mid-May, mid-July, and mid-September across land uses. Because plants were flowering in May and senescing in July and September, I calculated the average number of flowers for May and seedpods for July and September. The first thirty plants of each transect were measured, and for each time period encompass plants measured in eight transects on managed grasslands and six transects along roadsides and in each rangeland. Plant characteristics with asterisks denote significant differences during that time period for both years. Additionally, there was a difference in the number of stems in July 2016. Letters next to measurements denote differences between treatments.

		May				July				September			
Year	Land Use	Height*	Width*	Stems*	Flowers or Seedpods	Height*	Width*	Stems*	Flowers or Seedpods	Height*	Width	Stems	Flowers or Seedpods
2015	Managed grasslands (a)	31.16 ± 0.79^{d}	32.54 ± 1.45	2.1 ± 0.14	8.95 ± 1.62	39.33 ±0.76^{b}	25.25 ± $1.05^{b,e}$	1.44 ± 0.06	0.77 ± 0.1	16.77 ± 0.55	18.87 ± 0.87	1.49 ± 0.1	0.27 ± 0.11
	Roadsides (b)	27.02 ± 0.8 $4^{a,d}$	36.28 ± 1.61^{d}	2.5 ± 0.19	9.45 ± 1.78	19.7 ± 0.87	19.74 ± 1.26	1.92 ± 0.16^{a}	0.28 ± 0.11^{a}	15.81 ± 1.16	16.47 ± 2.22	1.32 ± 0.15	0.21 ± 0.13
	Range-Prior Spring Burn (c)	27.18 ± $0.87^{a,d}$	36.25 ± 1.8^{d}	2.19 ± 0.16	7.9 ± 1.84	32.85 ± 1.03^{b}	29.35 ± 1.7^{b}	1.65 ± 0.1	0.4 ± 0.09^{a}				
	Range-Same Spring Burn (d)	18.9 ± 0.48	31.81 ± 1.49	1.78 ± 0.1^{b}	5.39 ± 1.0	27.19 ± 0.75^{b}	28.54 ± 1.29^{b}	1.8 ± 0.1	0.42 ± 0.08^{a}				
	Range-Summer Burn (e)	29.88 ± 0.99^{d}	28.48 ± 1.59	1.6 ± 0.12^{b}	4.34 ± 0.91	34.94 ± 1.2^{b}	33.22 ± 1.9^{b}	2.01 ± 0.16^{a}	0.53 ± 0.12	13.57 ± 1.12^{a}	18.84 ± 1.72	1.32 ± 0.12	0.13 ± 0.06
2016	Managed grasslands (a)	25.94 ± 0.63^{c}	28.06 ± 1.15	1.61 ± 0.09^{b}	4.64 ± 0.86	28.33 ±0.93^{b}	24.5 ± $1.11^{b,e}$	2.04 ± 0.17	0.25 ± 0.06	21.11 ± 0.94	23.63 ± 1.6	1.6 ± 0.11	0.45 ± 0.14
	Roadsides (b)	27.32 ± 0.91^{c}	34.24 ± 1.46^{a}	2.41 ± 0.17	6.46 ± 1.074	23.6 ± 0.91	19.82 ± 1.19	1.5 ± 0.09^{a}	0.12 ± 0.04	23.1 ± 3.6	19.6 ± 3.2	1 ± 0	0
	Range-Prior Spring Burn (c)	30.32 ± 0.65^{d}	31.87 ± 1.23	1.66 ± 0.08^{b}	7.18 ± 0.96	35.28 ± $0.67^{a,b}$	28.46 ± 1.33^{b}	1.5 ± 0.07^{a}	0.35 ± 0.06				
	Range-Same Spring Burn (d)	25.15 ± 0.62	37.04 ± 1.41^{a}	2.01 ± 0.12	7.15 ± 0.94	29.45 ± 0.81^{b}	24.83 ± 1.09 ^{b}	1.56 ± 0.09^{a}	0.22 ± 0.06				
	Range-Summer Burn (e)	27.89 ± 0.63^{d}	33.29 ± 1.32	1.83 ± 0.08^{b}	7.81 ± 0.89	36.93 ± $0.81^{a,b}$	29.81 ± 1.28^{b}	1.61 ± 0.07^{a}	0.34 ± 0.08	15.6 ± 0.76^{a}	22.7 ± 1.3	1.6 ± 0.1	0.35 ± 1.3

Table 5. Number (mean ± SE) of *Asclepias viridis* plants and unexpected cycnia caterpillars (*Cycnia collaris*) per hectare during three time periods throughout the growing season in 2015 and 2016.

		Mid-May		Mid-July		Mid-September	
Land Use	Species	2015	2016	2015	2016	2015	2016
Managed Grasslands (n=8)	*A. viridis*	3191 ±671	2810 ± 981	1988 ±827	1540 ± 572	462 ± 154	233 ± 118
	C. collaris	0	20 ± 20	85 ±42	30 ± 16	22 ± 7	247 ± 215
Roadsides (n=6)	*A. viridis*	4453 ± 1818	4347 ± 1499	1253 ± 512	1333 ± 38	153 ± 53	64 ± 26
	C. collaris	0	20 ± 22	87 ± 35	87 ± 38	0	16.3 ± 7
Range-Prior Spring Burn (n=6)	*A. viridis*	1433 ± 510	1433 ± 89	1100 ± 379	953 ± 154	--	--
	C. collaris	133 ± 82	53 ± 32	27 ± 27	40 ± 18	--	--
Range-Same Spring Burn (n=6)	*A. viridis*	1120 ± 190	1567 ± 243	980 ± 195	973 ± 262	--	--
	C. collaris	0	20 ± 20	33 ± 22	47 ± 19	--	--
Range-Same Summer Burn (n=6)	*A. viridis*	913 ± 247	2100 ± 164	720 ± 240	1087 ± 104	133 ± 40	527 ± 129
	C. collaris	0	67 ± 59	13 ± 8	73 ± 66	20 ± 14	133 ± 4

Table 6. Total number of caterpillars collected in each land use for 2015 and 2016, and the proportion of these caterpillars that emerged as moths, ichneumonid wasps, or tachinid flies. Additionally, two braconid wasps emerged from rangelands each year and one caterpillar from a managed grasslands was infected by Eulopid wasps in 2016. Proportions for 2016 are as of April 25, 2017 as 30% were still overwintering as pupae at that time.

Year	Land Use	Total Caterpillars Collected (n)	Moths	Ichneumonid Wasps	Tachinid Flies	Dead-Caterpillar	Dead-Pupa
2015	Managed Grassland	61	0.361	0.180	0	0.197	0.262
	Roadsides	83	0.494	0.072	0.024	0.181	0.229
	Range-Prior Spring Burn	57	0.368	0.087	0	0.211	0.316
	Range-Same Spring Burn	92	0.413	0.054	0.011	0.196	0.315
	Range-Summer Burn	54	0.382	0.073	0.091	0.182	0.273
	Range-All	212	0.377	0.094	0.024	0.189	0.307
2016	Managed Grassland	96	0.438	0.031	0.020	0.102	0.092
	Roadsides	105	0.400	0.067	0.076	0.029	0.133
	Range-Prior Spring Burn	51	0.333	0.118	0.020	0.039	0.235
	Range-Same Spring Burn	76	0.355	0.105	0	0.040	0.250
	Range-Summer Burn	129	0.256	0.078	0.155	0.047	0.155
	Range-All	261	0.303	0.088	0.081	0.042	0.188

Table 7. Organizations contacted in 2015 and 2016 for unexpected cycnia caterpillar (*Cycnia collaris*) observations. Additionally, a project was created on iNaturalist.org to aid in reporting observations. Organizations distributed the request to their members through email lists, social media, and newsletters; the method differed by group.

Name of Organization
1. Arkansas Master Naturalists
2. Botanical Club of Wisconsin
3. Butterflies of Oklahoma, Kansas, and Texas
4. Butterfly Society of Virginia
5. Carolina Butterfly Society
6. Central Arkansas Chapter of Master Naturalists
7. Delaware Native Plant
8. Florida Native Plant Society
9. Illinois Native Plant Society
10. Indiana Native Plant and Wildflower Society
11. Iowa Native Plant Society
12. Kansas Native Plant Society
13. Louisiana Native Plant Society
14. Michigan Botanical Club
15. Midwest Native Plant Society
16. Missouri Native Plant Society
17. Monarch Larvae Monitoring Project
18. Monarch Watch
19. Moths of Ohio
20. Native Plant Society of Texas
21. North Carolina Native Plant Society
22. Northwest Arkansas Master Naturalists
23. Oklahoma Native Plant Society
24. Pennsylvania Native Plant Society
25. Rhode Island Wild Plant Society
26. Tennessee Master Naturalists
27. Virginia Native Plant Society
28. Wild Ones (Wisconsin)

Table 8. Percent contributions of each environmental variable to the Maxent models for estimating habitat suitability for unexpected cycnia (*Cycnia collaris*).

