ECOLOGY OF MOTH POLLINATORS IN URBAN ENVIRONMENTS

By

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ABSTRACT

Moths live in increasingly urban environments. As a group, moths are involved in a variety of ecological interactions: prey-predator, plant-herbivore, and plant-pollinator, and these interactions are likely influenced by the effects of urbanization. Pollination is an important ecological function for the persistence and maintenance of biodiversity. Despite its importance, a significant portion of plant visitors have been largely omitted from pollination research: nocturnal pollinators. This thesis expands the literature on nocturnal pollination in urban environments, with an emphasis on moths, which are speciose and abundant in terrestrial ecosystems. In Chapter One, I introduce and review key concepts in moth biology, pollination, and urban ecology, which are central for the subsequent chapters. In Chapter Two, I outline the creation of a moth-pollen transport network, which revealed that an abundance of moths in the surveyed urban gardens carried pollen on their mouthparts. This two-year study indicated that moths were frequent, generalist plant visitors with the capacity to move pollen throughout their environment. In Chapter Three, I broaden my view to compare nocturnal pollinators as a community to diurnal pollinators also utilizing urban garden habitats. Combined with a selective pollinator exclusion experiment, this research demonstrated significant differences among pollinator communities and visitation behaviors between day and night, yet showed that both groups contributed significantly to plant reproduction. Diurnal floral visits tended to be very frequent, but short in duration compared to nocturnal floral visits, which were less frequent. I note that increased visitation frequency may increase exposure to pollinators, but that there can also be an increase in antagonistic visitors, influencing the overall effectiveness of floral visitor communities. Finally, in Chapter Four, I describe an elementary

education project which takes the study of urban moths into the classroom, using a low-cost, easy to use moth trap to teach students about ecological research through the lens of moth biology. As scientists, one of the most important actions we can take is sharing our research with the broader community. As cities continue to expand, and we find new and improved ways to support biodiverse, functional ecosystems within these novel urban habitats, it is worth getting to know our unique, pollinating neighbors.

It gets better, I promise.

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CHAPTER ONE: INTRODUCTION

Moths as pollinators in urban environments

In this chapter, I introduce literature on moths as a group, pollination biology, and urban ecology. My goal is to provide the reader background information that will be relevant to understanding the subsequent chapters.

Moths are the largest and most diverse group of Lepidoptera and provide many ecosystem functions across landscapes. As juveniles, most moth larvae consume plants, some of which may be economically important, often making them targets of pest control (Young 1997). As adults, many moth families are nectarivorous, or nectar feeders. Through interactions with flowers, these moths provide pollination services that are important for plant reproduction (MacGregor et al 2015). Additionally, at all life stages, moths act as a food source to birds, bats, and other predators, playing a key role in local food webs (Buse et al. 1999, Vaughan 1997, Visser et al. 2006). Unfortunately, many moth populations are in decline (Conrad et al. 2006, Fox et al., 2014).

A variety of factors have influenced moth declines. Land use change, including urbanization, agricultural management such as the use of herbicides to remove weedy plant species, and habitat fragmentation have all decreased the amount of habitat available to moth species (Fox 2013, Fox et al. 2014, Kozlov 1996). In addition, increased use of artificial lighting at night is of concern. In recent years, many studies have assessed the effects of both direct lighting and “urban glow” on moths (Altermatt and Ebert 2016, Davies et al. 2013, Gaston et al. 2015). Though effects seem to vary based on species and light type, there is consistent evidence that night lighting has an effect on moth flight patterns and may decrease time spent reproducing (Davies et al. 2017) and foraging (Knop et al. 2017). Moths are also vulnerable to the effects of insecticide use, particularly aerial sprays (Longley & Sotherton, 1997). Even in cases where direct mortality does not occur, sub-lethal effects due to insecticide exposure have been observed such as decreased weight and dispersal capabilities (Longley and Sotherton 1997, New, 2004). Additionally, as nectarivores, adult moths may be vulnerable to the non-target uptake effects of systemic insecticides like neonicotinoids (Cresswell 2011). Though studies on the effects of this class of insecticide have not been conducted directly on moths, neonicotinoids have been shown to have sub-lethal effects on Hymenopteran insects such as decreased foraging behavior and navigation ability (Henry et al. 2012). Given the ecosystem functions carried out by moths, their decline may pose a risk for the stability of some environments (Conrad et al. 2006).

