

SPATIOTEMPORAL DRIVERS OF LARGE MOTH ACTIVITY ACROSS FOREST-
GRASSLAND HABITAT COMPLEXES IN CENTRAL ILLINOIS AND THEIR
IMPLICATIONS FOR THE CONSERVATION OF THE DECLINING EASTERN WHIP-
POOR-WILL, A MOTH SPECIALIST

BY

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THESIS

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ABSTRACT

Large moths are known to serve key roles in many ecosystems as herbivores, pollinators, and prey to diverse species. Nocturnal plants and animals that depend on moths often have narrow diel and seasonal activity windows due to restrictions such as cooler nighttime temperatures and limited light availability. Because of these limitations, increasingly well-documented declines in moths and species such as the Eastern Whip-poor-will (*Antrostomus vociferus*), a specialist moth predator, have raised concerns about potential mismatches in activity between moths and the taxa that rely on them for food or pollination. Since 2021, I have been working to investigate large moth activity in midwestern landscapes by conducting hundreds of hours of insect trapping using ultraviolet-light bucket traps on whip-poor-will breeding grounds in central Illinois. I distributed trapping efforts throughout the summer across forest and edge habitats and lit traps during one of three 90-minute time blocks (dusk, solar midnight, and dawn). Moths with a body length ≥ 10 mm were sorted out of these samples, counted, and massed to determine patterns and drivers of large moth activity on the landscape. Large moth abundance and biomass increased in forest interiors relative to forest/grassland edges and generally peaked in late June relative to the rest of the season, with those peaks largely driven by forests. Moth abundance and biomass were highest after dusk relative to solar midnight and dawn in forests and did not differ over the course of the night along edges. Moth captures and mean moth weight also differed between field sites and showed complex responses to interactions involving temperature, moon brightness, relative humidity, and wind speed. These insights into the spatiotemporal activity patterns of large moths highlight potential opportunities for the conservation of this important nocturnal group and species that depend on them for survival.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 BACKGROUND

The Eastern Whip-poor-will (*Antrostomus vociferus*, hereafter whip-poor-will) is a crepuscular insectivorous bird that breeds in eastern North America and has undergone significant population declines in recent decades (Cink et al., 2020, Sauer et al., 2017). Whip-poor-wills are part of the aerial insectivore feeding guild, a group whose members have suffered geographically widespread and taxonomically diverse losses over the past half-century that have been well documented in North America (Blancher et al., 2009, Nebel et al., 2010, Smith et al., 2015). Aerial insectivore declines are thought to be driven by a variety of factors, including habitat loss, reduced prey abundance, environmental contaminants, phenological shifts in prey availability, and changing climatic conditions in breeding, stopover, and wintering grounds (Spiller et al., 2019). Understanding how these factors interact to influence the success of aerial insectivore species is critical for the conservation of this increasingly threatened group. However, despite extensive research investigating whip-poor-will ecology and documenting population declines, the causes of their estimated 2.8% annual decline in North America between 1966 and 2015 remain largely unconfirmed (Sauer et al., 2017).

Multiple studies in recent years have demonstrated that moths, particularly large moths, constitute the primary prey of whip-poor-wills and similar nightjars (Souza-Cole et al., 2022, Mitchell et al., 2021, Garlapow 2007). In this study, as in Souza-Cole et al., 2022, I define large moths as those with a body length (front of head to tip of abdomen) ≥ 10 mm. Souza-Cole et al., 2022 found a positive correlation between the abundance of large moths and the abundance of whip-poor-wills in Illinois and a strong negative relationship between whip-poor-will abundance and the percentage of land covered by human development within 5 km of a site. Similarly,

researchers in southern Ontario found that whip-poor-will presence at the regional scale was positively associated with moth abundance (English et al., 2017). DNA metabarcoding, also conducted by Souza-Cole et al., 2022, detected lepidopterans in 91.7% of whip-poor-will fecal samples. These findings have taken place in the context of negative trends in large moth populations across Europe and North America, particularly in areas that have been developed or converted to agriculture (Conrad et al., 2006, Wagner et al., 2020). The negative association of both nightjars and moths with human development underscores its importance as a potential common source of population declines for both predator and prey. The increasingly well-established links between whip-poor-will and moth declines have understandably raised concerns in the scientific community over food availability for breeding nightjars.

In addition to declining prey abundance, several life history traits of whip-poor-wills and moths point to potential constraints on the ability of whip-poor-wills to find sufficient food to breed successfully. One such constraint is the number of hours per day that whip-poor-wills are able to forage. Daily activity analysis of breeding whip-poor-wills using automated telemetry systems shows significantly lower activity levels over a 24-hour period compared to diurnal species (Souza-Cole 2021). Whip-poor-will foraging windows are likely limited to crepuscular hours and nights with sufficient moonlight by which to see prey contrasted against the sky (Mills et al., 1986). Because of the reduced temporal foraging windows of this species, whip-poor-wills must make efficient use of the dusk and dawn hours that are their primary activity periods by catching a large number of prey, particularly at the height of the breeding season when they need to provision their young as well as themselves. However, spatiotemporal prey availability patterns on breeding grounds may not match the active intervals of whip-poor-wills, which could put a severe strain on breeding whip-poor-wills as moth populations decline.

Seasonal variation in large moth availability may also limit the ability of whip-poor-wills to breed successfully. Previous studies have shown that macro-moth abundance reaches multiple maxima throughout the summer, often reaching a peak in or around late June in temperate regions (Busse et al., 2022, Shewring et al., 2022). Although our study followed the Souza-Cole et al., definition of large moths as any individual with a body length ≥ 10 mm, macro-moths are generally larger than other moth species and are thus roughly comparable to our large moth category in size (Waring and Townsend 2017). Studies showing peaks in moth abundance in June coincide with recent evidence that whip-poor-wills likely time their breeding season so that moonlight and moth availability overlap when they are most in need of food (English et al., 2018). However, this evolutionary strategy may become more difficult in the context of climate change, which is potentially altering the timing of moth emergence relative to whip-poor-will migration and breeding (English et al., 2018, Macgregor and Scott-Brown 2020).

Yet another restriction on whip-poor-will foraging capacity comes from spatial patterns of moth activity, which may be highly variable within the patchwork of forest and open areas that make up whip-poor-will breeding grounds. Moth abundance may not be consistently high at the forest edges where whip-poor-wills often forage, depending on the local moth community composition (Slade et al., 2013).

The abiotic factors influencing the activity of large moths may also be crucial for understanding their conservation and that of their predators. Previous research has indicated that whip-poor-will vocalization and activity increase during periods of greater moonlight availability (Souza-Cole et al., 2022, English et al., 2018, Mills 1986, Wilson et al., 2006). If moth activity is also limited by certain abiotic conditions, whip-poor-will foraging opportunities could be constrained even further by mismatches in activity with their prey due to intensifying pressures

such as artificial light at night and climate change. For example, artificial light and elevated temperatures may interfere with communication between moths and the plants they pollinate, resulting in altered patterns of moth activity throughout the night (Macgregor and Scott-Brown 2020). To understand potential constraints on moth activity and their relationship with whip-poor-will foraging opportunities, future work should investigate patterns of large moth activity by combining spatiotemporal insect surveys across habitats and time blocks with monitoring of ambient moonlight and other meteorological factors.

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CHAPTER 2: SPATIOTEMPORAL DRIVERS OF LARGE MOTH ACTIVITY ACROSS FOREST-GRASSLAND HABITAT COMPLEXES IN CENTRAL ILLINOIS

2.1 INTRODUCTION

Moth and butterflies (Order Lepidoptera) serve key roles across diverse ecosystems as herbivores, pollinators, indicators of ecological health, and prey for other wildlife (Chapman et al., 2003, Kitching et al., 2000, Oostermeijer et al., 1998). Diurnal lepidopterans, especially butterflies, have historically received disproportionate attention from researchers and conservationists, despite making up only 15-25% of the diversity in the order and being poor indicators of the moth community (Kawahara et al., 2017, Ricketts et al., 2002, Thomas 2005). As awareness of declines among many insect taxa, and moths in particular, has grown over the past two decades, a flurry of recent studies has investigated the ecology of large moths by focusing on factors that influence their community assemblages or population trends (Conrad et al., 2004, Conrad et al., 2006, Wagner 2020, Burner et al., 2021). This research has demonstrated the importance of land use, plant and animal communities, and abiotic factors such as elevation and climate for moth biodiversity and abundance (Rabl et al., 2020, Slade et al., 2013, Fox et al., 2014, Macgregor and Scott-Brown 2020).

Despite the growing body of knowledge on moth ecology, spatiotemporal activity patterns of large moths remain understudied, especially at the diel and landscape scales. Studies that have investigated moth activity at these scales have often focused on either overall diversity (e.g., Kadlec et al., 2009) or specific taxa, providing information that is limited to a single species or family (e.g., Danthanarayana et al., 1976, Broadhead et al., 2017, Zhang et al., 1998, Moreno et al., 2021). Studies that consider large moths as a whole often focus on seasonal peaks in abundance or meteorological factors that may influence trapping efforts (e.g., McGeachie

1989, Yela and Holyoak 1997) but rarely address questions pertaining to when and where large moths are active at the diel scale on landscapes containing multiple habitat types (but see Mestdagh 2021). Understanding the factors that affect large moth activity at these scales is especially important because it will help clarify the constraints placed on taxa that depend on moths as pollinators or prey.

Beyond moths, many other nocturnal species also shape their activity patterns based on spatiotemporal and environmental factors such as time of night, availability of moonlight, time of the year, and habitat type. Plants that rely on large moths as pollinators time their nectar production so that visits to conspecifics by pollinators are maximized (Macgregor and Scott-Brown 2020, Raguso et al., 2003, Balducci et al., 2020). Similarly, nocturnal species that depend on large moths for food, many of which are declining aerial insectivores such as bats and nightjars, rely on patterns of abundance and available biomass of large moths as key determinants of their ability to forage effectively (English et al., 2017, Arrizabalaga-Escudero et al., 2015, Hecker and Brigham 1999).

The declining Eastern Whip-poor-will (*Antrostomus vociferus*) specializes in moths, particularly large-bodied moths, as its primary food source (Souza-Cole et al., 2022). Additionally, due to limited food availability and high predation risk during the day as well as low visibility at night, the whip-poor-wills generally limit foraging to dusk and dawn hours and nights with bright moonlight (Sauer et al., 2020, Souza-Cole 2021). Because of these limitations, whip-poor-wills depend on high prey abundance during key windows in space and time, during which they likely gorge themselves to support energetically expensive undertakings such as rearing young and migrating (English et al., 2018, Souza-Cole et al., 2022). Understanding the spatiotemporal patterns and drivers of large moth abundance and biomass in critical habitats for

their nocturnal predators is therefore an important step toward assessing their foraging opportunities and managing for increased prey availability.

To understand the factors shaping the activity of large moths, I employed ultraviolet light trapping across gradients of space, time, and moonlight availability in whip-poor-will breeding habitats over three breeding seasons. I also collected weather data to account for meteorological factors influencing capture rates. I predicted that moth abundance, biomass, and average individual mass in my traps would decrease with increasing moon illumination mediated by cloud cover, decrease as wind speed increased, and increase with relative humidity and air temperature. In terms of temporal patterns, I predicted that moth activity metrics would reach diel peaks after dusk, declining through solar midnight until dawn with seasonal peaks in June and July, and these trends would be consistent across habitats and years (Busse et al., 2022). Based on previous habitat comparisons in Illinois and elsewhere, I predicted that moth abundance would be greater in forest interiors compared to forest/grassland edges (Safford 2018, Mestdagh 2021). Because whip-poor-wills are often observed foraging along edges at dusk and dawn, I predicted that edge moth abundance would be closer to forest abundance and greater relative to solar midnight during crepuscular hours (Wilson and Watts 2008). Ultimately, my goal was to understand when and where moths are available as prey or pollinators on forest-grassland landscapes, as well as the drivers and conservation implications of those activity patterns are for moths and the species that require them as food.

2.2 METHODS

2.2.1 *STUDY SITES*

I sampled moths at three field sites in west-central Illinois over three summers from 2021 to 2023. In 2021, fieldwork was conducted between mid-May and mid-August at two

field sites near the city of Havana, in central Illinois, USA. The first of these sites, Sand Ridge State Forest (“Sand Ridge”), is a 3,035-hectare dry sand forest with a patchwork of roads and open areas including dry sand savanna, dry sand prairie, ponds, and former agricultural fields. This large state forest also contains several extensive sections of pine plantations and recreation areas such as trails and campgrounds (Marcum et al., 2013). Sand Prairie-Scrub Oak Nature Preserve (“Scrub Oak”) is a 590-ha natural area consisting of oak-dominated sand forest and remnant sand savannas, dry sand prairies, and successional fields (McClain et al., 2008). Both Sand Ridge and Scrub Oak have maintained robust whip-poor-will breeding populations in recent decades, in contrast with much of central Illinois (Bjorklund 1983, Souza-Cole et al., 2022).

In 2022, a third field site, Jim Edgar Panther Creek State Fish and Wildlife Area (“Panther Creek”) was added to foster a comparison of insect community assembly and abundance between the two original sites and a nearby natural area where whip-poor-will populations have declined in recent years (Souza-Cole et al., 2022). Panther Creek is a 6,698-ha complex of deciduous forest, farm fields, prairies, and wetlands with poorer soil drainage than the two original sites (Illinois DNR n.d.), both of which have excessively drained soils because of their high sand content (NRCS 2009). All three field sites are located near the Illinois River and are generally surrounded by row-crop agriculture.

2.2.2 ULTRAVIOLET LIGHT INSECT TRAPPING

Four nights per week beginning in mid-May and ending in early August 2021, I deployed three bucket traps (BioQuip Products, Inc. #2851A, Safford et al., 2018) with 24W ultraviolet blacklight lures (390-405 nm wavelength) in 150-m transects at either Sand Ridge or Scrub Oak.

Lures were composed of a 2-m blacklight LED strip wound tightly around a 30-cm length of white PVC pipe. These lures were surrounded by three clear-plastic vanes that insects lured into proximity of the traps would collide with and fall into a funnel below (Fig. 1). The light strip illumination status was controlled by programmable timers linked to an 18 amp-hour 12V battery. Traps were lit for a 90-minute period beginning at civil dusk (when the center of the sun's disc is 6° below the horizon, approximately 30 min. after sunset).

To avoid oversampling insects in any one location, Sand Ridge and Scrub Oak were visited on alternating nights and traps were rotated between 8 transect locations at each site, for a total of 16 transect locations, which were spaced at least 100 m apart. All transects were perpendicular to a woodland/grassland edge and contained two traps. I spaced each trap 75 m apart from other traps spanning forest and forest/grassland edge habitats. Each trap contained a small jar of ethyl acetate covered in mesh. The vapors from the ethyl acetate acted as the killing agent for insects in the trap; the collected insects were placed in a freezer upon returning to the field station to be preserved for future processing.