Variable	Climate and Elevation Model	Climate, Elevation, and Land Cover Model
Mean diurnal range (BIO 2)	4.1	1.8
Max. temperature of the warmest month (BIO 5)	7.2	4.4
Min. temperature of the coldest month (BIO 6)	12.7	9.2
Mean temperature of the wettest quarter (BIO 8)	22.2	10.5
Annual precipitation (BIO 12)	47.8	42.8
Elevation	6	1.3
Land Cover	NA	30

Table 9. Milkweed (*Asclepias* spp.) species used by unexpected cycnia (*Cycnia collaris*). Citizen scientists reported finding unexpected cycnia caterpillars on 15 different milkweed species. Bess (2005) reported use of *A. syriaca* as being uncommon; however, several people reported finding caterpillars on it. Common names are based on the USDA plants database (plants.usda.gov) (USDA).

Scientific name	Common name
*A. amplexicaulis**	clasping milkweed
A. asperula	spider milkweed
A. curassavica	bloodflower
*A. hirtella**	green milkweed
A. humistrada^	pinewoods milkweed
A. incarnata	swamp milkweed
A. purpurascens	purple milkweed
A. speciosa	showy milkweed
A. stenophylla	slimleaf milkweed
A. sullivantii	prairie milkweed
*A. syriaca**,[+]	common milkweed
*A. tuberosa**	butterfly milkweed
*A. verticillata**	whorled milkweed
*A. viridiflora**	green comet milkweed
*A. viridis**	green antelopehorn milkweed

Sources that also documented use by unexpected cycnia for the recorded species included: *Bess 2005; ^Nishio 1980; [+]Delaney et al. 2008

Figure 1. Unexpected cycnia (*Cycnia collaris*) undergo five instars as caterpillars. Instar stages for this species are determined by size and setae/hair density (setae/hairs are located in distinct clumps and the number of hairs in a clump increases with instar stage) of the caterpillar, with each subsequent instar getting increasingly larger and more hairy.

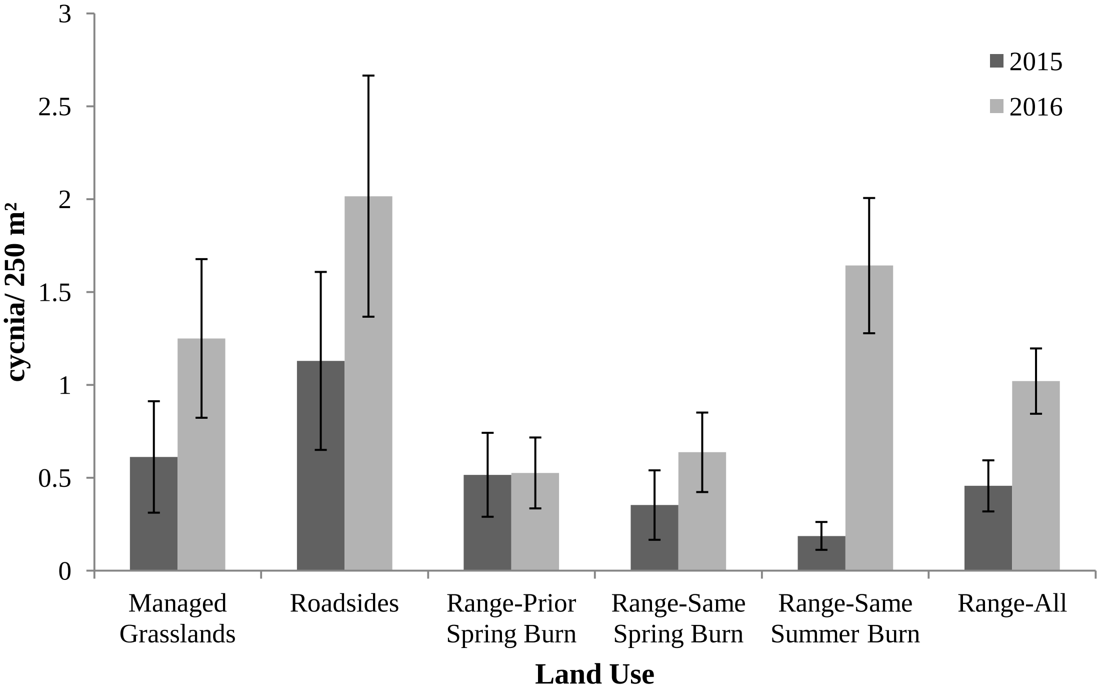

Figure 2. Density of unexpected cycnia caterpillars (*Cycnia collaris*) across land uses and associated land management practices averaged across the entire growing seasons of 2015 and 2016. Error bars denote standard error. Densities did not differ across land uses for either year (2015: F=1.123, $df_{(4,361)}$, p=0.345; 2016: F=1.999, $df_{(4,349)}$, p=0.0942).

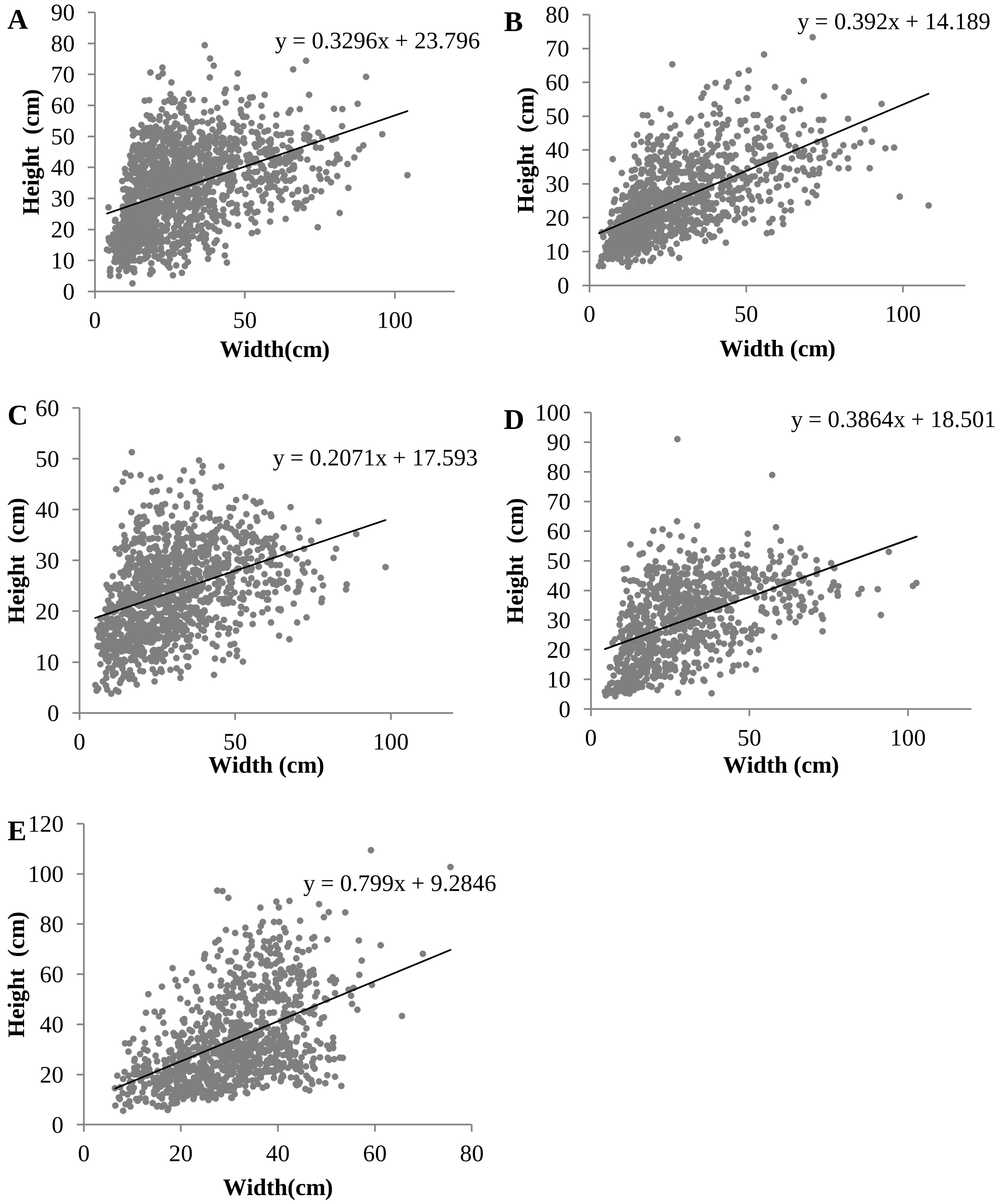

Figure 3. Correlations between plant height and plant width for 2015 for (A) managed grasslands (r=0.424), (B) roadsides (r=0.624), (C) same spring burn sites (r=0.395), (D) summer burn sites (r=0.496), and (E) previous spring burn sites (r=0.494). All correlations were significant (p<0.001).