Pollination

Pollination is important to the generation and maintenance of biodiversity in terrestrial ecosystems. It has been estimated that 87.5% of flowering plants rely on biotic pollination for subsistence (Ollerton et al. 2011). Unfortunately, many pollinating insects, like moths, have undergone significant declines in recent years (Potts et al. 2010). In habitats with reduced pollinator numbers, plants are at risk of pollen limitation, reduced seed set, and insufficient fruit production (Ashman et al. 2004, Potts et al. 2010). These effects on plant fecundity can lead to changes in plant diversity and overall health of a given habitat (Ashman et al. 2004). Considering the importance of pollination as an ecosystem function provided by pollinating guilds, their decline puts habitat stability at risk (Garibaldi et al. 2013).

One way that pollination behavior can be described is by using a type of interaction network called a pollination network. These schematics are used to display interactions between plants and their pollinators in a given environment. Within the network, each plant or pollinator is a node, and their connections illustrate pollination interactions between them. Once constructed, these networks can be analyzed using various metrics in order to describe the vulnerability or strength of the community. For example, characterizing the number of redundant interactions, those carried out by multiple species in the network, can inform how robust the network is to perturbation. Robustness of a network can be used to predict how resilient the pollination network may be when stress is placed on the system (Blüthgen and Klein 2011). Contrastingly, if the network is dominated by complimentary interactions, this means that pollinators are carrying out unique interactions that are not repeated by multiple groups within the network. Niche complementarity can be associated with increased biodiversity and decreased interspecific competition, but the specialized nature of the interactions can also leave the network more vulnerable to disturbance within the system (Loreau et al. 2001). Information organized through pollination networks can be used to predict the effects of disruption to the network such as habitat disturbance, biological invasion, and pollinator conservation efforts (Bascompte and Stouffer 2009, Bewick et al. 2013, Memmott et al. 2004). Characterizing plant-pollinator interactions wholistically can be key in informing targeted conservation efforts.

The majority of research on pollination services to date has focused on the work of diurnal (day flying) pollinators (Macgregor et al. 2015). However, nocturnal pollinators such as moths, which have also shown signs of decline (Conrad et al. 2006, Fox et al. 2014), may represent a significant and underreported portion of plant-pollinator interactions (Hahn and Brühl 2016). Understanding the role of these nocturnal pollinators in ecological communities is important for informing conservation practices as well as making predictions for how plant-pollinator interactions may shift in response to environmental changes.

Pollination by moths may be an advantageous strategy in some plants. Studies comparing generalist plants pollinated by both nocturnal moths and diurnal pollinators have found that moth pollination can provide a few key benefits. One benefit is moths' longer-distance pollen dispersal due to their ability to carry pollen grains for long periods of time and to cover long distances rapidly (Miyake and Yahara 1998, Young 2002). A study comparing diurnal and nocturnal pollinators of Common Milkweed (*Asclepias syriaca*) concluded that nocturnal pollinators were higher quality pollinators due to the ratio of seed pods produced per visitation. Visitation by a nocturnal pollinator, primarily moths, was twice as likely to result in seed pod production than visitation by a diurnal pollinator, primarily bumblebees (Jennersten and Morse 1991). In a case comparing nocturnal and diurnal pollination of *Lonicera japonica*, moths were found to be more effective pollinators than their diurnal counterparts, removing 10 times less pollen for the same pollination effect (Miyake and Yahara 1998). This was attributed to diurnal pollinators often collecting pollen to provision their young while moth pollinators do not. This last point indicates that predominantly moth-pollinated plants are potentially able to invest less resources in pollen production without compromising potential reproductive success.

Some work has been done to explore the varying roles that nocturnal pollinators like moths play in larger interaction networks. One study in a boreal pine forest in Scotland collected pollen from moth bodies for two years to create a nocturnal pollen-transport network. In their system, they found 25 moth species (8% of total moths) carried pollen of 12 plant taxa which they assembled into a network that was found to be highly nested and dependent on core generalists (Devoto et al. 2011). Another study in an estuary system in southern Portugal created a nocturnal pollen-transport network where 76% of moths carried pollen for 26 plant taxa. The authors inferred, based on the high proportion of moths carrying pollen in the estuary system, that previously assembled diurnal pollinator networks for the area likely underestimated pollination redundancy of the system by omitting nocturnal pollination activity (Banza et al. 2015). These studies demonstrate that focusing solely on diurnal pollinators may lead to an incomplete understanding of local pollination networks. For example, some plant species may only be pollinated by one or a few diurnal pollinators, but may also be pollinated by nocturnal pollinators, thus decreasing their risk of pollen limitation (Macgregor et al*.* 2015). Otherwise stated, moths may provide pollination networks functional niche redundancy. In habitats where pollinators are facing declines, pollination networks that feature redundancy are likely to be more resilient than those that do not.