In 2022, to investigate variation in moth activity over the course of an evening in each habitat, the number of traps per transect was expanded to six, with each of the three traps in each habitat running for 90 minutes at a different time of night (Fig. 2). The first trap was lit starting at civil dusk (when the center of the sun's disc is 6° below the horizon), the second was lit starting 45 minutes before solar midnight (the midpoint between dusk and dawn), and the third was lit starting 90 minutes before civil dawn. To accommodate the addition of a third field site while avoiding oversampling, I reduced the number of transects at each field site to 6 and rotated through the three sites every three trapping nights. Additionally, to avoid oversampling within a single habitat each night, I spread the three traps located in each habitat in a transect 75 m apart

to accommodate the traps' estimated sampling radius of $\leq 30\text{m}$ (Fig. 2, Muirhead-Thompson 1991, Beck and Linsenmair 2006). To maintain a high sample size in 2022, I sampled two separate transects at the same site nightly.

To maintain continuity in our dataset across all three years in 2023, I again focused our efforts at Sand Ridge and Scrub Oak during the 90-minute time block starting at civil dusk. As in 2021, two-trap transects were spread across forest and forest/grassland edge habitats with traps 75 m apart. Eight transects (four at each field site) were visited four times between early May and late June.

2.2.3 MOON SCORE, WEATHER, AND DOMINANT TREE COVER DATA

I accessed hourly weather data through the Iowa Environmental Mesonet Automated Airport Surface Observing Systems (ASOS) Archive (Herzman 2023). Weather data for Sand Ridge were collected from General Wayne A. Downing Peoria International Airport, located approximately 30 km northeast of the forest. Sand Prairie-Scrub Oak and Panther Creek weather records were collected from Abraham Lincoln Capital Airport, located in Springfield, Illinois, approximately 40 km east-southeast of Panther Creek and 50 km southeast of Scrub Oak.

Weather data accessed through the ASOS Archive consisted of hourly measurements of air temperature, wind speed, cloud cover, relative humidity, and hourly precipitation. Insect trapping did not occur on nights with a predicted chance of rain of $\geq 20\%$. In ASOS, cloud cover observations are categorized as clear, few, scattered, broken, or overcast. I converted these to an ordinal numeric factor called "sky code," which ranged from 0 to 4, respectively. All weather measurements were averaged across a three-hour period overlapping the range of times when traps were lit over the course of the season for each of the three nightly time blocks: 8:00 pm-

11:00 pm for the after-dusk time block, 11:30 pm-2:30 am for the midnight time block, and 3:00 am-6:00 am for the before dawn time block. I acquired moon illumination fraction as well as moonrise and moonset times using the “SunCalc” package version 0.5.1 (Thieurmel et al., 2022) in R version 4.3.2 (R Core Team 2022). Moon score for a given sampling period was defined as the percentage of the moon illuminated multiplied by the proportion of minutes during the sampling window that the moon was above the horizon.

Dominant tree cover (coniferous or deciduous) was defined as the tree type that covered the majority of the tree canopy within 30 m of each insect trap location. This parameter was assessed first via satellite imagery and later confirmed in person at each trap location during fieldwork.

2.2.4 INSECT SAMPLE PROCESSING

Insect samples were stored in -20°C freezers in zip lock bags until processing. Samples were processed using forceps in glass sorting trays. Large insects with a body length ≥ 10 mm were separated from smaller individuals. Body length was defined as the distance from the front of the head to the tip of the abdomen, excluding appendages such as mouthparts, antennae, and ovipositors. Only insects that had flight-capable wings and met this size requirement were included in the sorting, counting, and weighing process. Insects from each trap sample were then sorted by taxonomic order into four categories: Lepidoptera, Coleoptera, Blattodea, and Other. Large, flight-capable moths, beetles, and cockroaches were chosen to be sorted out from other insects because they are believed to be the primary prey species of whip-poor-wills based on previous fecal metabarcoding results (Souza-Cole et al., 2022, Garlapow 2007). Once sorting was completed, the number of individuals in each category was recorded and the wet mass of the

insects in each category was measured the nearest 0.001 g using a digital scale. For a step-by-step protocol of the sorting and massing process, please see Appendix A.

2.2.5 STATISTICAL ANALYSIS

2.2.5.1 Overview

To gain a complete picture of the prey pool available to whip-poor-wills across time and space during the breeding season, I modeled three measures of large moth availability: abundance, total biomass, and average mass of an individual moth (“mean moth weight”). Before modeling, samples that did not represent 90 minutes of trapping due to known insect escapes during collection, timer errors, or light malfunctions, and samples that were missing critical information such as the time of night they were collected were excluded from the data set. I also excluded any sample collected while precipitation was recorded at more than trace levels, because precipitation frequently caused malfunctions in the traps that may not have been detectable and substantial moisture in the traps made insect samples difficult to process accurately.

I evaluated models based on Akaike’s Information Criterion corrected for small sample sizes (AICc) as calculated by the “dredge” function in the MuMIn package version 1.47.1 (Bartoń 2022) in R version 4.3.2 (R Core Team 2022). Each of the three measures of prey availability was modeled using a two-stage model ranking process, with the first stage including weather and moon-related variables and the second containing temporal and habitat-related variables.

The first stage consisted of a single round of model-ranking, with the following five environmental covariates included in models: air temperature, average wind speed, relative

humidity, sky code, and moon score. None of the continuous environmental variables were highly correlated ($|r| \geq 0.5$) and I did not restrict which variables were included in models together. I constructed a global model with the additive effects of all five explanatory variables in addition to the following three potential interactive effects: air temperature \times average wind speed, air temperature \times relative humidity, and sky code \times moon score. The top ranked model from this stage was carried on to the next model-ranking stage.

The best-fitting model from the first stage became a fixed set of terms for the second stage, which consisted of multiple rounds of model-ranking due to the high number of terms included in the analysis. Models considered the following six spatiotemporal variables: habitat type, time of night, sampling round, field site, dominant tree cover, and moon score. In addition to the additive effects of all six covariates, I evaluated eleven interactions in this stage: moon score \times time of night, field site \times sampling round, field site \times time of night, habitat \times sampling round, habitat \times dominant cover, habitat \times time of night, time of night \times sampling round, habitat \times field site, dominant cover \times sampling round, habitat \times moon score, and time of night \times dominant cover. To simplify each round of ranking in the second stage, all rounds of model-fitting –except the final round– included a cap on the number of terms allowed in a model beyond any intercept and random effect terms. In the first round, this maximum was derived by adding four to the number of fixed terms from the previous stage.

After the candidate models in each round were ranked by AICc, the lowest-ranking interaction term was eliminated from future model ranking rounds unless the highest-ranking model containing that term was within two AICc units of the top model. In each round, models were forced to select from a list of interaction terms from models within two AICc units of the top model in the previous round. Interaction terms that had been on this list in the previous round

and were included in the top model of the current round became fixed terms in the next round. After each round, I reset the parameter limit to four plus the number of terms in the most heavily-parameterized option in the list of interaction terms plus the number of fixed terms from previous rounds.

These rounds continued until either the top model included all possible remaining interaction terms or a model with the maximum number of terms being considered in a given round did not rank within two AICc units of the top model. Once one of these conditions was met, the best-fitting model from that round was carried forward into a final model-ranking. In this final round, all interaction terms not present within 2 AICc units of the top model of the previous round were excluded, no fixed terms besides those carried over from the first stage were included, and the minimum number of terms was set equal to the number of terms in the top model from the first round of ranking in stage two, with no maximum number of terms. Unless otherwise noted, the highest-ranking model from this final model-ranking was used to estimate parameter effect sizes and create figures of predicted values.

2.2.5.2 Abundance modeling

To estimate the abundance of large insect prey available to whip-poor-wills at a given time and place, the above model-ranking process was applied to a generalized linear mixed modeling approach with a negative binomial underlying distribution. Models were run using the “nbinom1” or “nbinom2” family within the “glmmTMB” package, and that family was kept consistent for each model-ranking procedure (Brooks et al., 2017). A random effect of trap relative position (left, middle, or right relative to a person facing from grassland to forest habitat) nested within transect identity was applied to all models.

2.2.5.3 Available biomass and mass-per-individual modeling

To estimate the relative available biomass of large insect prey to whip-poor-wills at a given time and place, the model-ranking procedure described above was applied to a generalized least squares modeling approach. This same approach was also used to model the mass-per-individual large moth in a given sample. For both dependent variables, the “gls” function within the “nlme” package version 3.1-162 was used to run all models (Pinheiro et al., 2023). A compound symmetric covariance structure was used to apply a random effect of trap relative position nested within transect identity to all models. Additionally, all models included a heterogeneous variance structure that accounted for discrepancies in variance between habitats, times of night, and sampling rounds, as well as interactions between those variables.

2.3 RESULTS

2.3.1. OVERVIEW

The 2022 analyses included a total of 374 insect samples representing 561 hours of trapping between May 15 and August 10. In our three-year 2021-2023 analysis that included only dusk trapping at Sand Ridge and Scrub Oak, a total of 216 samples were analyzed, representing 324 hours of trapping. In total, 498 unique 90-minute samples were analyzed across the three years of data, representing 747 hours of trapping.

In 2022, counts of large moths in each 90-minute sample ranged from 0 to 212 with a median of 23 and an average of 32.6 ± 1.6 (mean \pm se). Moths accounted for 69.1% of winged large insects (body length ≥ 10 mm). Total biomass of large moths in each sample ranged from 0 to 16.89 g, with a median of 1.56 g and a mean of 2.12 ± 0.11 g. Moths accounted for 57.0% of the biomass of winged large insects collected in 2022. The mean mass of an individual large

moth was 0.065 g. The mean mass of an individual moth in each sample ranged from 0.009 to 0.714 g, with a median of 0.063 g and a mean of 0.075 ± 0.003 g.

Across the 2021-2023 dusk samples from Sand Ridge and Scrub Oak, large moth counts ranged from 0 to 206, with a median of 26 and a mean of 37.2 ± 2.2 . Moths accounted for 70.2% of the large, winged insects in the samples. The total mass of large moths per sample ranged from 0 to 16.89 g, with a median of 1.71 g and a mean of 2.42 ± 0.18 g. Moths accounted for 45.9% of the biomass of winged large insects at dusk. The mean mass of an individual large moth was 0.063 g. The mean mass of an individual moth in each sample ranged from 0.013 to 0.182 g with a median of 0.061 g and a mean of 0.068 ± 0.002 g.

2.3.2. *DIEL-SCALE ANALYSIS (2022 ONLY)*

The highest-ranking model explaining large-moth abundance in 2022 carried an AICc weight of 0.304 and included an additive effect of relative humidity as well as the following seven interaction terms and their corresponding additive effects: temperature \times wind speed, moon score \times time of night, field site \times sampling round, field site \times time of night, habitat type \times sampling round, habitat type \times dominant tree cover, and habitat \times time of night. This was also the most heavily parameterized model in the set, with a total of 19 terms. Moon score \times time of night, sampling round \times field site, and field site \times time of night appeared in all six models with a delta AICc of ≤ 4 in addition to the additive effects of all spatiotemporal factors considered except dominant tree cover.

The top model predicting biomass of large moths in 2022 was simpler than the top model for abundance, including a total of five interaction terms and their additive effects: temperature \times wind speed, moon score \times habitat, field site \times habitat, moon score \times time of night, and sampling

round \times time of night. This model carried an AICc weight of only 0.118 and ranked only 0.19 AICc units above the second-highest model, which carried a weight of 0.107 and included all terms in the highest-ranking model in addition to a habitat \times time of night interaction. Because it was more heavily parameterized, the second-highest-ranking model was used to create all figures for this ranking. All additive effects and two interactions –sampling round \times time of night and habitat \times field site– appeared in every model within 4 AICc units of the top model, and the sum of AICc weights for models containing those interactions were 0.99 and 0.91, respectively. The sum of AICc weights for models containing the moon score \times habitat, habitat \times time of night, moon score \times time of night, and interactions were 0.62, 0.58, and 0.52, respectively.

The top model describing the drivers of average moth weight in 2022 was relatively complex, containing the additive effect of sky code and the following seven interaction terms: temperature \times wind speed, temperature \times relative humidity, field site \times sampling round, field site \times time of night, time of night \times sampling round, habitat \times field site, and habitat \times moon score. The most influential spatiotemporal factors, which were included in all models within 4 AICc units of the top model, were the interactions between habitat and moon score, sampling round and field site, and sampling round and time of night, as well their corresponding additive effects. The sums of weight for models containing these three interactions were 0.94, 0.98, and 1.00, respectively. For models containing the other two spatiotemporal interaction terms contained in the top model –field site \times time of night and habitat \times field site– AICc sums of weights were 0.55 and 0.51, respectively.

The influence of moon score on all three measures of large moth availability varied depending on either time of night or habitat. Moon score had a fairly strong negative effect on large moth abundance at solar midnight, with a much milder negative effect at dusk and a slight

positive effect at dawn (Fig. 3). Under moonless conditions, the model predicts approximately 1.5× higher moth abundances at dusk and solar midnight than at dawn (Fig. 3). Predicted moth biomass was similarly negatively influenced by increasing moon score at dusk and solar midnight and positively correlated with moon score at dawn (Fig. 4). Moon score also produced opposite small but notable effects on mean moth weight in different habitats, positive in forest and negative along edges (Fig. 5).

In addition to moonlight, time of night interacted with habitat, field site, and sampling round to influence large moth availability in 2022. Forests had more variability in both moth abundance and biomass over the course of a night than edges, with the number of large moths in the forest starting at approximately double the edge abundance at dusk and declining through solar midnight until the two habitats have similar moth abundances at dawn (Fig. 6). Biomass showed a similar pattern with a smaller decline in forests of only 0.8× from dusk to dawn. Across all field sites, moth abundance declined between dusk and dawn, although the largest decline took place between civil dusk and solar midnight at Panther Creek and between solar midnight and civil dawn at Sand Ridge and Scrub Oak (Fig. 7). In contrast, predicted moth weight increased from dusk to dawn at Panther Creek, while it remained relatively consistent over the course of an evening at both Sand Ridge and Scrub Oak (Fig. 8).

Moth biomass and mean weight showed similar responses to the interaction between time of night and sampling round. At dusk, both variables peaked during June and bottomed out at the end of the season, while at both solar midnight and dawn, total biomass and individual mass peaked at the start of the season, declined through June and July, and increased slightly at the end of the season (Figs. 9 & 10). Sampling round also interacted with field site to influence moth abundance and mean weight. Moth abundance declined sharply from early season highs between

June and July in all field sites and recovered somewhat in late July at Panther Creek and Sand Ridge, but not Scrub Oak (Fig. 11). Average mass of a moth generally declined as the season progressed across field sites, decreasing sharply from May-July at Panther Creek and Sand Ridge before recovering slightly late in the season, while at Scrub Oak mean individual mass rose to a peak in June and declined the remainder of the season (Fig. 12).