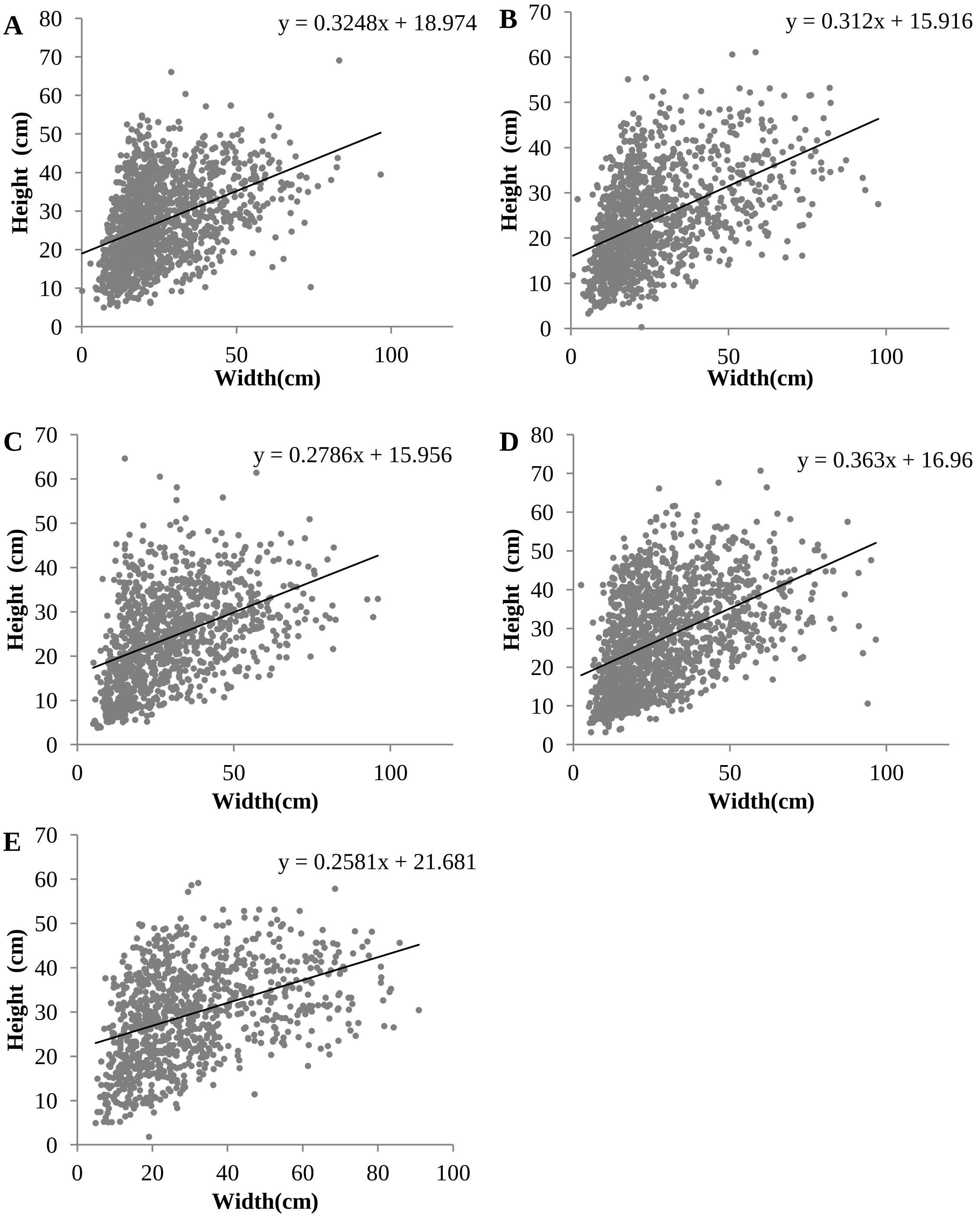

Figure 4. Correlations between plant height and plant width for 2016 for (A) managed grasslands (r=0.421), (B) roadsides (r=0.485), (C) same spring burn sites (r=0.434), (D) summer burn sites (r=0.468), and (E) previous spring burn sites (r=0.411). All correlations were significant (p<0.001).

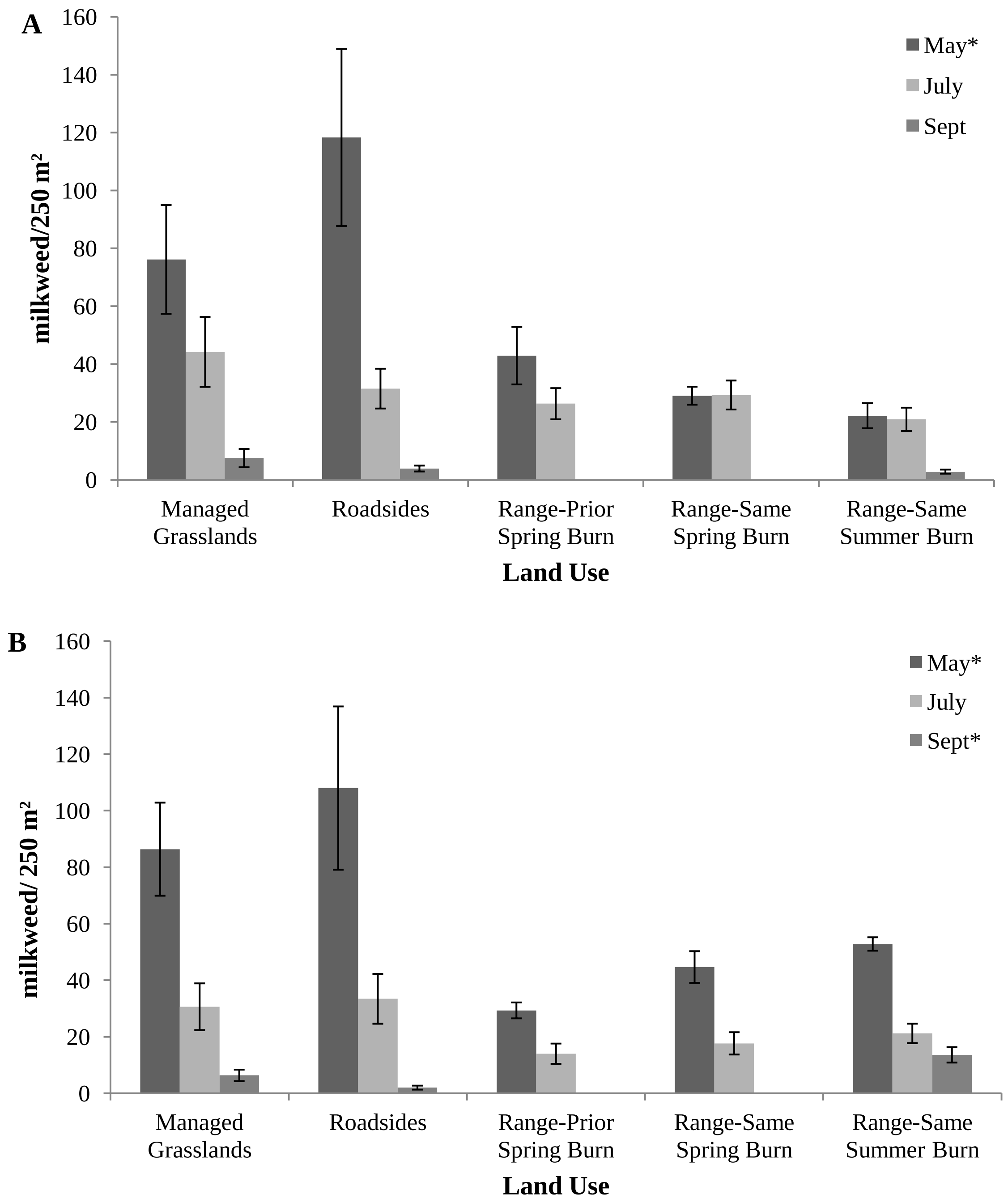

Figure 5. Average density of *A. viridis* plants on each land use during three time periods throughout the growing (May, July, and September) in 2015 (A) and 2016 (B). Error bars denote standard error. Months with asterisks had significant differences in densities among land uses.