Moth pollination is traditionally divided into two categories of ‘pollination syndromes’. These syndromes are ‘sphingophily’ and ‘phalaenophily’. Sphingophily is pollination by hovering moths in the family Sphingidae, and phalaenophily is pollination by flower settling moths in other moth families (Willmer 2011). Of the research that has been done on moth pollination, the majority has focused on sphingophily (NRC 2007). However, moths in the family Sphingidae comprise less than 2% of the 11,000 moth species in North America (BAMONA 2017). Flower settling moths are much more diverse and numerous than the hovering moths of the family

Sphingidae by comparison (Atwater 2013). Though precise estimates do not exist for how many flower settling moths there are, this group comprises the majority of the 11,000 moth species in North America. Due to their high diversity, it has been proposed that flower settling moths may often be more common pollinators than Sphingid moths (Okamoto et al. 2008). Given their potential importance as pollinators, a better understanding of moths' roles in pollination networks and how that may shift in changing environments could broaden and clarify our understanding of how best to conserve vital pollination services.

Urban Ecology

Urban ecology is a subfield of ecology in which ecological research is done in an urban environment. Traditionally, ecology is the study of how organisms interact with their environment. In urban ecology, organisms are interacting with an urban environment composed of built spaces, or areas predominantly covered with human-made structures such as buildings, parking lots and roads, and green spaces, or areas covered by plants such as golf courses and parks (Forman 2010, Forman 2014). The study of urban ecology carries increasing importance now that more than 50% of the human population lives in urban environments (UN 2014). In 1950 only 30% of humans lived in urban environments, and now some estimates predict 66% of the human population will live in urban environments by 2050 (UN 2014). If these trends persist, urban development is likely to increase greatly in coming years.

Urban ecology is a relatively new subfield of ecology. Historically, ecologists have focused on studying ecological interactions in what were considered natural environments (Forman 2014). However, in the 1970s many ecologists took an interest in the ecological interactions that take place in urban environments. French botanist Jean-Marie Pelt published

L’homme re-naturé (Re-Naturalized Human) in 1977 within which he pioneered the concept of applying ecological ideas to an urban environment (Pelt 1977). Shortly thereafter, a researcher in London surveying ground arthropods with pitfall traps found that the best indicator for species diversity was the proportion of land devoted to greenspace within the city, showing that urban environments had factors affecting diversity in ways that had previously been unknown in other non-human impacted environments (Davis 1978). Two landscape ecologists first distinguished urban environments from other landscapes in 1986 when they divided all landscapes into five broad types based on human influence, ranging from pristine landscapes to urban centers (Forman and Godron 1986). Now established as a field in its own right, urban ecology studies have expanded, with researchers investigating many different aspects of urban environments.

An area of emerging importance in urban environments is urban gardening. Specifically, interest has grown in the role urban gardens play in maintaining biodiversity in the face of increasing urbanization (Gaston et al. 2005). Though individual garden habitats may be small, they can be numerous, contributing relatively large proportions of overall urban green space (Gaston et al. 2005). Studies have shown that the value of urban gardens for maintaining local biodiversity may be considerable due to their abundance and the diversity of resources, such as forage and nesting space, that they provide (Akinnifesi et al. 2010, Davis 1978, Owen 1991). For example, a survey of four urban areas in the United Kingdom estimated that residential urban garden space comprised 24-36% of overall city space and contained 54-83% of pollinator species recorded in those areas (Baldock et al. 2019). If estimates on growing urban development as the human population in urban areas increases hold true, an empirical understanding of the nature and role of urban gardens as greenspace in an urban environment will only grow in importance.

Conclusion

In a rapidly changing world, maintaining ecological function will be key in preserving healthy ecosystems. Though individual species may exhibit differential responses to anthropogenic disturbance, such as urbanization, maintaining biodiverse communities can help mitigate the effects of this change by sustaining ecological function. Pollination is a function that plays a key role in terrestrial ecosystem health, and pollination network theory has shown that networks with functional redundancy may be more resilient to disturbance. Pollination network research that accounts for variability, such as temporal variability, gives a holistic view of pollination activity in that environment, and can help when anticipating response to environmental change. Moths, and nocturnal pollinators as a whole, represent a group previously omitted from the majority of pollination research, despite life histories that include frequent interaction with flowering plants. Inclusion of these groups in pollination studies can provide a clearer view of the structure and function of pollination networks. In the face of pollinator decline, different pollinating taxa will have differential responses to urbanization, an understanding of which will help to inform conservation practices.