The interactions between habitat type and dominant tree cover and between habitat and sampling round show more consistent spatiotemporal patterns than interactions containing time of night. Although all sampling rounds show more moths in forests than edges, that difference became starkest during mid-late June in 2022 (Fig. 13). Forests also contained greater moth biomass than edges across all field sites; the difference was largest at Panther Creek, followed by Scrub Oak and then Sand Ridge (Fig. 14). The interaction between habitat and dominant tree cover shows deciduous forests to have greater moth abundance than coniferous forests, while no such difference existed along edges (Fig. 15). Deciduous areas experienced more extreme differences in moth abundance between forest and edge than coniferous dominated forests at our field sites (Fig. 15).

In addition to habitat, the additive and interactive effects of air temperature and wind speed were among the most influential factors driving large lepidopteran availability in 2022. Moth abundance rose swiftly with rising temperatures, an effect that shrank but did not disappear as wind speed increased (Fig. 16). Because of this wind speed \times temperature interaction, at low temperatures, higher wind speeds led to relatively greater moth captures while lower wind speeds maximized moth abundance at high temperatures (Fig. 16). Individual moth mass showed a similar trend, with the largest predicted moth masses occurring on cold, windy nights and warm, calm nights (Fig. 17). The effects of the wind speed \times temperature interaction on large moth

biomass were similar to those on abundance, with a strong positive effect of temperature on biomass at low wind speeds that diminished as wind speed increased.

Increasing relative humidity also had a notable positive effect on moth abundance (Fig. 18) and positively influenced mean moth weight at high temperatures but had no effect at low temperatures (Fig. 19). Sky code was only included in the best-fitting model for one of the 3 response variables; captured moths were 40% lighter on average as cloud cover increased from clear to overcast skies (Fig. 20).

2.3.3. DUSK ACROSS YEARS ANALYSES (2021-2023)

Under our top model, the main drivers of dusk moth abundance across the three years of our study were the additive effects of moon score and study year as well as the interactions between sampling round and field site, habitat type and field site, and temperature and relative humidity. The top model carried a weight of only 0.101, but the model averaged sums of weights for the spatiotemporal factors year, sampling round \times field site, and habitat \times field site were 0.88, 0.69, and 0.61, respectively, with the only other factors included in the final round of model-fitting, habitat \times sampling round, field site \times study year, and the additive effect of dominant cover carrying sums of weights equal to 0.30, 0.28, and 0.17, respectively.

The highest-ranking model predicting biomass of large moths at dusk included the additive effects of study year, temperature, relative humidity, and moon score, plus three interaction terms: sampling round \times field site, field site \times habitat, and habitat \times sampling round (Table 2). This model carried an AICc weight of 0.159, with the model averaged sums of weights for all terms in the top model ranking at or above 0.58.

The top terms predicting mean moth weight at dusk were sky code, sampling round, and the interactions between habitat and study year, habitat and moon score, and temperature and wind speed. The best model had an AICc weight of 0.528 and all terms in the model carried a model averaged sum of weights of 0.90 or greater.

Differences in moth abundance and biomass at dusk between field sites grew as the season progressed, with both sites starting the season with approximately 30 moths or 2 grams per sample and Scrub Oak ending the season with approximately 34 moths and 2 grams per sample compared to Sand Ridge's 18 moths and around 1.3 grams per sample (Figs. 21 & 22). Differences between habitats also varied across field sites; forests had about 1.75× the number of moths and 1.8× the biomass of moths as edges at Sand Ridge, while those differences grew to approximately 2.25× and 2.25× at Scrub Oak, respectively (Figs. 23 & 24). These changes were primarily driven by increases in forest abundance and biomass when shifting from Sand Ridge to Scrub Oak, as edge abundances and biomasses remained relatively consistent between sites.

In addition to variability across sites, habitat type also interacted with temporal factors within and across field seasons to influence moth activity. At dusk, moth biomass peaked between mid-June and early July in both habitat types with the forest biomass at 1.9× next-highest sampling round, from mid-May to early June (Fig. 25). The difference between forests and edges was also at its most extreme during the mid-June to early July period with the expected moth biomass in forests at 2.45× the edge biomass (Fig. 25). Average moth weight also varied with sampling round, peaking between mid-June and early July, but the relative weight of moths between habitats did not change between sampling rounds (Fig. 26). Average moth weight also varied between habitats across study years, with heavier moths in edges in 2021 and 2022 and in forests in 2023 (Fig. 27). Large-moth abundance and biomass also generally increased as

study year increased, with predicted abundance increasing from 25 to 35 moths per sample and biomass increasing from 1.5 to 3 g per sample between 2021 and 2023.

As in our 2022 analyses, the moon score influenced all three response variables. Increasing moon score resulted in declines in moth abundance and biomass at dusk across all years. Moon score also showed a similar interaction with habitat to influence mean moth weight as it did in 2022, suggesting that heavier moths are found in forests during brightly moonlit periods, and show a very slight preference for edge habitat during moonless periods (Fig. 28).

Temperature, wind speed, relative humidity, and sky code again strongly influenced large-moth availability in our multi-year analysis. Moth biomass at dusk increased with temperature across all years of our study, and temperature interacted strongly with relative humidity to shape moth abundance (Figs. 29 & 30). At 45% relative humidity, increasing temperature from 12°C to 27°C increased expected abundance from 20.5 to 63.5, while at 95% humidity, abundance was relatively stable between 19 and 20 over the same temperature change (Fig. 30). Wind speed and temperature interacted in a very similar way to our 2022 analysis to influence individual moth mass at dusk from 2021-2023, indicating that the average moth captured is more than double the mass on 12°C nights with 12 mph winds (0.089 g) relative to 12°C nights with 0 mph winds (0.043 g, Fig. 31). On 27°C nights, 0 mph winds led to an expected large moth mass of 0.085 g and 12 mph winds led to an expected mass of 0.045 g. Sky code also showed a moderate negative effect on mean moth weight, with the average moth becoming 38% lighter as cloud cover increased from clear to overcast.

2.4 DISCUSSION

Our research demonstrates that a variety of spatiotemporal and meteorological factors predict availability of large moths. These factors serve not only as indicators of potential

windows of opportunity for moth predators and plants that depend on moth pollination, but also as clues as to how human activity may contribute to declines in moth populations and biodiversity and how these effects could be addressed through conservation and management.

One of the most important drivers of both moth abundance and biomass across all our analyses was habitat type. Like much of midwestern North America, our study sites were made up of complexes of wooded and/or grassland natural areas surrounded by abundant row-crop agriculture. In this context, our results uniformly showed substantially higher availability of large moths in forests relative to forest/grassland edges, although the scale of this difference varied based on the moon score, study site, time of night and sampling round. This fits with previous research that has measured higher moth abundance in forests relative to adjacent grasslands in Illinois (Safford 2018).

Although the possibility remains that shaded conditions in forests may have systematically biased forest traps to attract more insects relative to traps along edges, an interaction between moon score and habitat type did not emerge in the top model describing moth abundance in either analysis. The habitat \times moon score interaction did emerge in the top models for moth biomass in 2022, but the overall biomass interaction showed a clear preference of moths for forest traps even under moonless conditions, with the preference growing only slightly under bright moonlight. Another caveat to consider relating to the difference in moth availability between forests and edges is the differential attractiveness of ultraviolet light lures on different macromoth taxa. Because we are investigating large moth availability as a whole, we did not consider the taxonomic affinity of moth species in this study. However, it is important to note that the taxonomic composition of the community in different habitats and at different times

may have influenced capture rates, as some macro-moth taxa are more attracted to light lures than others (Merckx et al., 2014).

Habitat type also affected mean moth weight by interacting with moon score, possibly indicating that larger moths are relatively more attracted to light traps in shaded areas when the environment is brighter. However, our analyses suggest that moonlight does not interact strongly with habitat type to influence large moth count or biomass. The interaction between moonlight and habitat type influencing moth weight could instead imply a defensive response of moths to open areas due to potential aerial insectivore predation (Safford 2018), which may be especially important for larger moths because they are more likely to be targeted by whip-poor-wills at our sites, particularly under brightly lit conditions (Souza-Cole 2021, Souza-Cole et al., 2022). In contrast, the decline in mean weight along edges with increasing moon score while abundance remains relatively consistent may suggest that lighter large moths –which may be less attractive to insectivores– shift their activity away from forest interiors on brightly moonlit nights (Hecker and Brigham 1999).

The most extreme differences in moth availability between habitats across all our analyses consistently occurred between mid-June and early July. These differences are likely driven by plant phenology and could make forests particularly important for the Eastern Whip-poor-wills that breed at our study sites and provision their young during that time, meaning greater benefits from the exceptionally high availability of moths (Busse et al., 2022, Souza-Cole et al., 2021, Stewart 2023). The differences in individual moth mass between habitats across years were less consistent than those within each season. The heavier moths collected in our traps in forests in 2023 compared to the heavier moths along edges in previous years may have resulted from a lack of sampling later in the season in 2023.

Differences between habitats also varied across field sites, with Panther Creek having the highest difference in total biomass between forest and edge in 2022, followed by Scrub Oak and then Sand Ridge, a pattern that held for the latter two sites in our three-year dusk analysis, along with a similar trend in moth abundance. These differences demonstrate the variable availability of moths between even seemingly similar sites depending on factors such as the plant community, soil type, and human activity. One particularly notable difference in plant composition between our sites was the presence of monoculture pine plantations at approximately half of the transects at Sand Ridge, which possibly had a negative impact on moth abundance and diversity relative to more natural forest composition at the other field sites (Marcum et al., 2013). The potential negative impact of the pine plantations on moth abundance was further supported by traps in deciduous-dominated forests showing greater moth abundance than those in coniferous-dominated forests, with essentially no difference in abundance between edges, when pine plantations at Sand Ridge accounted for the majority of coniferous dominated trap locations in 2022. Previous studies have also shown some indication of increased biomass of Lepidoptera in deciduous forests relative to coniferous plantations during the summer months (Falconer et al., 2021, Kirkpatrick et al., 2017). Additionally, Stewart (2023) found that whip-poor-will home range size increased with pine cover at Sand Ridge, likely indicating reduced foraging efficiency in that habitat.

In 2022, habitat also drove moth abundance and total biomass through clear interactions with time of night, showing a decrease in moth availability in the forest as the night progressed while both measures of moth activity remained at lower levels throughout the night along edges. The flurry of activity at dusk in the forest may be driven by competition for floral nectar resources, production of which maximizes for some nocturnally pollinated plants around dusk

(e.g., Balducci et al., 2020, Raguso et al., 1996). The relatively consistent lower levels of moth abundance and biomass in edge habitats suggest that activity in those areas may not be as important for floral resource competition and may be used by large moths for other purposes, such as a “highway” for moving between foraging grounds or seeking mating opportunities. Future research on moth activity patterns should attempt to quantify foraging and mating activities by moths along edges relative to forest interiors.

Another set of variables that interacted strongly in both our analyses were sampling round and field site. Differences in peak moth abundance and individual moth mass between field sites in 2022 are relatively minor and likely explained by plant community and phenology differences. However, even minor differences between these nearby and relatively similar field sites emphasizes potential for high variability in insect phenology and across spatial scales larger than those covered in this research, implying that caution is needed when attempting to predict moth phenology, particularly based on only a single year of data (Dunn et al., 2023). The lower variability in both abundance and biomass between field sites in our three-year dusk analysis implies a more consistent regional phenology when averaged over multiple years. Differences between sites for both response variables grew as the season progressed, but these differences may have been driven by a lack of sampling during the mid-July to early August sampling in 2023. On the other hand, increasing gaps in both abundance and biomass between sites as the season progresses may suggest that plant community has an increasing effect on moth availability as the growing season progresses.

The diverse interactions involving time of night in 2022 showcase the importance of diel cycles for moth activity. Declines in abundance over the course of a night across all three field sites suggest that competition for nectar resources may be an important driver of large moth

activity, and differences in the timing and magnitude of abundance changes through the night indicate potential effects of moth and plant community composition on the total number of moths active on the landscape (Moreno et al., 2021, Macgregor and Scott-Brown 2020). These community level differences between sites are also suggested by the interaction's effect on individual large moth mass, showing an increase as the night progresses at some sites while remaining relatively consistent at others. The differences in moth communities between sites are further evidenced by the sharp decline in whip-poor-will abundance at Panther Creek relative to our other field sites in recent years despite comparable if not greater moth availability at that site, suggesting that differences in community composition may also drive breeding instead of simply availability of moths in general (Souza-Cole et al., 2022).

Predicted moth count and biomass in 2022 was also driven by a complex interaction between time of night and moon score. These relationships were expected, given previous studies demonstrating the negative impact of ambient moonlight on moth captures in UV light traps (Yela and Holyoak 1997, McGeachie 1989). The stronger effect of moonlight on moth abundance at solar midnight is likely explained by overall darker conditions at solar midnight than civil dusk when some lingering twilight remains. Although I expected a similar negative effect to that seen at dusk, the slight positive impact of moon score on both moth abundance and biomass before civil dawn in our study suggests that bright moonlight in the early morning increases moth activity. The mechanism for this increase could be the subject of future research on moth activity and capture rates. This before-dawn increase in activity on moonlit nights may also partially explain why some predators, such as the eastern whip-poor-will, increase the duration of their activity on nights with greater ambient moonlight relative to moonless nights (Souza-Cole et al., 2021).

The sampling round also interacted with the time of night, likely demonstrating that shifts in moth community composition as the season progresses drive changes in total biomass and mean individual mass of large moths between different times of night (Summerville and Crist 2003). Although moth declines are not uniform across regions or families, and some generalist taxa are experiencing increases in temperate areas (Wagner et al., 2021), reductions in abundance of some moths, particularly in taxonomically unique or ecologically specialized groups, could result in inconsistent activity levels of large moths during specific periods on diel and seasonal scales. These inconsistencies could lead to periods of low moth availability that may have negative consequences for a variety of ecosystem functions provided by moths, particularly their role as prey. Prey availability for predators that rely on moths and pollination for threatened plant species that depend on specialist moths are both already threatened by human activity and a shifting climate and could both be further endangered by spatiotemporal mismatches in activity (Souza-Cole et al., 2022, Summerville and Crist 2003, Macgregor and Scott-Brown 2020). Future research could further address questions about moth availability by focusing on taxa that are known to be consumed by declining aerial insectivores or pollinators of endangered plants and measuring their unique traits and activity patterns in time and space.

For species that depend on moths as a source of food or pollination, another potential source of repeated breeding success is consistently available moth resources across years. In our study, dusk moth abundance and biomass increased every year, suggesting positive trends in moth populations at our sites during this short period. Longer-term monitoring would be required to confirm this trend since a three-year study could easily be influenced by meteorological conditions (Holyoak et al., 1997) and especially because trapping in 2023 did not include sampling in July or August, when moth availability generally decreased at our sites. However,

the changes in moth abundances seen in our short study do provide some evidence that moth populations are variable between years, which may have ripple effects on the breeding success of many other plant and animal species.