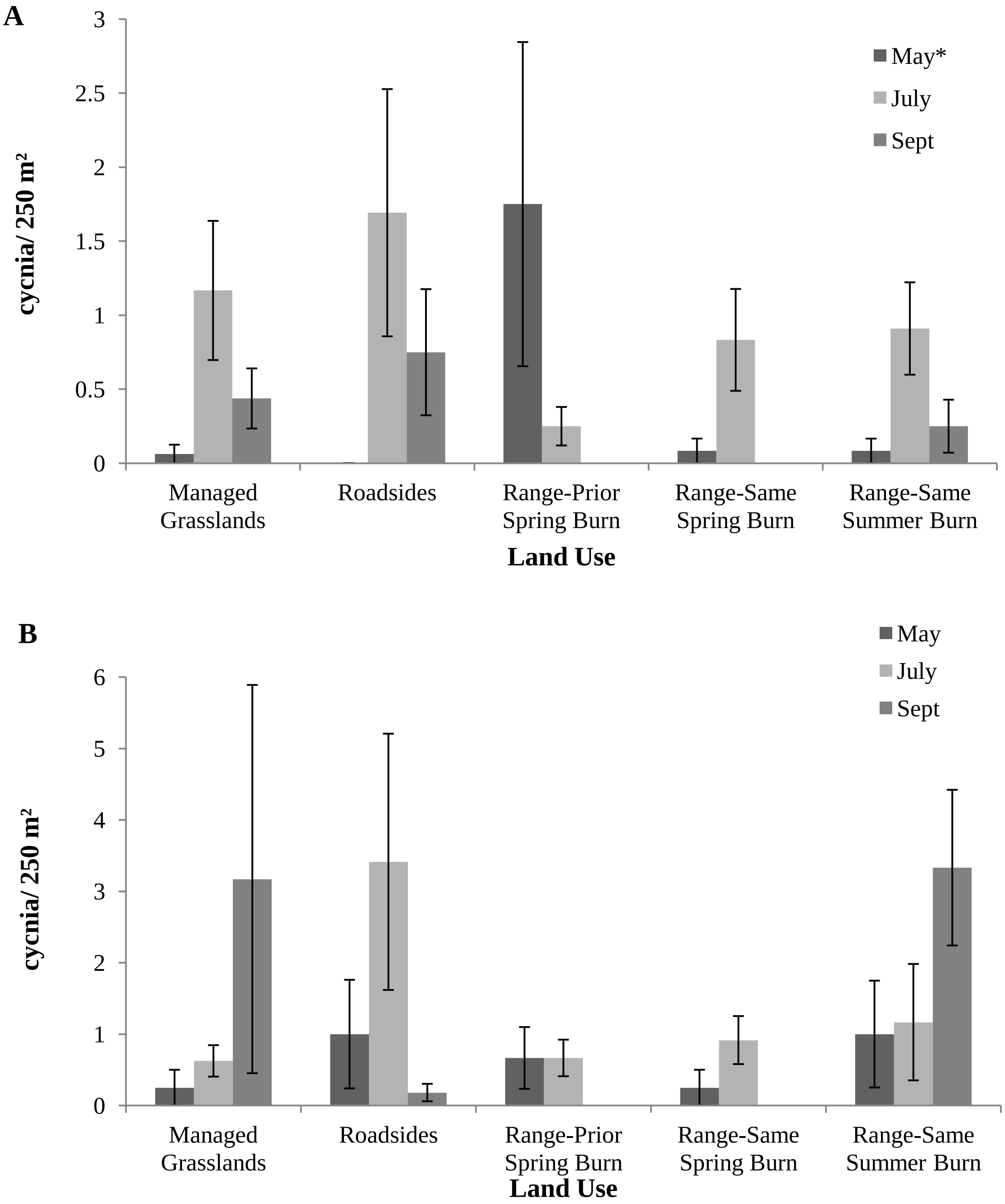

Figure 6. Average density of unexpected cycnia caterpillars (*Cycnia collaris*) on each land use during three time periods throughout the growing seasons (May, July, and September) of 2015 (A) and 2016 (B). Error bars denote standard error. Months with asterisks had significant differences in densities among land uses.

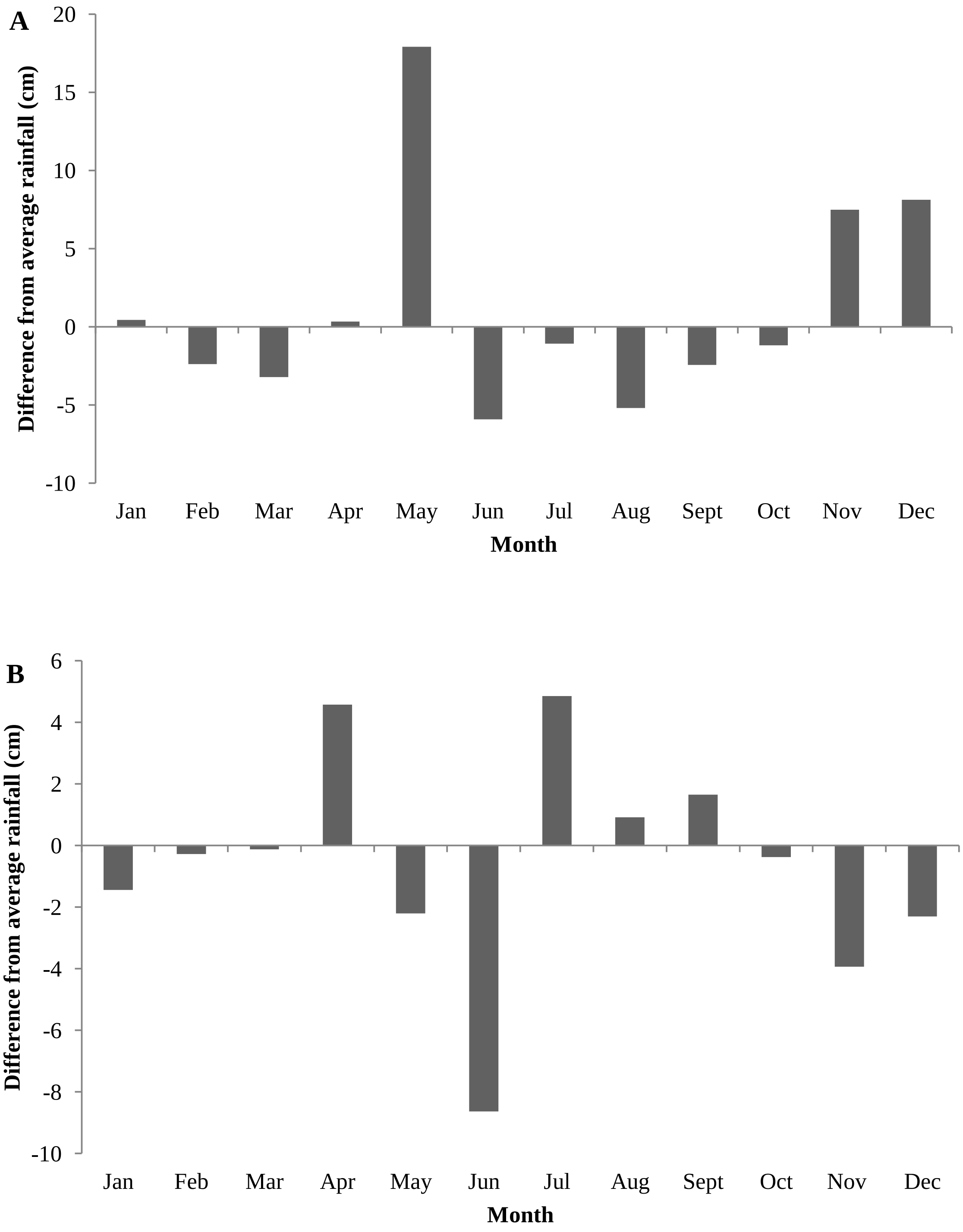

Figure 7. Difference from average rainfall (in centimeters) during January through December 2015 (A) and 2016 (B). Data were compiled from the Oklahoma Mesonet station nearest to the study sites (Marena, OK) for which long-term data were available.

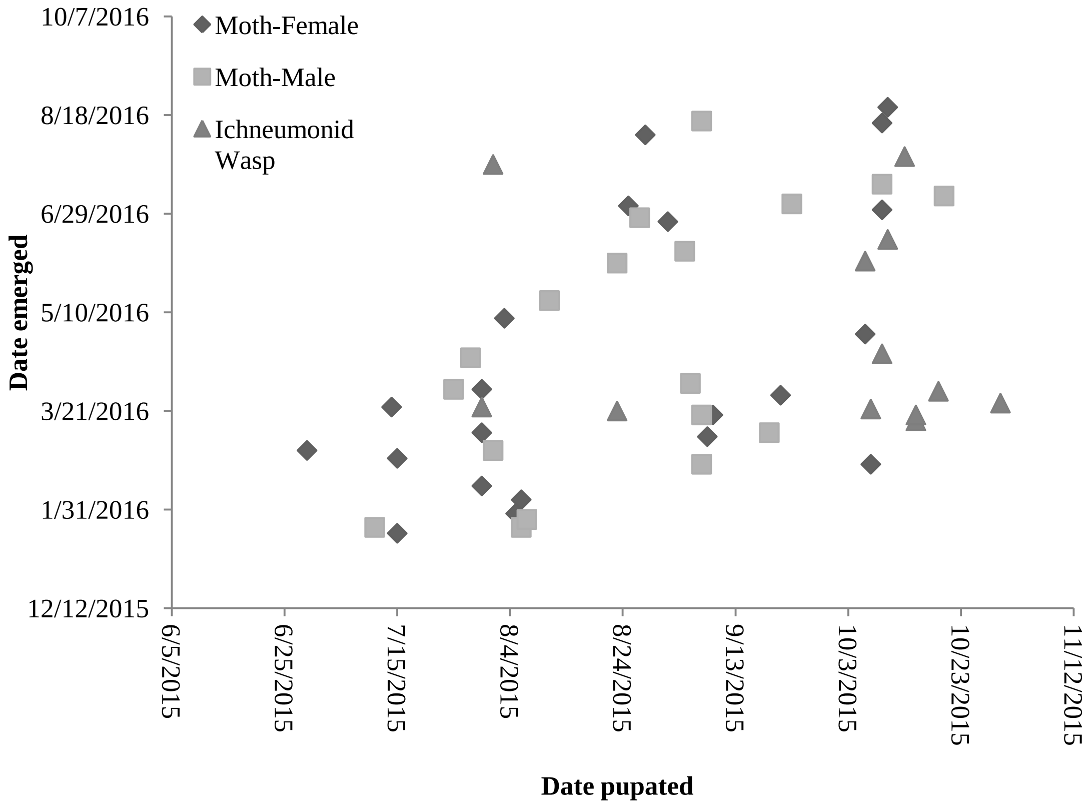

Figure 8. Emergence dates of caterpillars collected in 2015 that overwintered as pupa. All caterpillars were kept at lab temperature in individual containers.

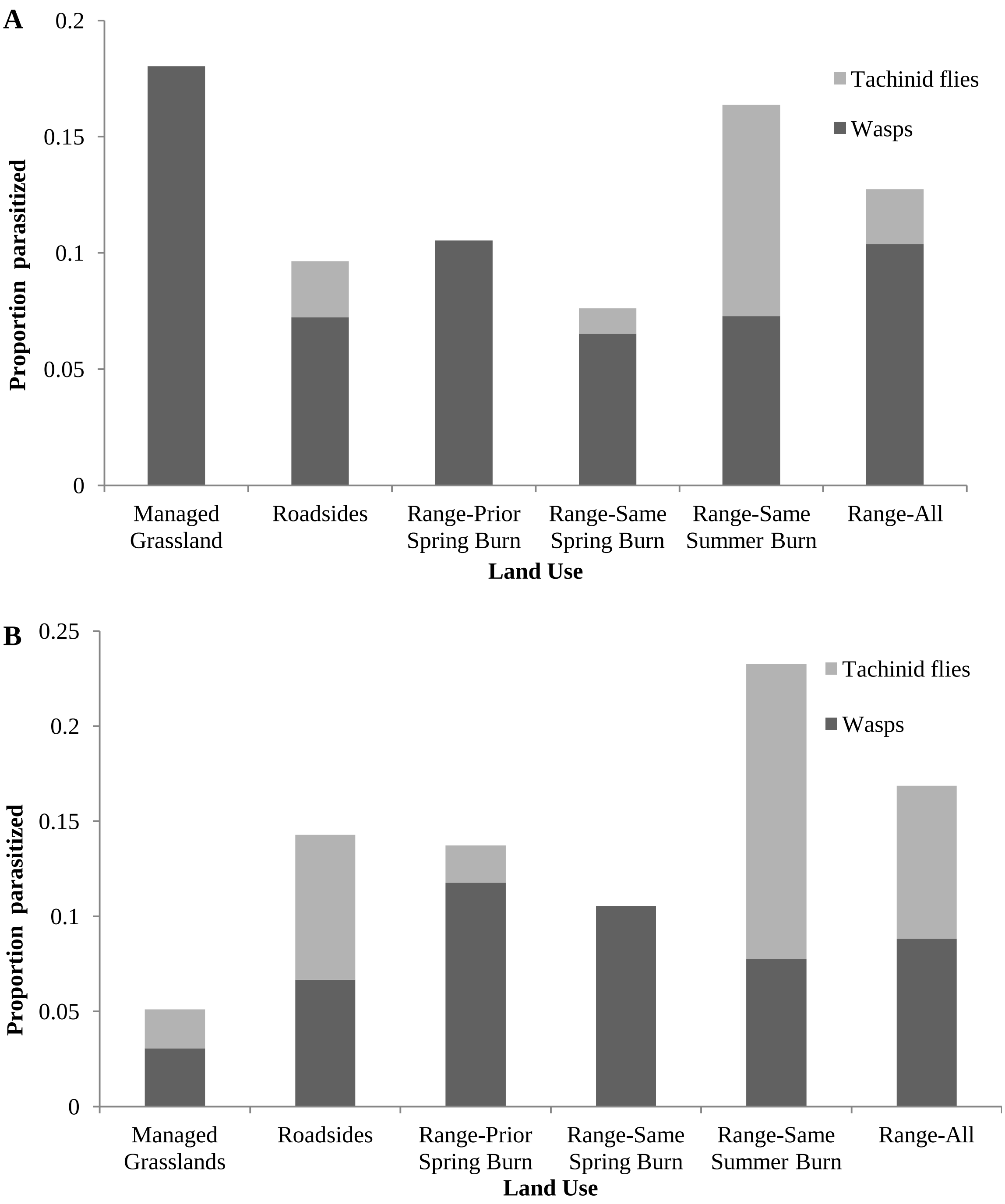

Figure 9. Unexpected cycnia caterpillar (*Cycnia collaris*) parasitism across land uses in 2015 (A) and 2016 (B). Wasps included ichneumonid wasps and braconid wasps. In 2015, no tachinid flies emerged from caterpillars collected from managed grasslands or prior spring burn plots. In 2016, wasps also included one caterpillar infected by eulophid wasps, and no flies emerged from caterpillars collected in the same spring burn sites. All parasitoids were combined into one category, and the three rangeland sites were combined into a single land use for the statistical analysis.