The strong impact of meteorological factors on large moths provides important clues as to how a changing climate will shape moth activity in the future. The positive correlations between moth abundance and temperature and between abundance and relative humidity were expected based on previous work on moth activity; however, nuanced interactions between temperature and wind speed and between temperature and humidity to influence abundance suggest potentially more complex relationships than previously thought (McGeachie 1989, Yela and Holyoak 1997). In our three-year dusk analysis, temperature had only a positive impact on moth abundance at lower relative humidity values, suggesting that dry conditions potentially cue moths to concentrate foraging at dusk, perhaps to avoid depleted nectar reserves later in the evening due to evaporation (Borges et al., 2016). Conversely, in 2022 individual moth mass increased with temperature only under humid conditions, indicating that when the whole night is taken into account, heavier moths may prefer to forage under warm, humid conditions, potentially because they have a competitive advantage over smaller moths and therefore can take advantage of the most energetically efficient conditions under which to forage.

Mean individual moth mass varied with wind speed and temperature, suggesting that heavier and lighter moths may also partition activity depending on favorable conditions for flight. As mentioned above, heavier moths likely have the competitive advantage when it comes to nectar resources, and so can become active during favorable conditions (warm, calm nights), forcing smaller moths to forage at less energetically efficient times (warm, windy nights and cold, calm nights). On windy nights, heavier moths are more successful at directional flight than

other moths (Kuenen and Cardé 1993), and on cold, windy evenings, they may take advantage of this fact to monopolize nectar resources. The negative relationship between increasing cloud cover and mean individual moth mass was consistent across both analyses, suggesting that heavier moths likely prefer clear skies to overcast, although further study will be required to explain this relationship.

Although many factors combine to influence patterns of large moth activity in a landscape, focusing on a select few could provide major benefits for the conservation of moths – and the species that depend on them– in managed natural areas. Healthy forests appear to be a relatively important habitat for moth populations in typical midwestern landscapes, as large moth abundance and biomass both were greater in forest interiors relative to forest/grassland edges. Additionally, minimizing human disturbance through artificial lighting, pesticides, and other means in forests during the second half of June, the peak of the breeding season for many species and the time when the biomass of moths is highest relative to edges would allow natural processes such as pollination by and predation of moths to take place without interference. Dusk appears to be the time with the highest moth biomass, particularly in forests during the same June time period, indicating that minimal disturbance in forests during those time blocks would lead to disproportionate benefits for moths. By following patterns of moth activity, land managers interested in conserving nocturnal species can make simple changes that may create lasting positive effects for these understudied and underappreciated insects and the species that depend on them to flourish.

2.5 FIGURES



Figure 1. A bucket trap in the field at Sand Ridge State Forest. The battery and timer controlling the LEDs are behind the trap in this image.

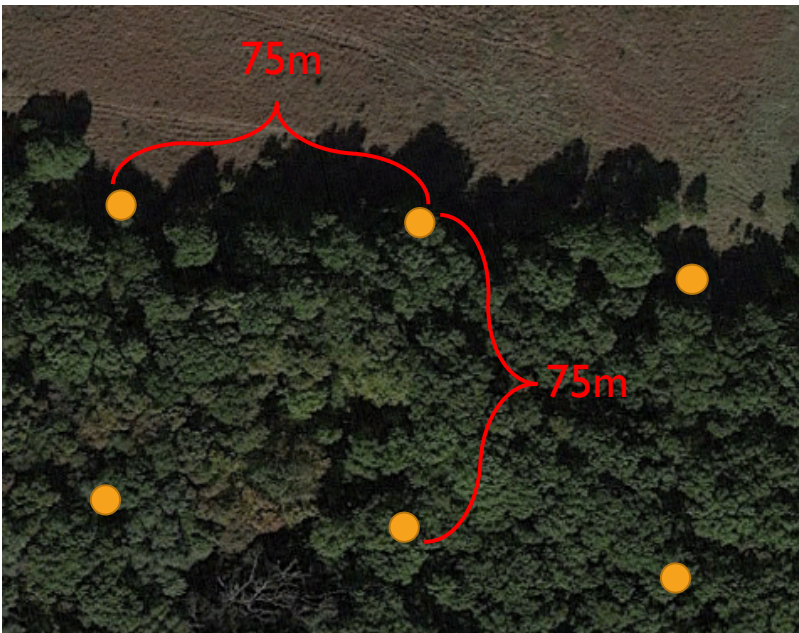


Figure 2. 6-bucket trap transect layout for 2022. 150×75m transect spanning forest and edge habitat. Orange dots represent individual bucket traps. In 2021 and 2023, only one trap was placed in forest interior and one along forest/grassland edge.

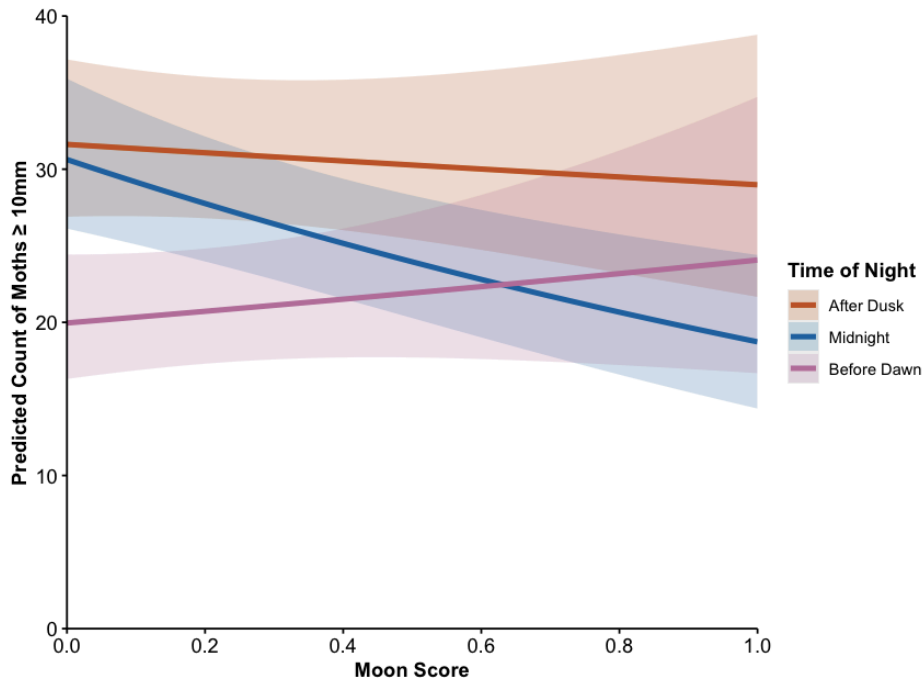


Figure 3. Predicted count of moths ≥ 10 mm body length as a function of moon score and time of night in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

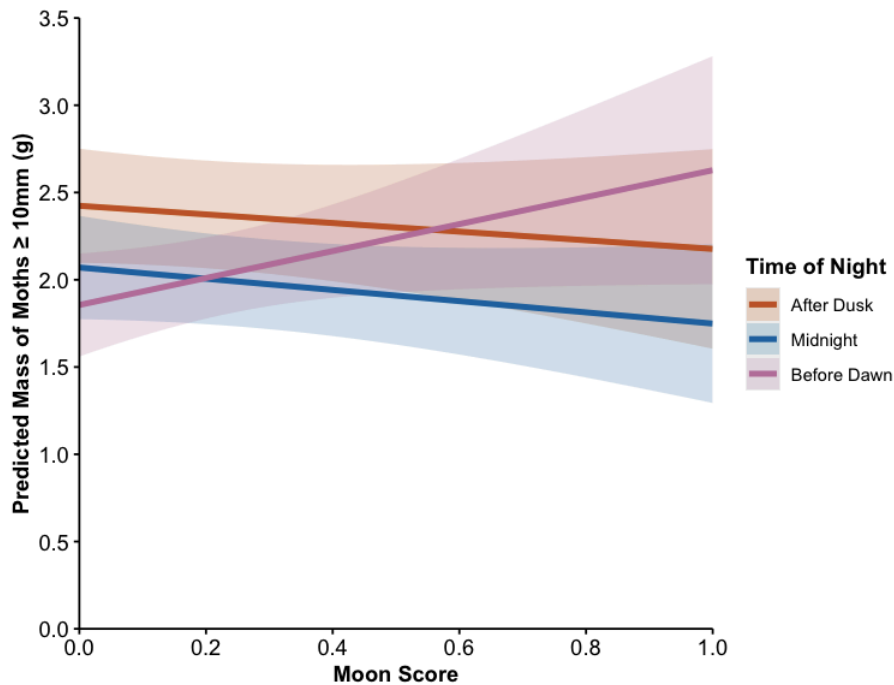


Figure 4. Predicted biomass of moths ≥ 10 mm body length as a function of moon score and time of night in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

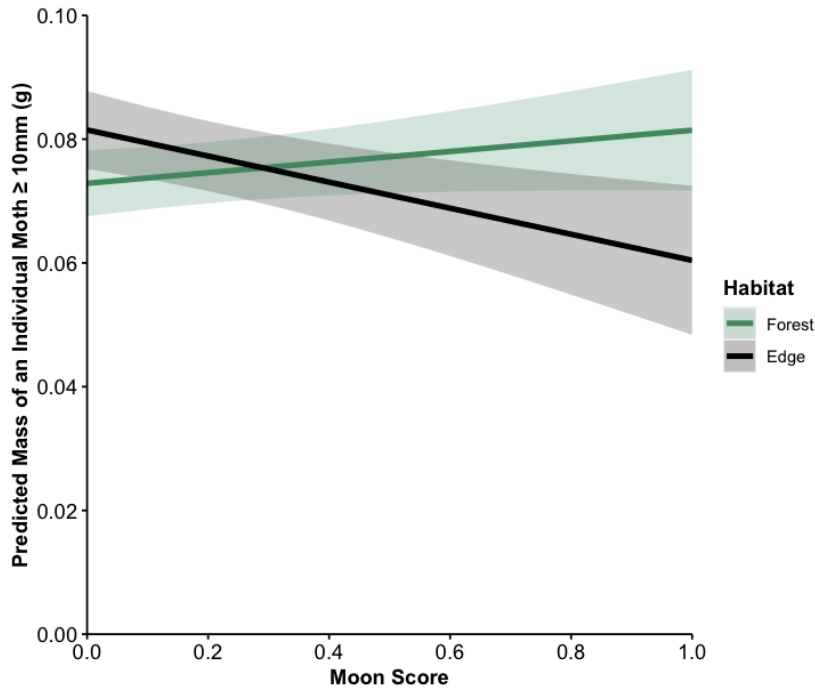


Figure 5. Predicted mass of an individual moth ≥ 10 mm body length as a function of moon score and habitat type in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

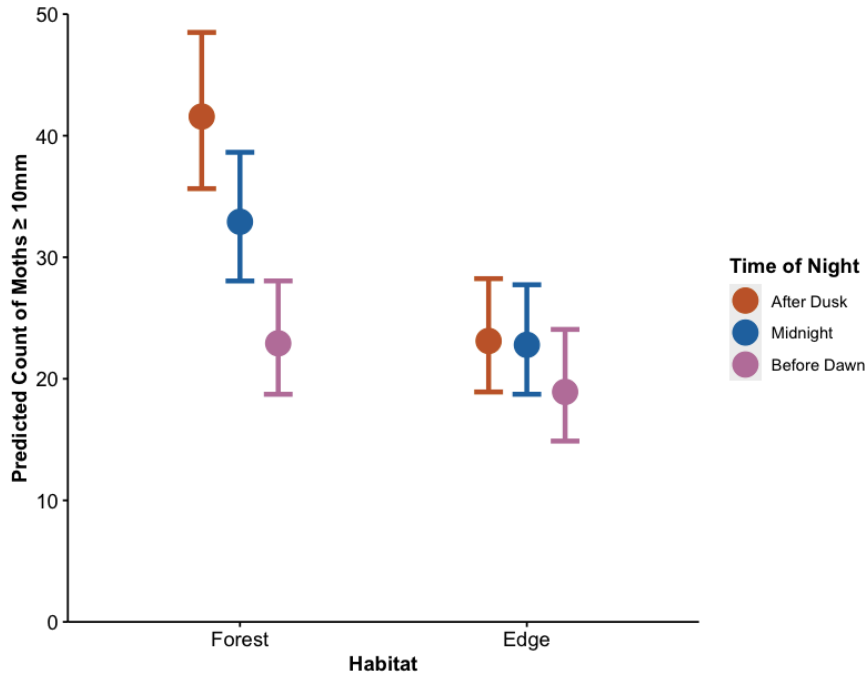


Figure 6. Predicted abundance of moths ≥ 10 mm body length as a function of time of night and habitat type in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

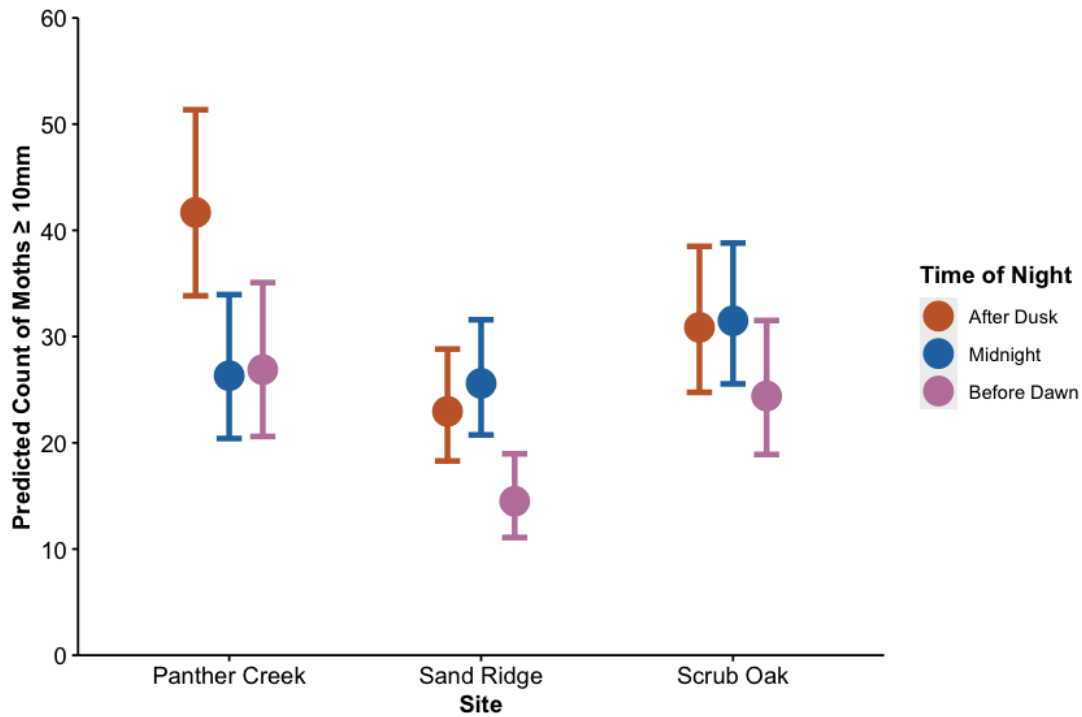


Figure 7. Predicted abundance of moths ≥ 10 mm body length as a function of time of night and field site in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

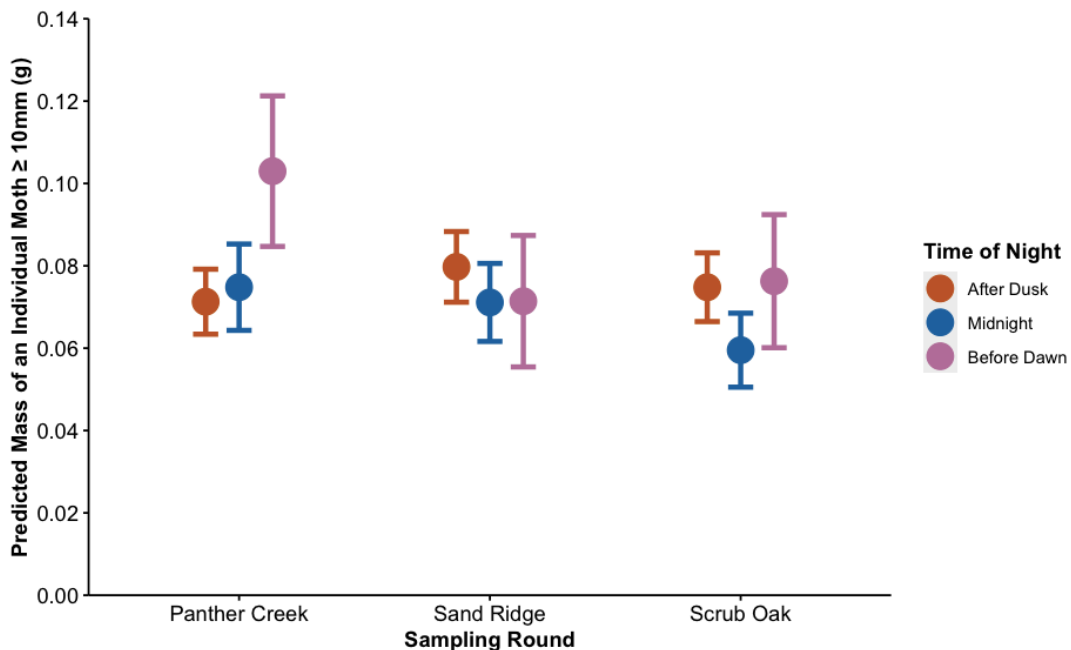


Figure 8. Predicted mass of an individual moth ≥ 10 mm body length as a function of time of night and field site in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

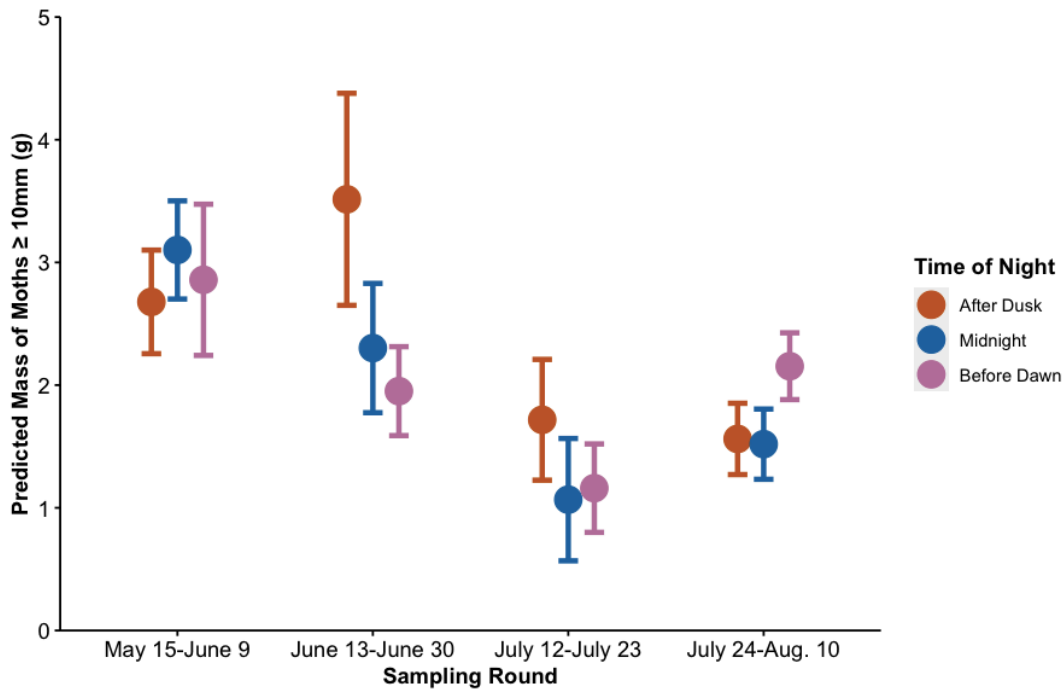


Figure 9. Predicted biomass of moths ≥ 10 mm body length as a function of time of night and sampling round in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

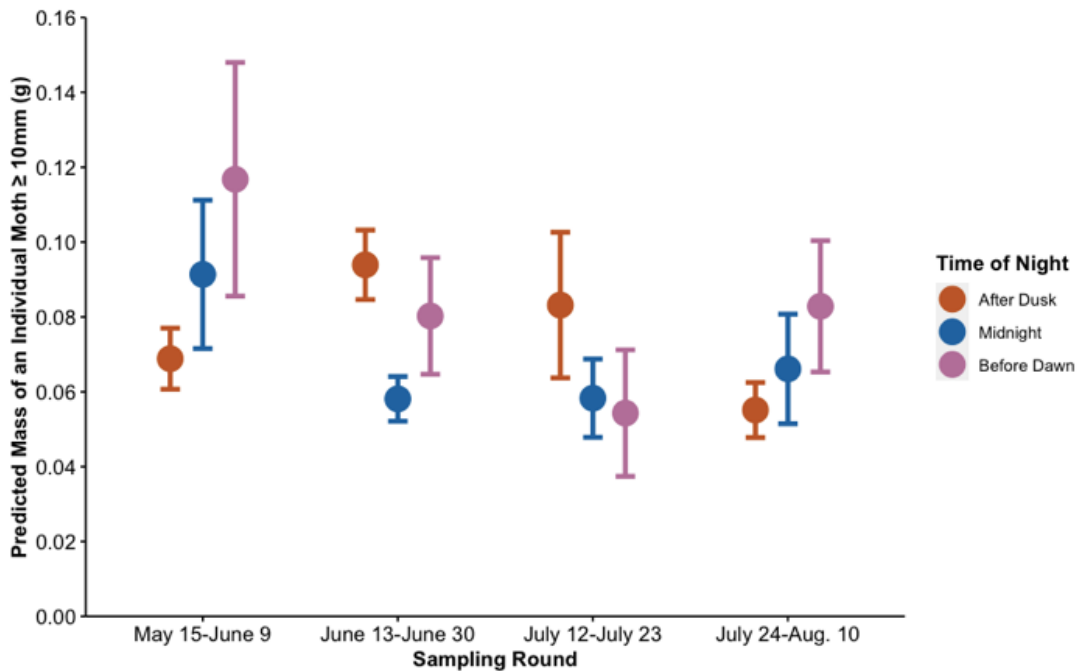


Figure 10. Predicted mass of an individual moth ≥ 10 mm body length as a function of time of night and sampling round in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

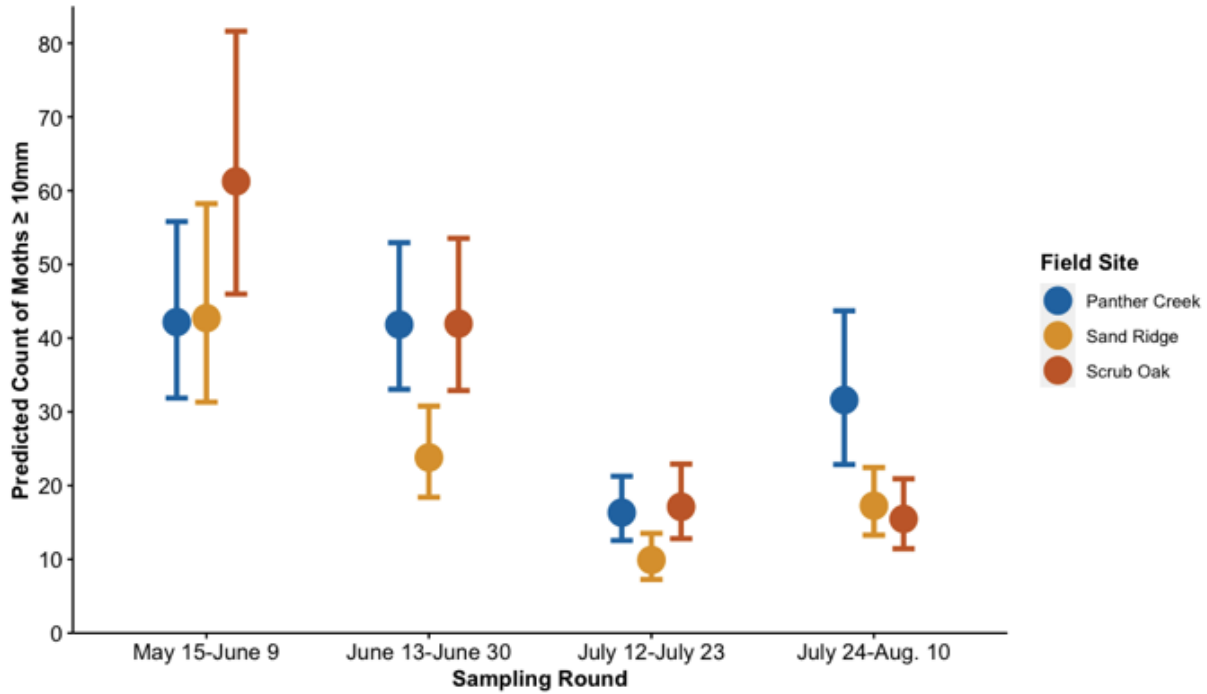


Figure 11. Predicted abundance of moths ≥ 10 mm body length as a function of field site and sampling round in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

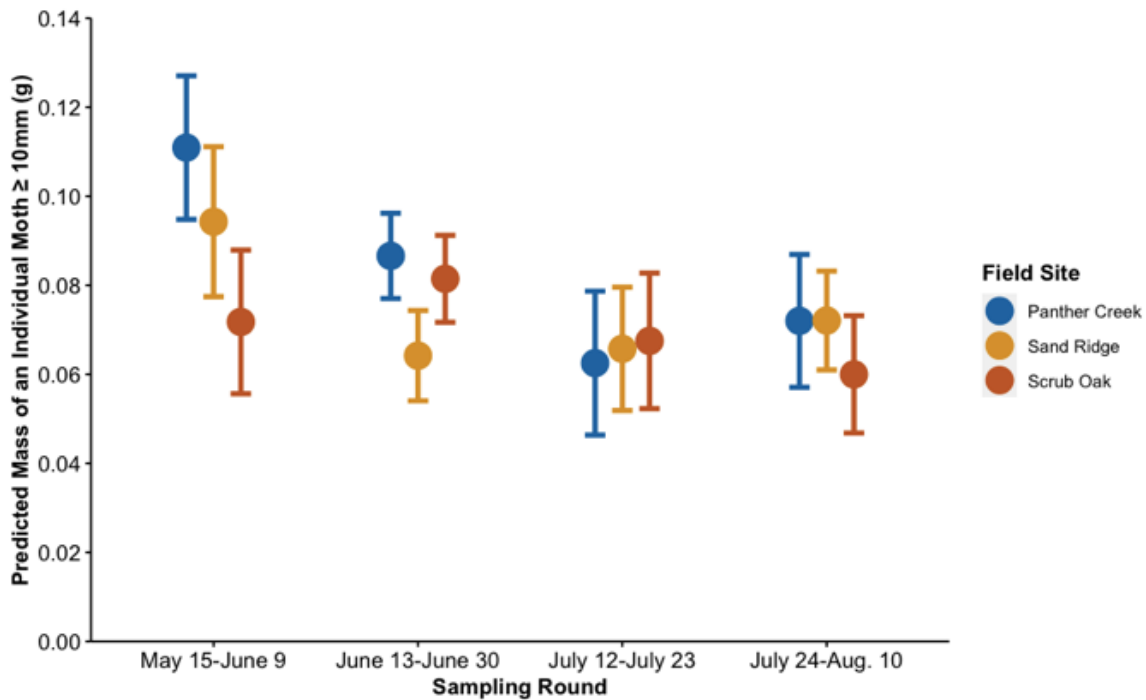


Figure 12. Predicted mass of an individual moth ≥ 10 mm body length as a function of field site and sampling round in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

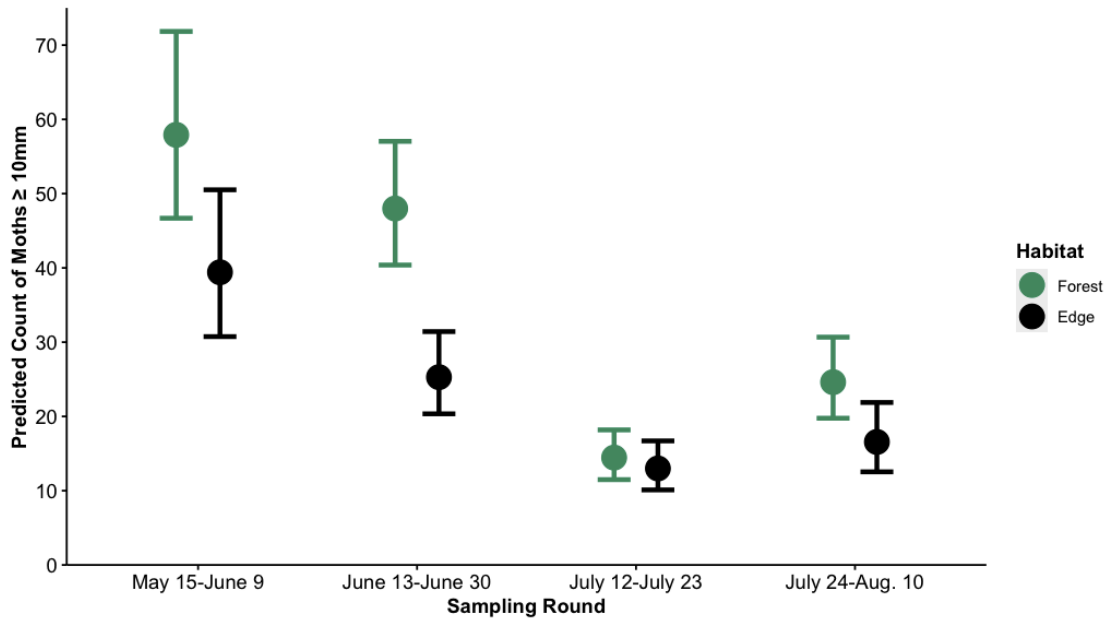


Figure 13. Predicted abundance of moths ≥ 10 mm body length as a function of habitat type and sampling round in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