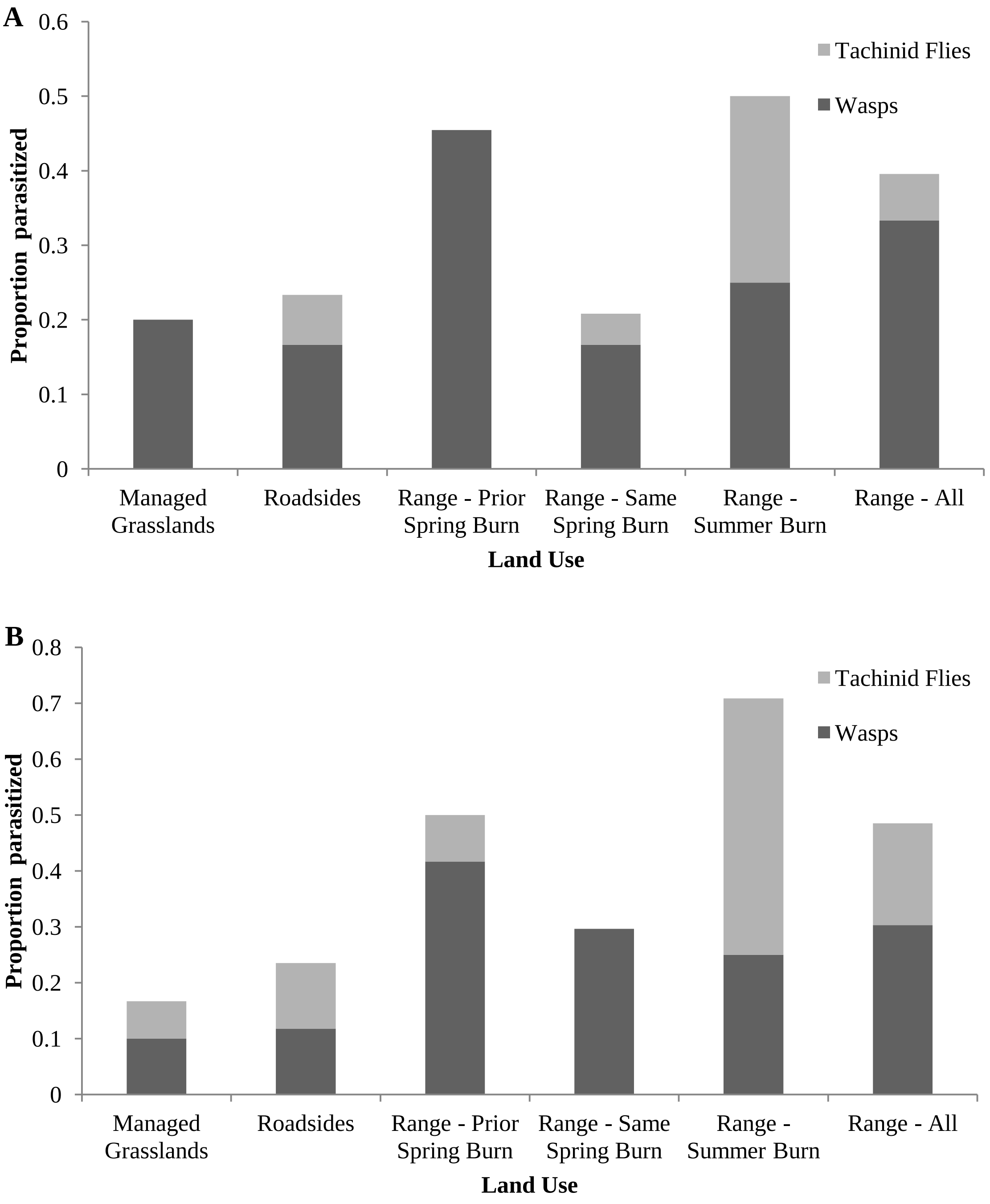

Figure 10. Unexpected cycnia caterpillar (*Cycnia collaris*) parasitism across land uses with parasitoids that emerged during the same season for 2015 (A) and 2016 (B). No tachinid flies emerged from caterpillars collected from managed grasslands or plots burned the previous spring in 2015. Wasps include ichneumonid wasps and braconid wasps. All parasitoids were combined into one category, and the three rangeland sites were combined into a single land use for the statistical analysis.

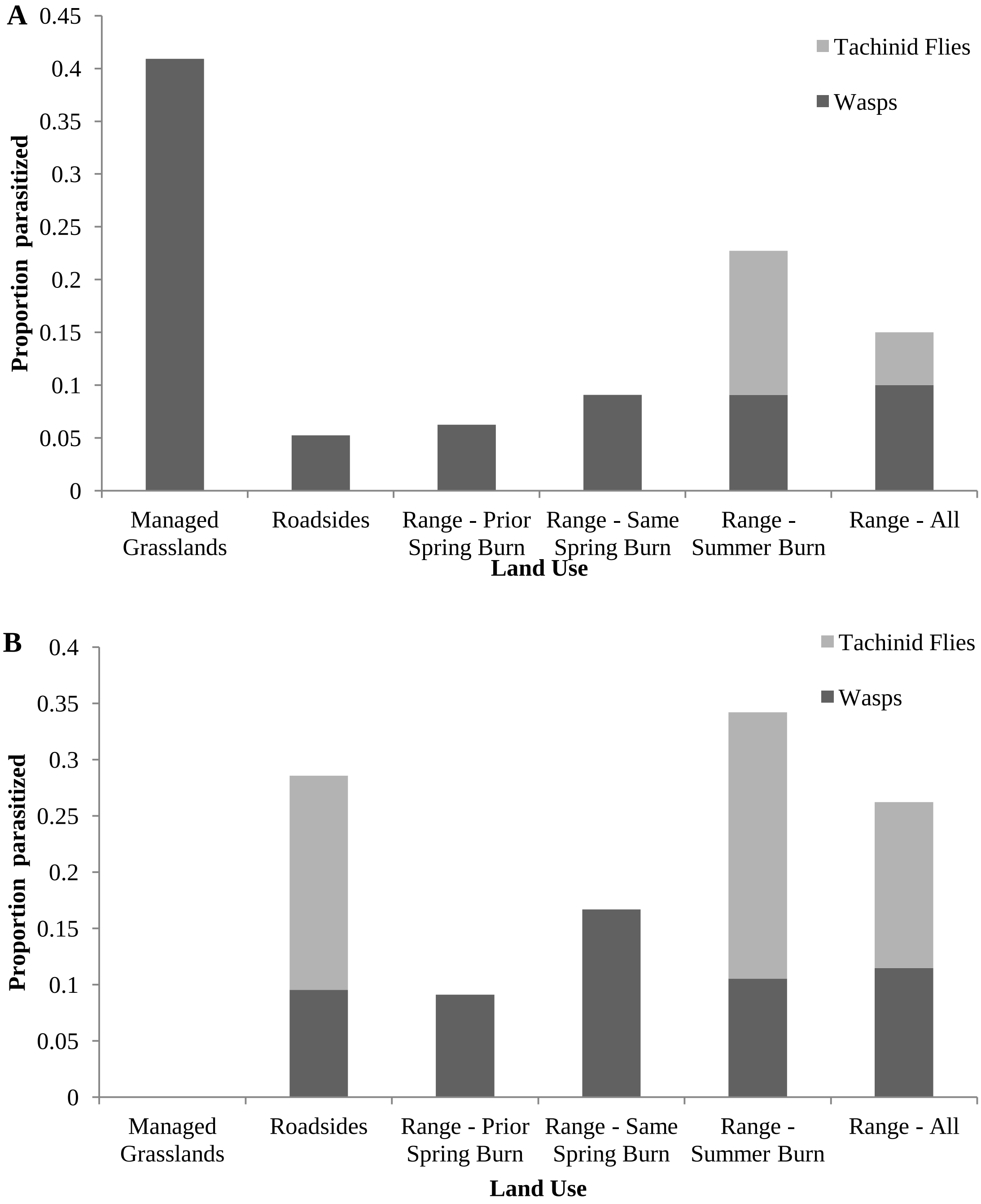

Figure 11. Unexpected cycnia (*Cycnia collaris*) parasitism across land uses with parasitoids that overwintered in the host pupae for 2015 (A) and 2016 (B). Tachinid flies only emerged from summer burn plots from caterpillars collected in 2015. Ichneumonid wasps were the only parasitoid wasp type to emerge from overwintering pupae. Results for 2016 only include those whose final outcome is known. All parasitoids were combined into one category, and the three rangeland sites were combined into a single land use for the statistical analysis.