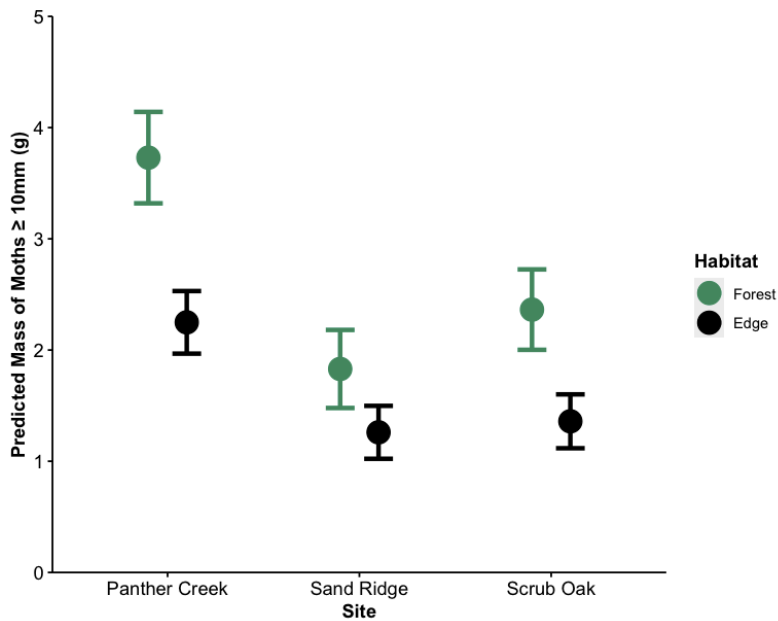


Figure 14. Predicted biomass of moths ≥ 10 mm body length as a function of habitat type and sampling round in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

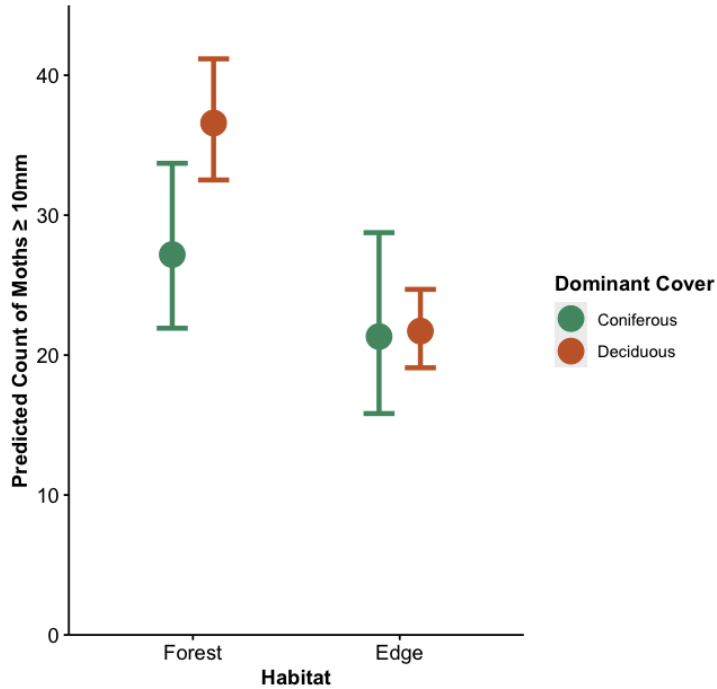


Figure 15. Predicted abundance of moths ≥ 10 mm body length as a function of habitat type and dominant tree cover in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

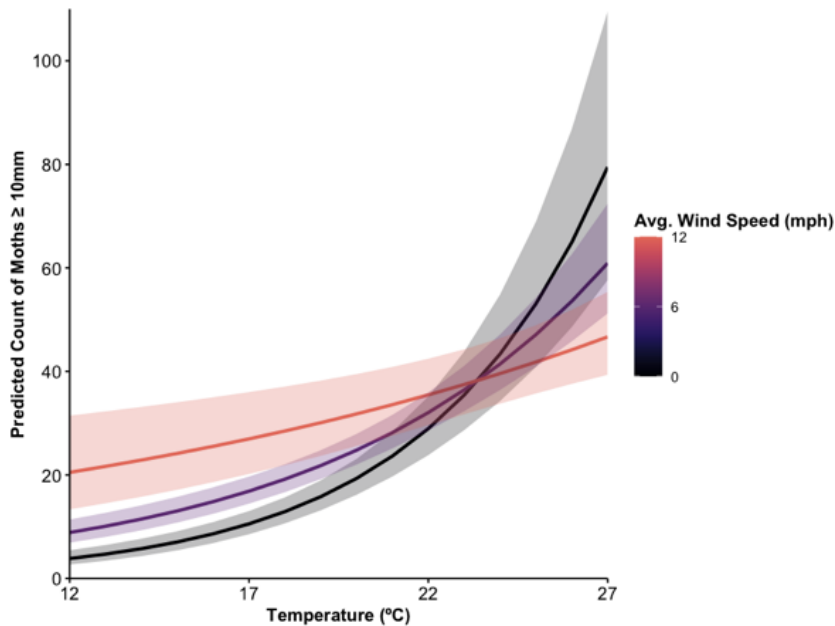


Figure 16. Predicted abundance of moths ≥ 10 mm body length as a function of air temperature and mean hourly wind speed in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

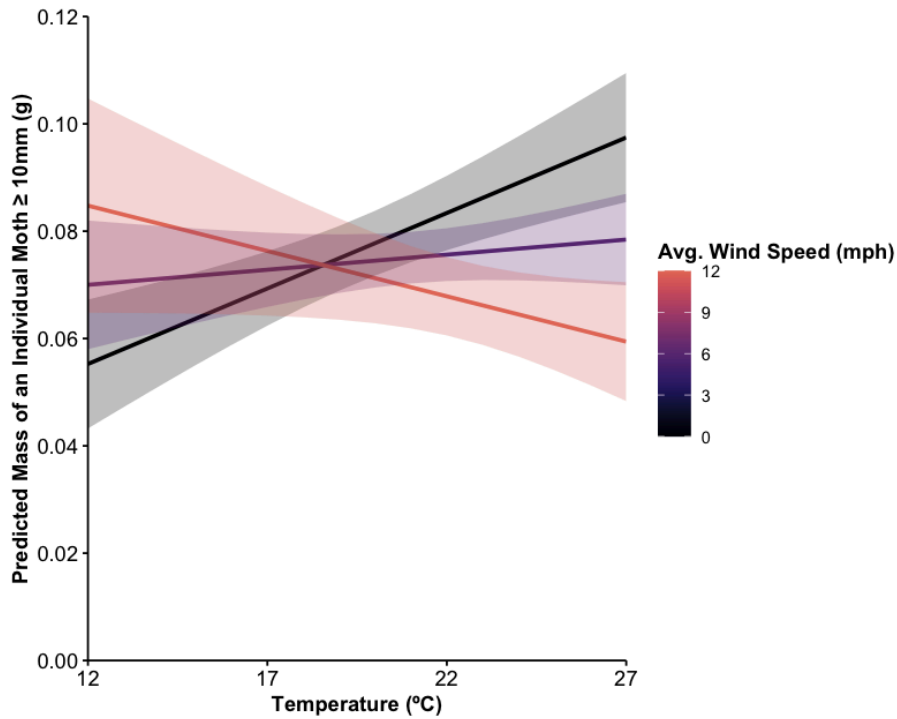


Figure 17. Predicted mass of an individual moth ≥ 10 mm body length as a function of air temperature and mean hourly wind speed in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

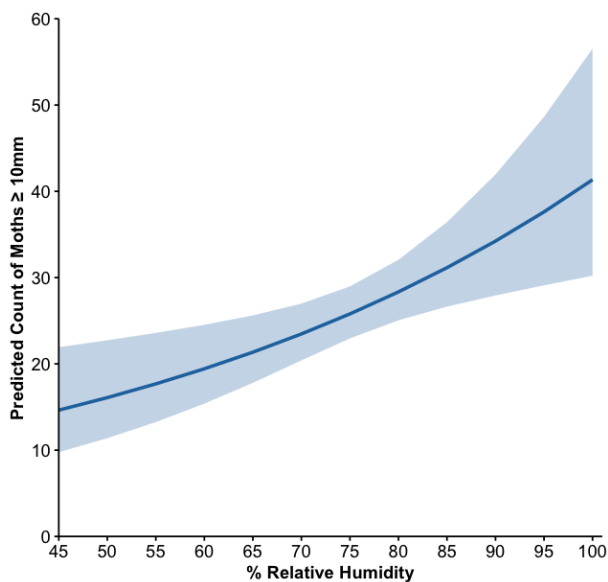


Figure 18. Predicted abundance of moths ≥ 10 mm body length as a function of relative humidity in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

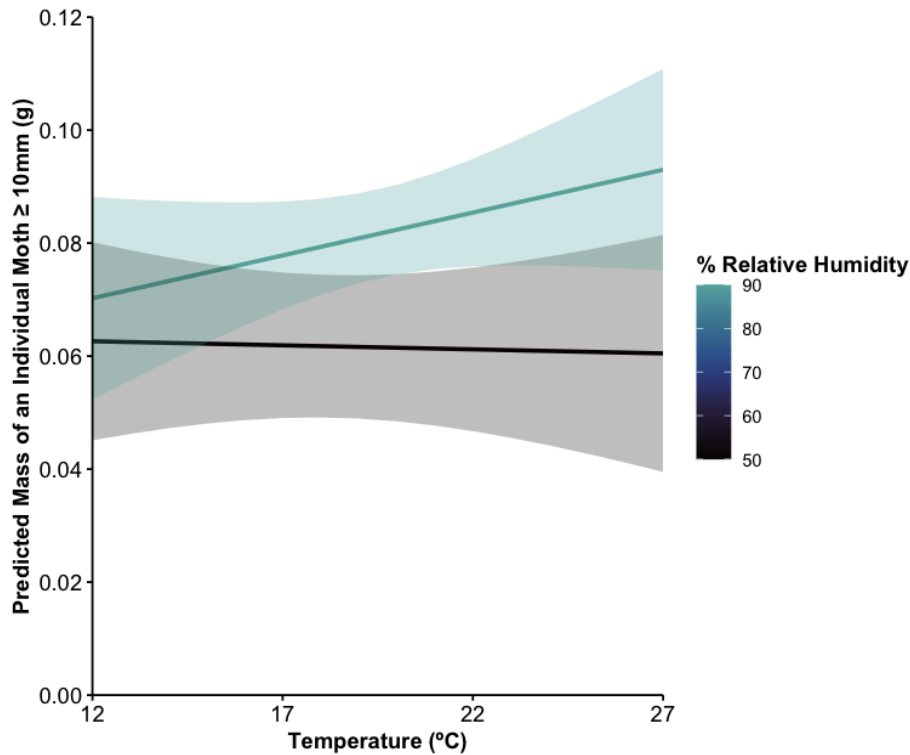


Figure 19. Predicted mass of an individual moth ≥ 10 mm body length as a function of relative humidity and air temperature in 2022. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

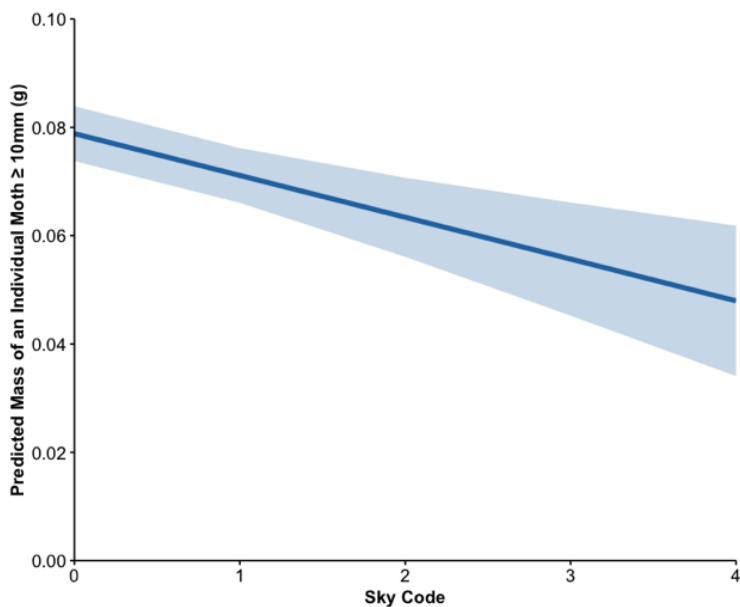


Figure 20. Predicted mass of an individual moth ≥ 10 mm body length as a function of cloud cover in 2022. 0 represents clear skies and 4 represents overcast skies. Based on data from UV light insect bucket trapping after dusk, at solar midnight, and before dawn in forest and edge habitats in central Illinois in 2022.