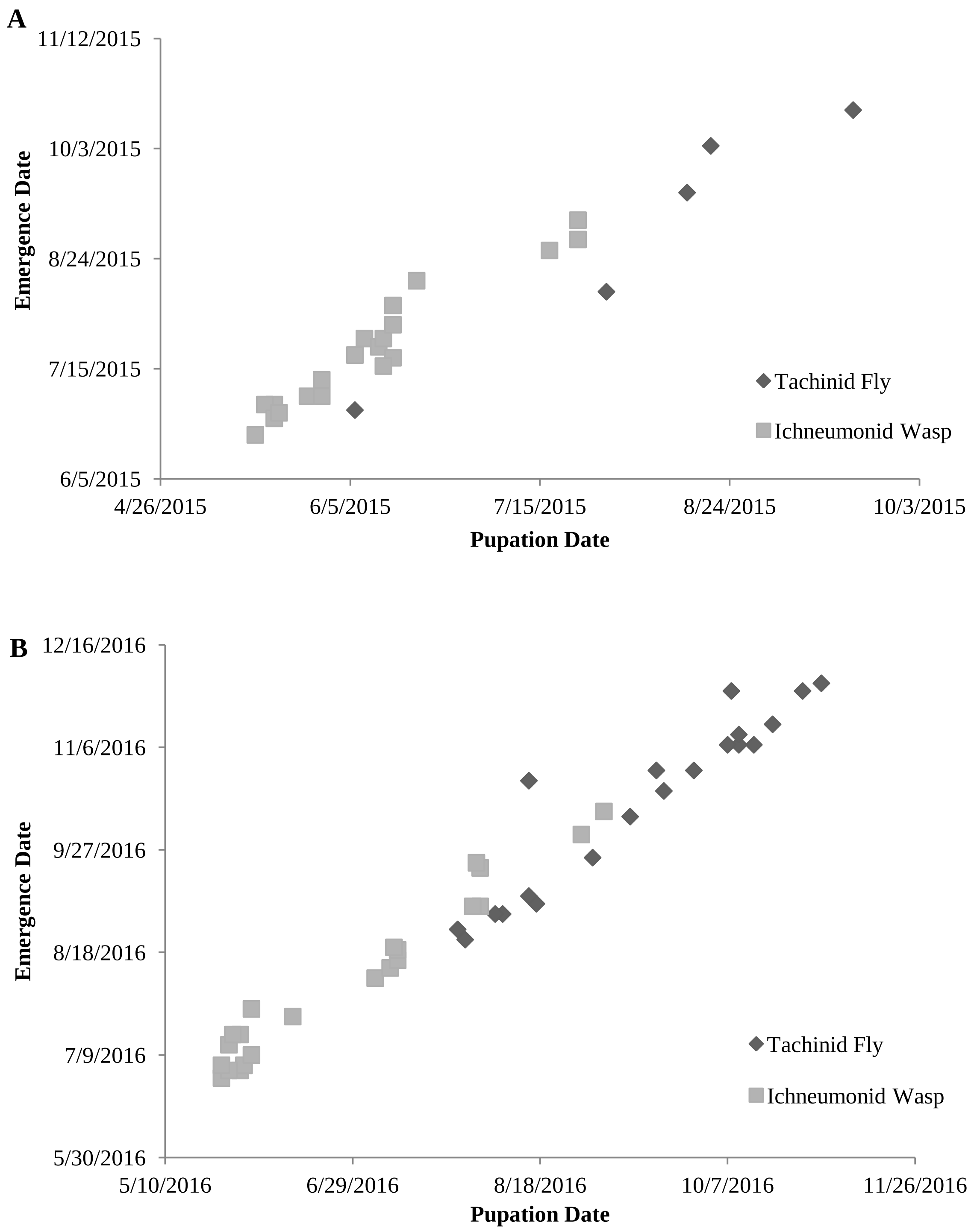

Figure 12. Emergence dates for parasitoids that emerged during the same season during 2015 (A) and 2016 (B).

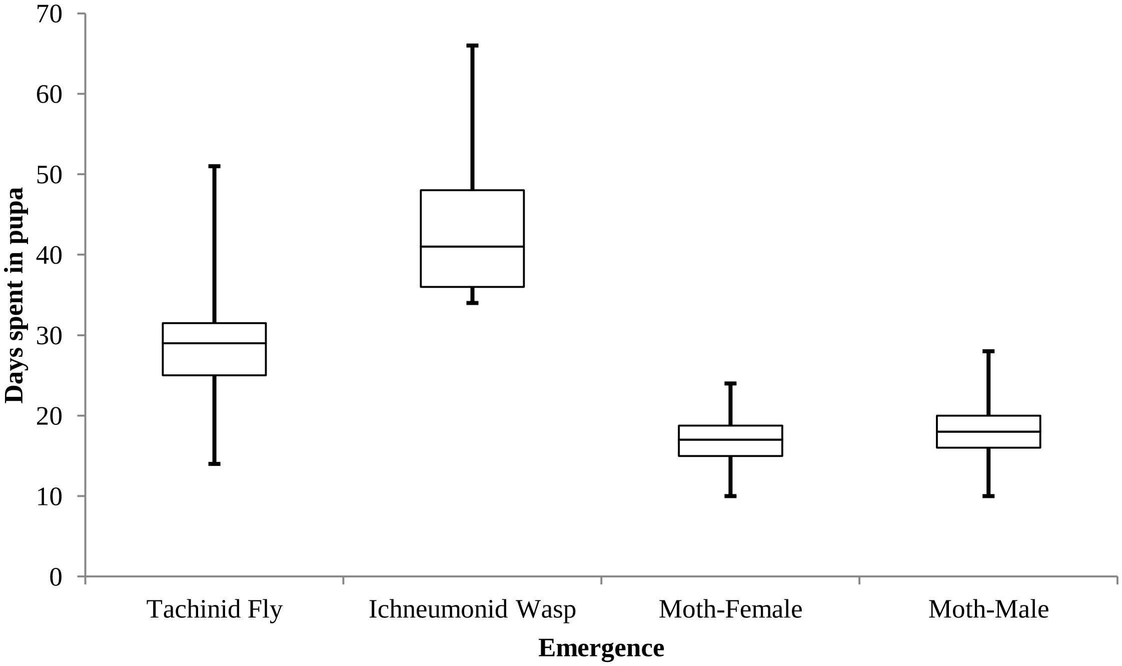

Figure 13. Number of days spent in pupa before emergence during the same season of tachinid flies (n=23), ichneumonid wasps (n=45), female moths (n=66), and male moths (n=68) for caterpillars collected in 2015 and 2016.

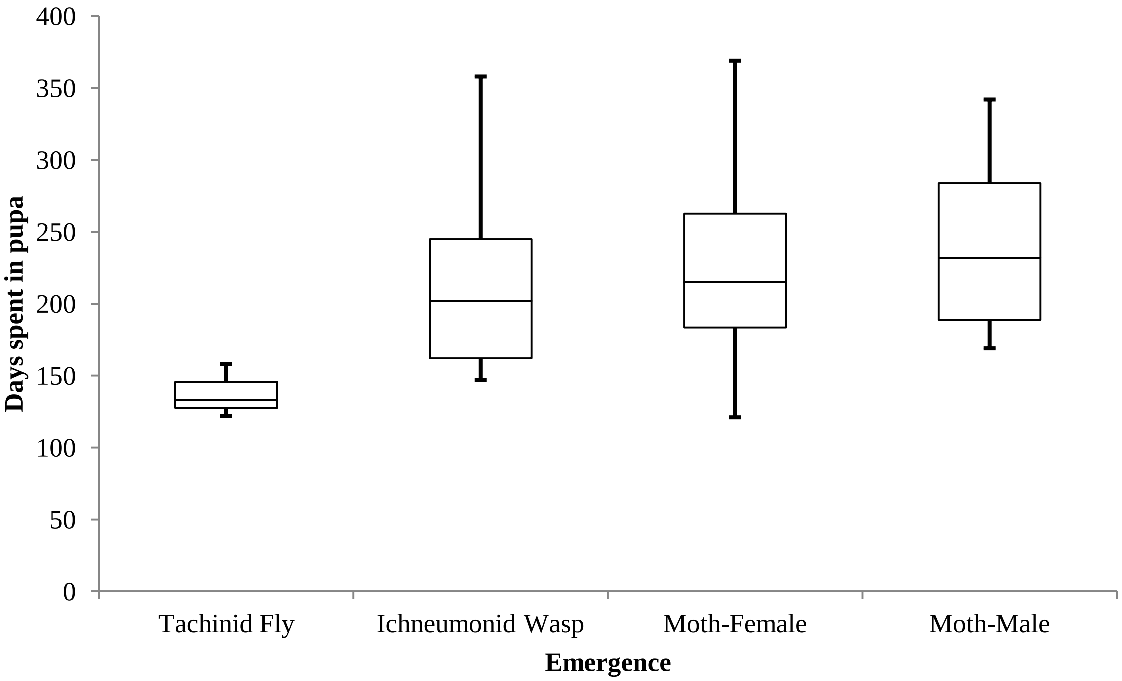

Figure 14. Number of days spent in pupa for caterpillars collected in 2015 that emerged after a diapause as tachinid flies (n=3), ichneumonid wasps (n=12), female moths (n=22), and male moths (n=15).