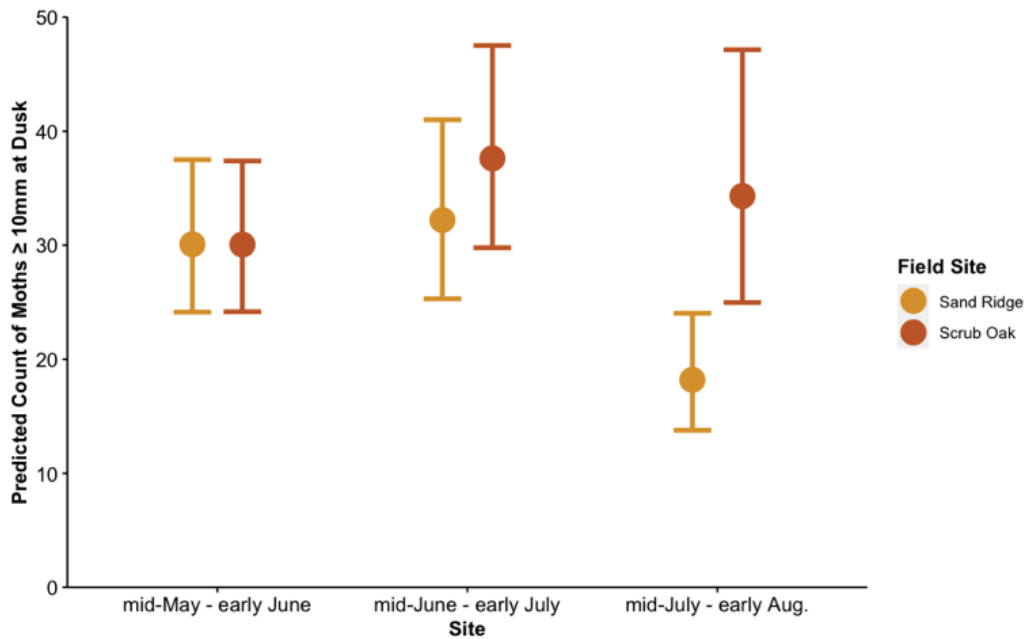


Figure 21. Predicted abundance of moths ≥ 10 mm body length as a function of sampling round and field site after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

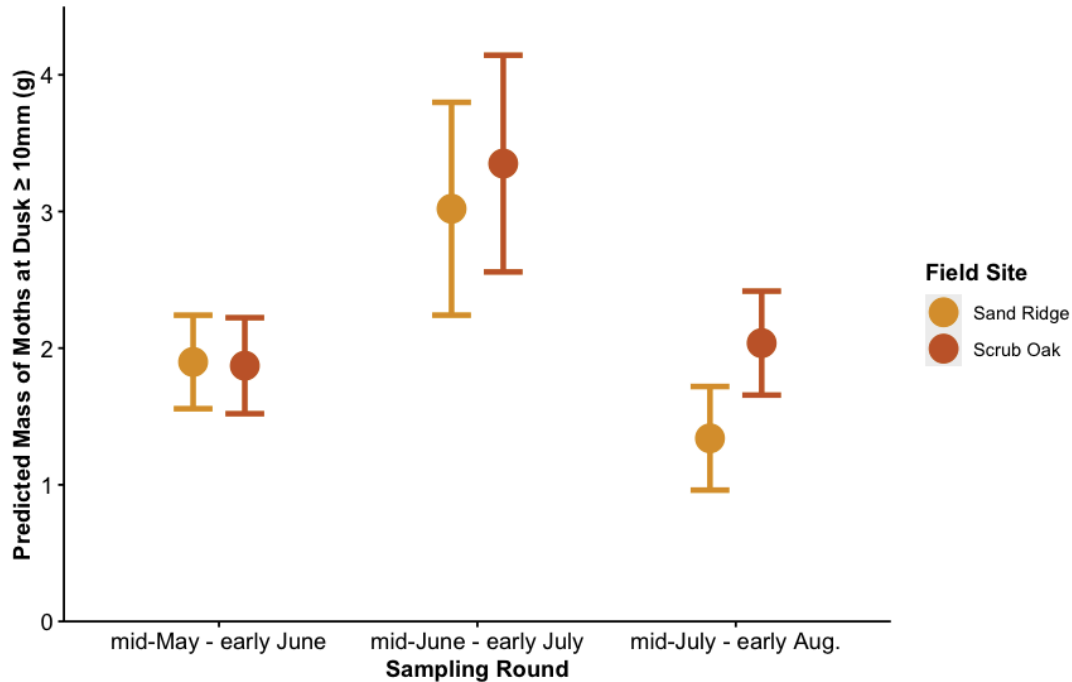


Figure 22. Predicted biomass of moths ≥ 10 mm body length as a function of sampling round and field site after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

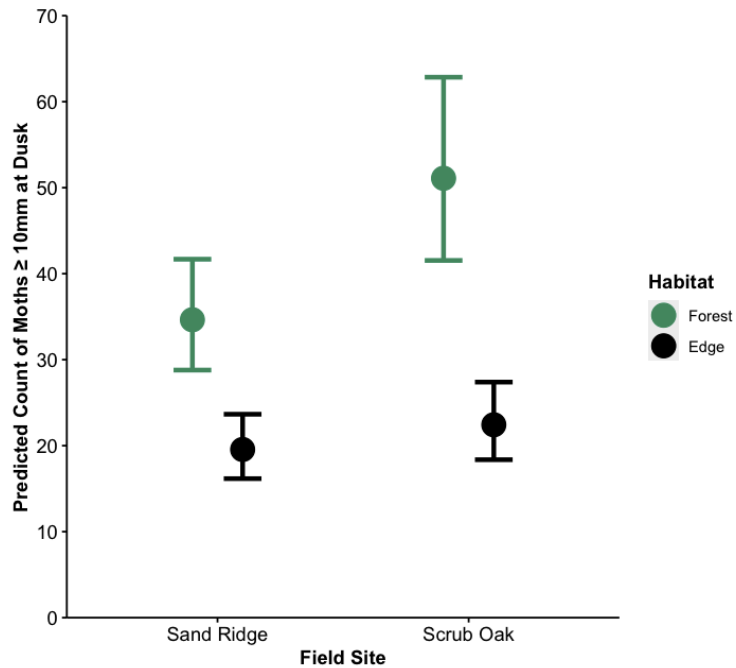


Figure 23. Predicted abundance of moths ≥ 10 mm body length as a function of habitat type and field site after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

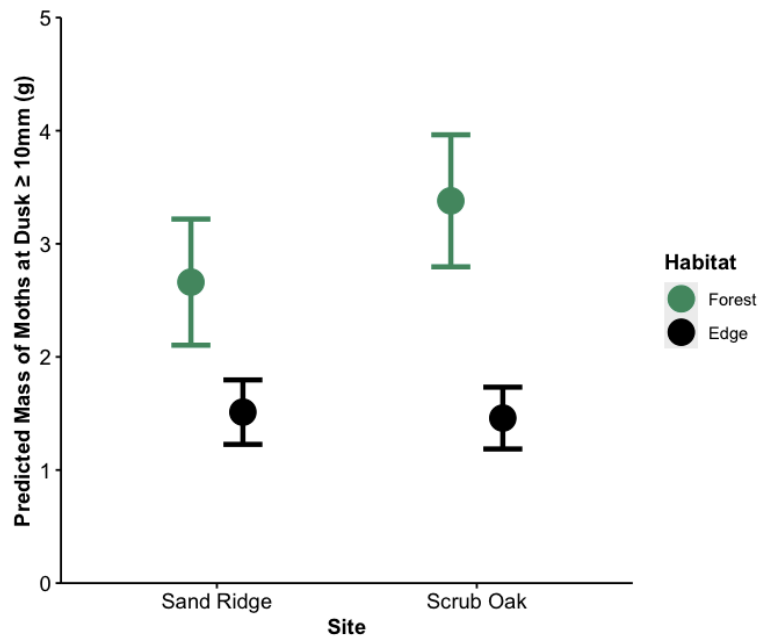


Figure 24. Predicted biomass of moths ≥ 10 mm body length as a function of habitat type and field site after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

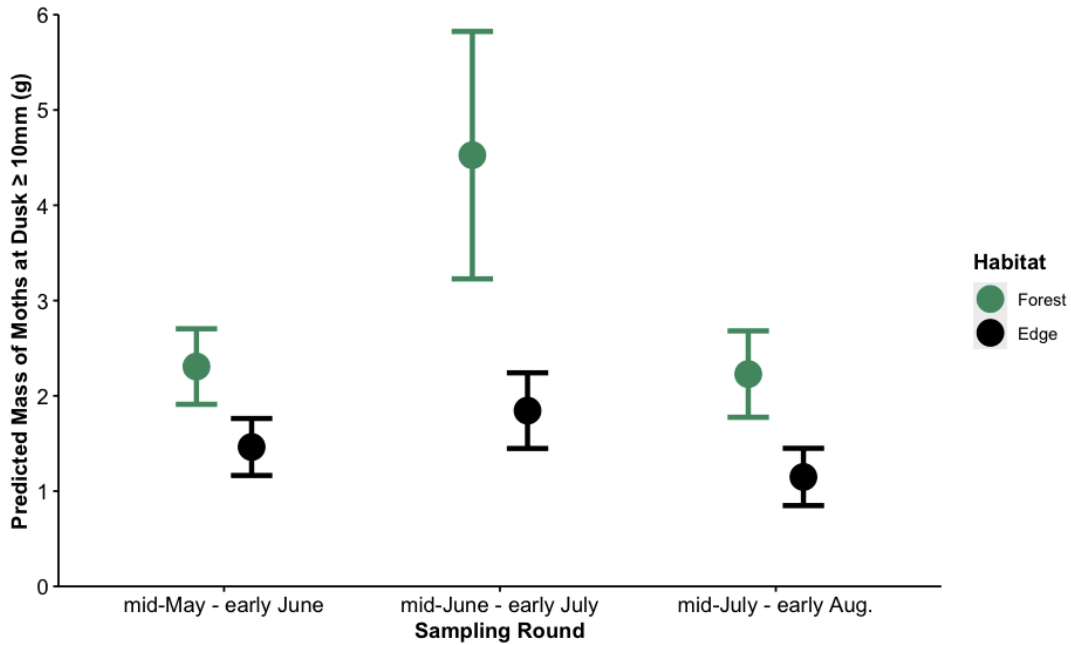


Figure 25. Predicted biomass of moths ≥ 10 mm body length as a function of habitat type and sampling round after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

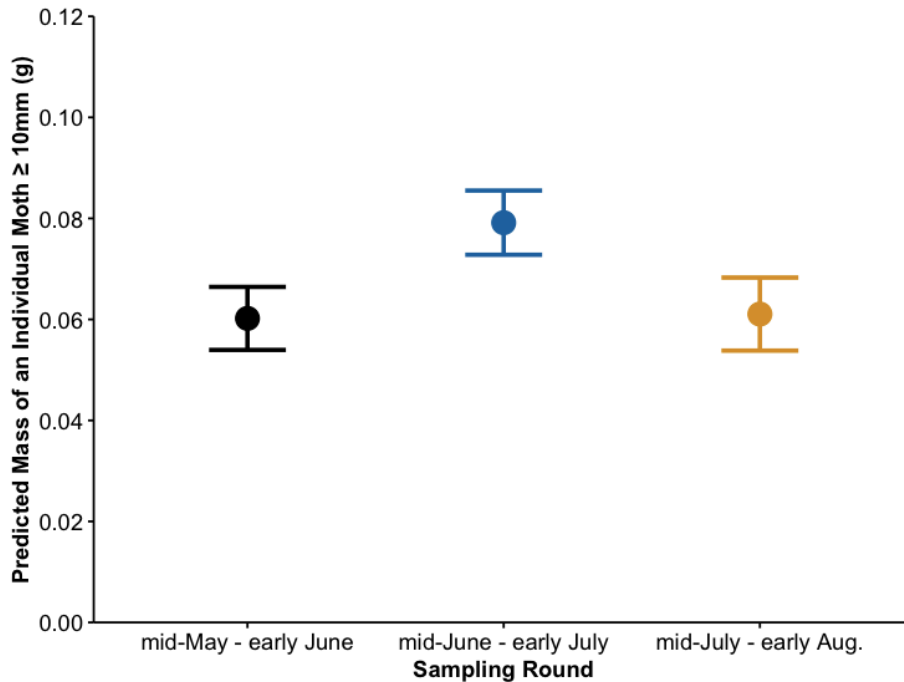


Figure 26. Predicted mass of an individual moth ≥ 10 mm body length as a function of sampling round after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

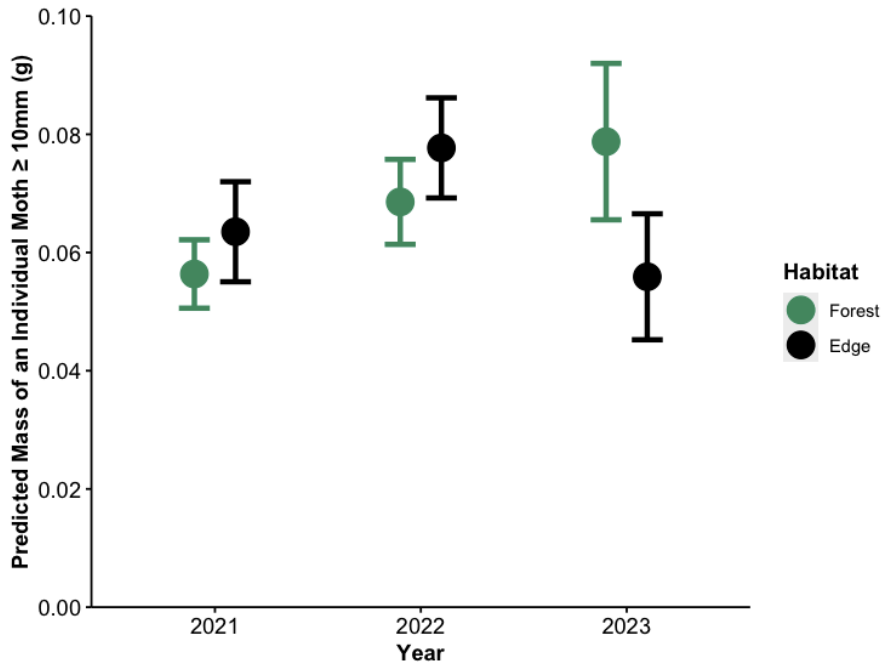


Figure 27. Predicted mass of an individual moth ≥ 10 mm body length as a function of habitat type and study year after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

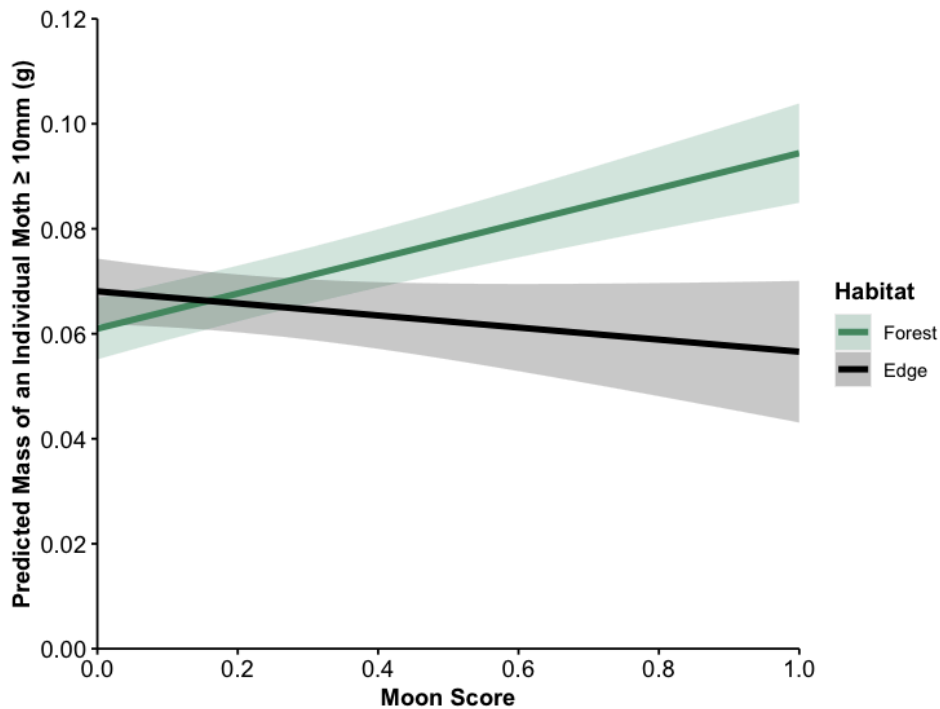


Figure 28. Predicted mass of an individual moth ≥ 10 mm body length as a function of habitat type and moon score after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

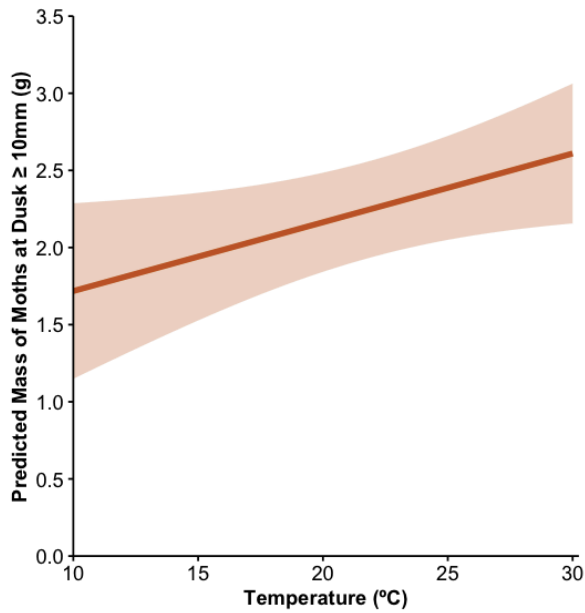


Figure 29. Predicted biomass of moths ≥ 10 mm body length as a function of air temperature after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

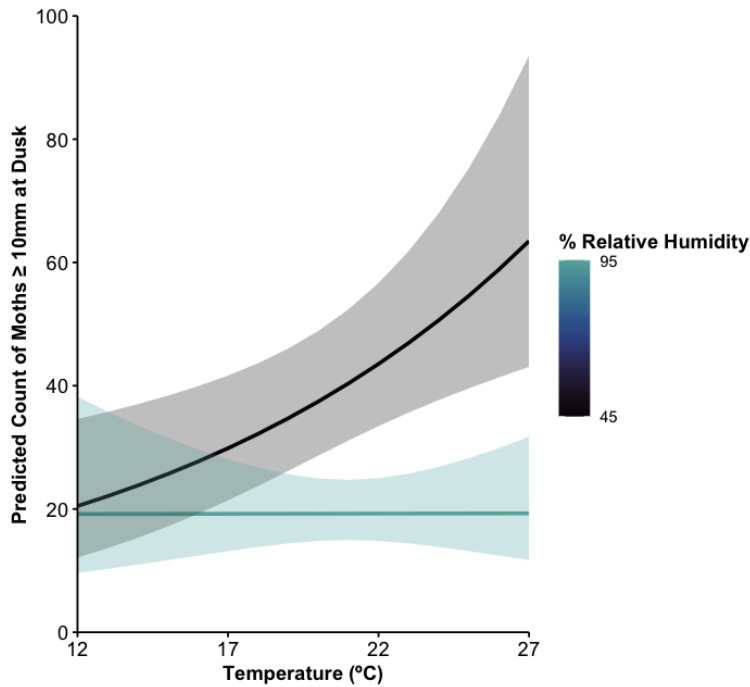


Figure 30. Predicted abundance of moths ≥ 10 mm body length as a function of air temperature and relative humidity after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

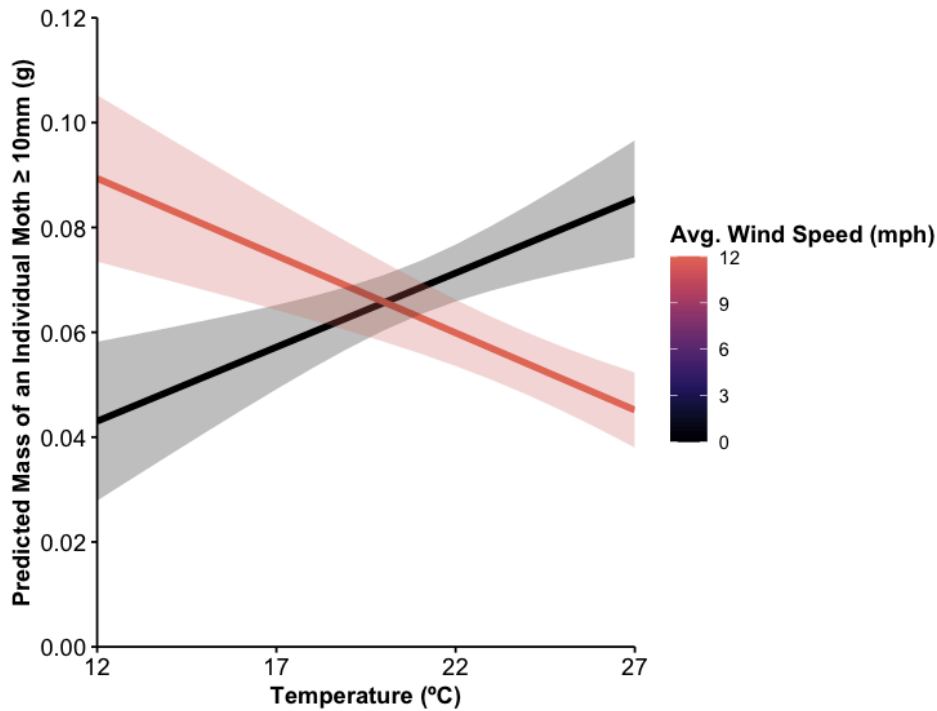


Figure 31. Predicted mass of an individual moth ≥ 10 mm body length as a function of air temperature and average wind speed after dusk. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

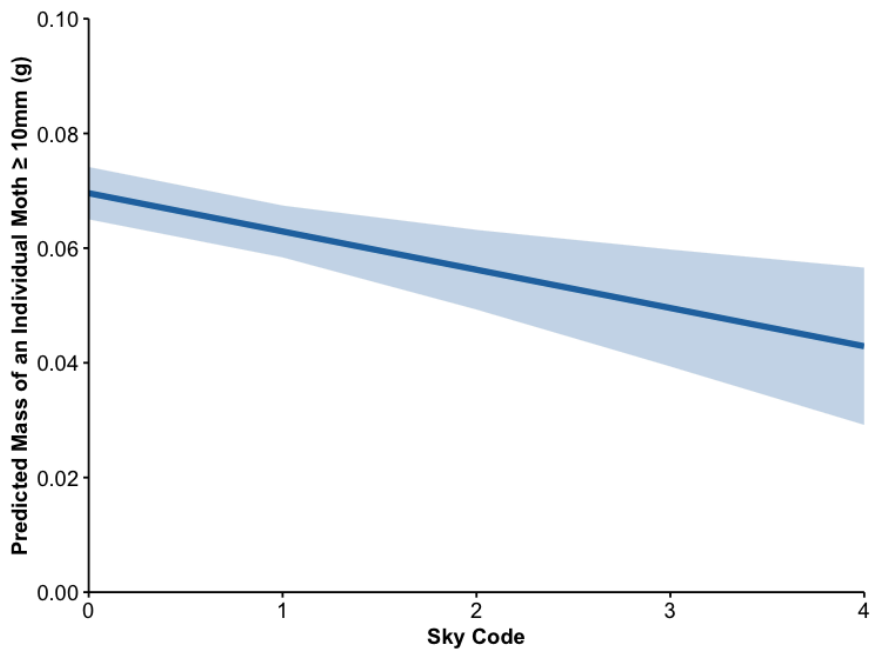


Figure 32. Predicted mass of an individual moth ≥ 10 mm body length as a function of cloud cover after dusk. 0 represents clear skies, and 4 represents overcast skies. Based on data from UV light insect bucket trapping after dusk in forest and edge habitats in central Illinois from 2021-2023.

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CHAPTER 3: GENERAL CONCLUSION

Our research shows that large moth species, like many other taxa, exhibit diel and seasonal activity patterns across habitat types. When taken as a whole, our data suggest that the large moth community may have developed spatial activity patterns at our sites that avoid foraging whip-poor-wills. Whip-poor-wills are most active along forest edges at dusk, when moths are also most active, but concentrated in forests. Moths are also most abundant in June, when breeding whip-poor-wills require surplus food resources to care for their young, but that peak is again driven by forests, not edges. Whip-poor-will activity increases as the moon gets brighter, but heavier, presumably more nutritious moths move into forest interiors during those periods while lighter moths move to edges. In combination, the patterns exhibited by the large moths at our sites suggest that the community and/or behavior of large moths has been shaped by whip-poor-will predation. Although this is not necessarily harmful to whip-poor-wills, additional pressures on moth availability, whether they come from weather or human activity, could reduce moth activity in key areas or during key times, disrupting the nuanced interactions between predator and prey and leading to population declines.

Ultimately, the success of whip-poor-wills and other moth-dependent species are driven by the accessibility of moths on the landscape. Land managers can take lessons from our research to determine what actions will be most beneficial for moths and the species that depend on them. Maintaining a healthy, diverse forest with small open areas for foraging whip-poor-wills and minimizing human disturbance during key periods are relatively straightforward steps that may have been overlooked in the past by conservationists at our sites. Still, the availability of large moths alone is likely not enough to ensure the success of whip-poor-wills, as demonstrated at our field site Panther Creek where whip-poor-wills have declined sharply in

recent years despite relatively high moth availability. Future researchers should investigate the shared ecological and physiological traits of the taxa that whip-poor-wills are known to consume or prey upon (“predate” is less preferred) , as well as the factors shaping the availability of those taxa, in order to understand the drivers of successful foraging and breeding for whip-poor-wills in Illinois and beyond.

APPENDIX A: INSECT SAMPLE PROCESSING PROTOCOL

Part 1: Sorting

1. Get an unsorted sample from the freezer and record all relevant sample identification data in the appropriate spreadsheet (e.g. **2023 SARI SCOA Insect Processing**). Make sure all of your tools and surfaces (sorting trays, rulers, forceps, etc.) are relatively clean and do not have any insects from other samples in/on them. If there are other insects present, use a paper towel to wipe the tool clean. Carefully pour the specimens into a sorting tray and do your best to avoid damaging them during the sorting process (use forceps/tweezers and avoid moving the insects more than necessary). Dispose of any plant material or other non-arthropod debris in the trash.
2. Classify all specimens as adult moth/butterfly (Order Lepidoptera), adult beetle (Order Coleoptera), adult cockroach (Order Blattodea) or other adult insect (caddisflies, wasps, flies, grasshoppers, true bugs, etc.). Arthropods **without functional wings** (larvae, worker ants, spiders, harvestmen, cockroach nymphs, hemiptera nymphs, etc.) will not be sorted at all and should be returned to the main sample bag.
3. Sort into separate piles the **lepidopterans, coleopterans, and blattodeans** with a body length greater than or equal to 10 mm. We refer to these individuals as “Large.” Body length is measured from front of head to tip of abdomen, excluding wings and appendages such as antennae and mouthparts. (**Note: Optionally, you can count the insects at this point, during the sorting process, to save work later.**)
4. Sort out all remaining insects **with functional wings** that have a body length greater than or equal to 10 mm. These are categorized as “Other.”
5. All remaining insects with functional wings and a body length less than 10 mm can be returned to the main sample bag with the wingless insects.
6. (**Note: If you are planning to continue straight into counting and massing the sample you are working on, you can skip steps 6 & 7 temporarily and come back to them after massing is complete.**) Label a small Ziploc® baggie for each classification and measurement range (e.g. Lep \geq 10 mm, Col \geq 10 mm, Other \geq 10 mm, etc.) then place the corresponding specimens inside. Put all smaller baggies in the original main sample bag along with any wingless specimens. Make sure each ziploc bag is properly sealed.

7. Write “[the date] sorted protocol V5” (e.g. “8/29/2023 sorted V5”) in the top right corner of the main sample ziploc to indicate that initial sorting has occurred under the specified protocol. You may then continue on to Part 2 or return the sample to the freezer. If you return the sample to the freezer, place it with other sorted samples. Make sure all your equipment is cleaned of any insects or debris before starting a new sample.

Part 2: Biomassing & Counting

1. Get a sorted sample and find the relevant sample identification information in the appropriate spreadsheet. MAKE SURE every identifying column (e.g. night of, date, state, block, habitat, point number, etc.) exactly matches the sample you are working on.
2. Thoroughly check the main sample bag and all smaller baggies for any insects that were sorted incorrectly. Make sure that any winged insects with a body length greater than or equal to 10 mm are placed in the appropriate baggie, and make sure there are no insects with a body length smaller than 10 mm in baggies that should only contain large insects. Also, ensure that any insects sorted into baggies have been correctly identified and sorted as moths, beetles, cockroaches, or “other.”
3. Count the number of individual large “Other” insects and record it in the “Other \geq 10 mm Count” field. Mass the contents of the Other baggie and record the mass in the “Other \geq 10 mm Mass” field.
4. Repeat step 3 for the Large blattodeans, Large lepidopterans, and Large coleopterans.
5. Write “[the date] massed V5” in the top right corner of the large Ziploc (under previous progress labels) to indicate the sample has been massed. Return all smaller baggies to the larger Ziploc and return to the freezer with other massed samples.

APPENDIX B: LIST OF 20 COMMON LARGE MOTH TAXA IN OUR SAMPLES

Family	Species	Common Name (Beadle and Leckie 2012)
Geometridae	<i>Anavitrinella pampinaria</i>	Common gray
Erebidae	<i>Apantesis</i> sp.	<i>Apantesis</i> tiger moth sp.
Noctuidae	<i>Athetis tarda</i>	The slowpoke
Erebidae	<i>Caenurgina</i> sp.	<i>Caenurgina</i> looper sp.
Erebidae	<i>Catocala</i> sp.	Underwing sp.
Crambidae	<i>Desmia</i> sp.	Grape leafroller moth sp.
Geometridae	<i>Eusarca confusaria</i>	Confused eusarca
Erebidae	<i>Halysidota</i> sp.	<i>Halysidota</i> tussock moth sp.
Erebidae	<i>Haploa</i> sp.	Haploa sp.
Erebidae	<i>Hypena scabra</i>	Green cloverworm moth
Erebidae	<i>Hypoprepia fucosa</i>	Painted lichen moth
Noctuidae	<i>Lacinipolia renigera</i>	Bristly cutworm
Lasiocampidae	<i>Malacosoma americana</i>	Eastern tent caterpillar moth
Notodontidae	<i>Nadata gibbosa</i>	White-dotted prominent
Noctuidae	<i>Orhodes</i> sp.	<i>Orthodes</i> quaker sp.
Sphingidae	<i>Paonias myops</i>	Small-eyed sphinx
Geometridae	<i>Prochoerodes lineola</i>	Large maple spanworm
Erebidae	<i>Spilosoma</i> sp.	<i>Spilosoma</i> tiger moth sp.
Geometridae	<i>Timandra amaturaria</i>	Cross-lined wave
Erebidae	<i>Zale</i> sp.	<i>Zale</i> sp.

APPENDIX B REFERENCES

Beadle, D., & Leckie, S. (2012). *Peterson field guide to moths of northeastern North America*.

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