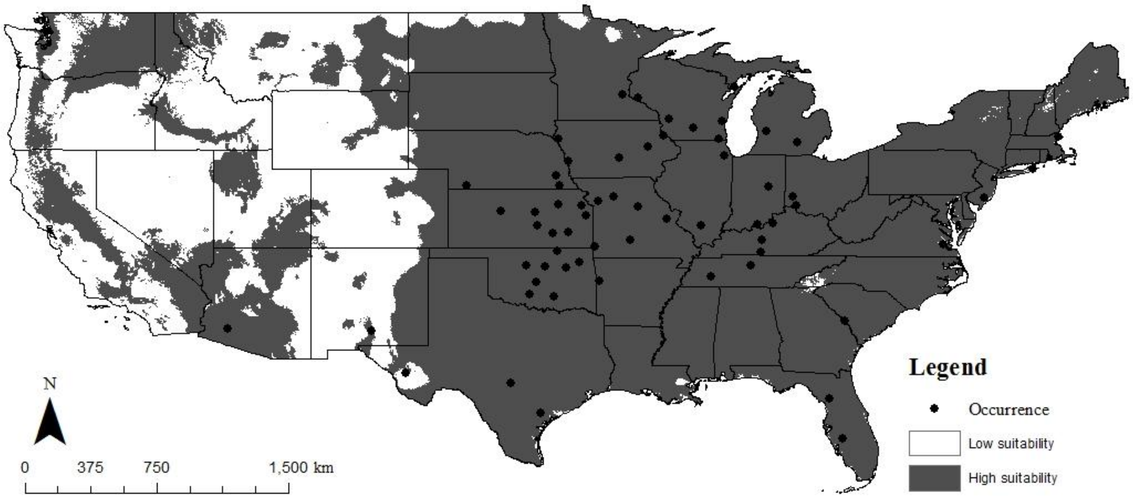

Figure 15. Potential suitable habitat for the unexpected cycnia (*Cycnia collaris*) using climatic variables and elevation as predictor variables (Mean AUC = 0.822) using the minimum presence threshold (0.0439). Unexpected cycnia occurrences were rarefied at 50 km.

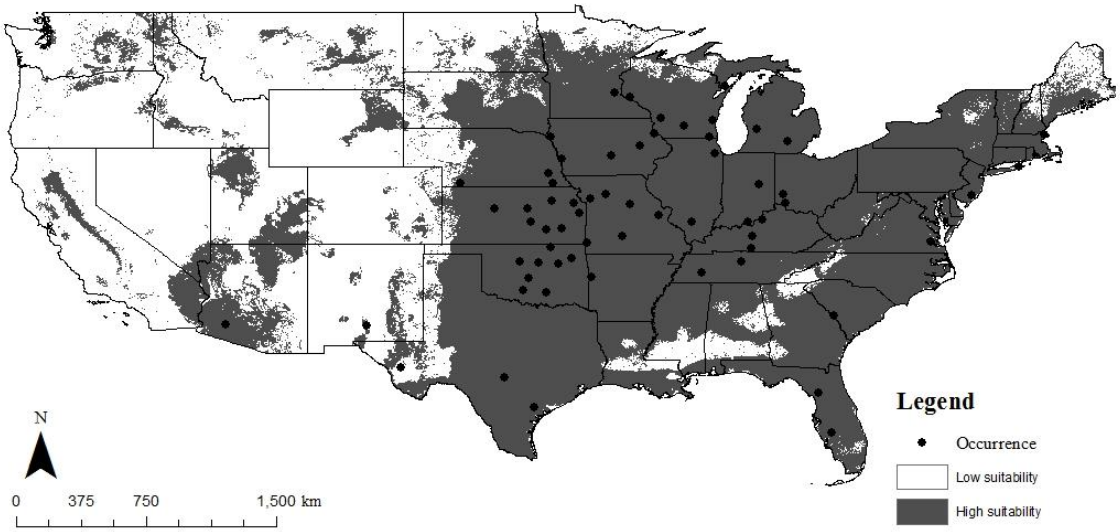

Figure 16. Potential suitable habitat for the unexpected cycnia (*Cycnia collaris*) using climatic variables, elevation, and land cover as predictor variables (Mean AUC = 0.835) using the minimum presence threshold (0.0752). Unexpected cycnia occurrences were rarefied at 50 km.

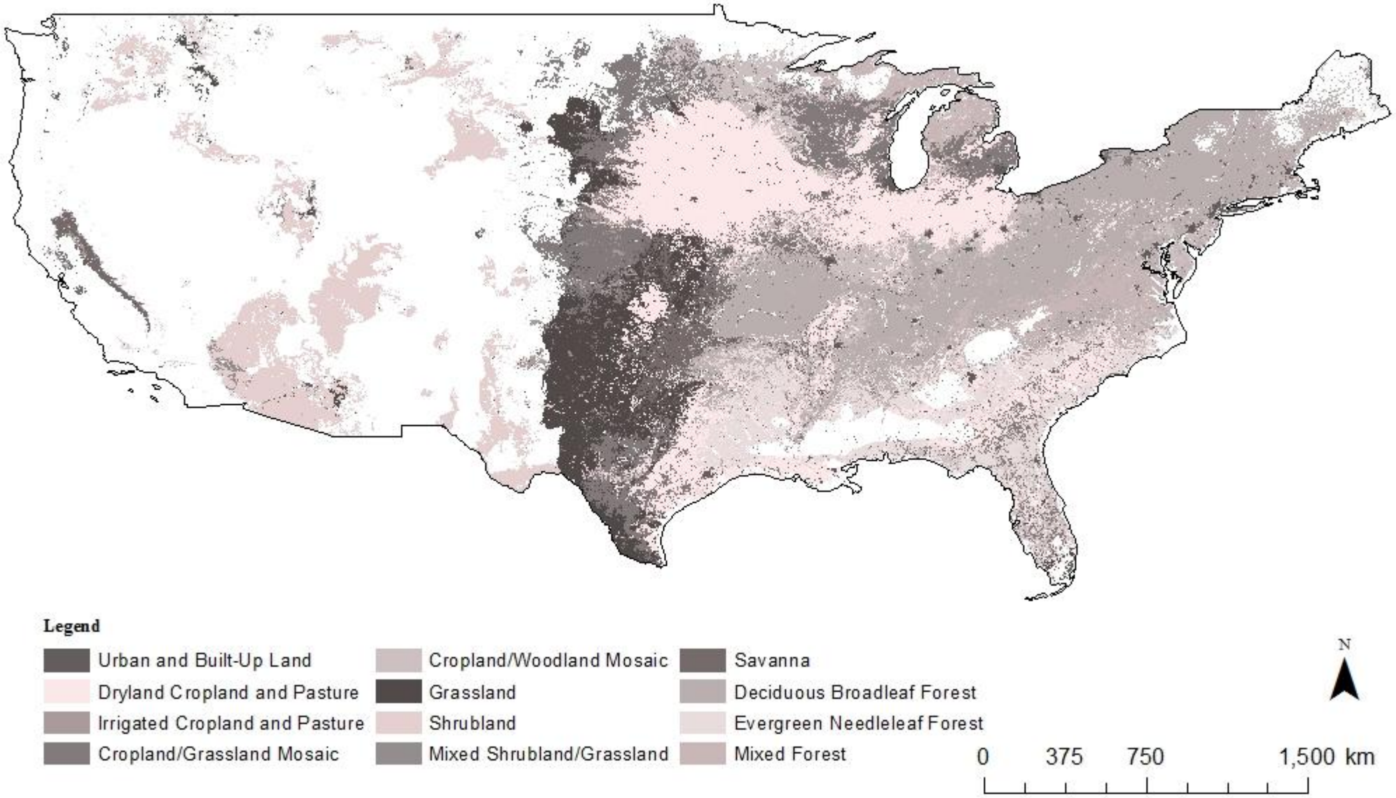

Figure 17. Land covers of the areas deemed as potentially suitable for the unexpected cycnia (*Cycnia collaris*) using climatic variables, elevation, and land cover as predictor variables (Mean AUC = 0.835) using the minimum training presence threshold (0.0752).

VITA

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Master of Science

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