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CHAPTER TWO

Associations between nocturnal moths and flowers in urban gardens: evidence from pollen on moths[1]

Abstract

Pollination is an important plant-animal interaction, and moths (Lepidoptera) are frequent flower visitors. With 11,000 moth species in North America, this group of organisms has potential to largely influence the plant communities they exist in. To date, most pollination research has focused on diurnal (day active) pollinators. However, nocturnal plant visitors, such as moths, may represent a significant and underreported portion of plant-animal interactions. Understanding the role of nocturnal pollinators in ecological communities is important for informing conservation practices as well as making predictions for how plant-insect interaction networks may shift in response to environmental changes, which may be especially important in disturbed habitats like urban gardens. We aimed to address this gap in our understanding by surveying moth-plant interactions in urban environments. We collected 260 moths over a two-year period, 68% of which were carrying pollen. By family—88% of Erebidae species, 89% of Noctuid species, and 92% of Geometrid species were pollen carriers. We conclude that moths frequently interact with a diversity of flowers in urban gardens.

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Introduction

Moths frequently interact with plants. Females of most species oviposit on host plants and caterpillars eat plant leaves. As adults, many moth families are nectarivorous, or nectar feeders (Scoble 1992). Through interactions with flowers, these moths may provide pollination services that are important for plant reproduction (MacGregor et al. 2015). With more than 11,000 moth species in North America, nectarivorous moths as a group have great potential to influence the flowering plants in their environment (BAMONA 2017). However, Lepidoptera-related pollination research to date has focused mostly on diurnal (day-active) groups.

Assemblages of moths frequently carry pollen from a diversity of plant species. This has been demonstrated in surveys of various habitat types that use pollen-transport networks to describe the pollination potential of moths in the environment. For example, one study in a boreal pine forest in Scotland collected pollen from moth bodies for two years to construct a nocturnal pollen-transport network (Devoto et al. 2011). In their system, they found 25 moth species (8% of total moths) carried pollen of 12 plant taxa (Devoto et al. 2011). Another study in an estuary system in southern Portugal constructed a nocturnal pollen-transport network where 76% of moths carried pollen for 26 plant taxa (Banza et al. 2015). The high proportion of moths carrying pollen in the estuary system indicated that previously constructed pollinator networks for the area were likely underestimating the pollination services contributed by nocturnal pollinators (Banza et al. 2015). While these are compelling examples, little is known about interactions between nocturnal moths and plants in urban environments.

To address this gap in our understanding, we set out to quantify the occurrence of pollen found on moths caught in urban community gardens. We chose this target habitat given their emerging importance and popularity in urban environments (Baldock et al. 2019). Pollen was collected from moths over a span of 3 months in the summers of 2017 and 2018. Here, we recount the taxonomic associations we recorded between nocturnal moth species and the species of plants whose pollen grains they carried.

Methods

Study region

This study was conducted at 14 garden sites in Ingham County, Michigan (population approx. 290,000). The gardens were all public community gardens, managed by the Greater Lansing Food Bank's Garden Project (https://greaterlansingfoodbank.org/programs/programs/garden-project). Gardeners were primarily growing fruits, vegetables, herbs, and cut flowers. Sites varied in distance from suburban area to city center and varied in size from 546 m^2 to 12,938 m^2.

Moth collection

Collection was done weekly from the beginning of June 2017 to the end of August 2017 (8 trapping events) and from May 2018 to July 2018 (10 trapping events) for 18 total trapping events per site. Moths were collected using sterilized Mercury Vapor UV Light Traps (BioQuip Rancho Dominguez, CA). Trapping was carried out on nights with temperature lows above 55°F and no precipitation or strong winds (i.e. <12 mph). This study focused on macromoths due to their ubiquity and the availability of identification resources.

During trapping events, the light traps were placed at the center of each garden on wooden stands 1m above the ground. With 12W U-shaped black lights, these traps have an estimated moth attraction range of 10-30m (Merckx et al. 2014). Traps were illuminated overnight from 20:00 until 06:00 using a timer. In the morning, samples were then transported back to the lab with moths still in the collection bucket in order to decrease the risk of pollen grains coming dislodged from the moth to which they were attached to.

Moths were identified using field guides (Handfield 2011, Beadle and Leckie 2012), reference collections, and BugGuide.net. Reference collections used were the Albert J. Cook Research Reference collection and the Peter White Lab collection, both at Michigan State University in East Lansing, Michigan.

Pollen analysis

All pollen work was carried out in a sterile environment. Each tool was cleaned with 95% ethanol between samples to decrease pollen contamination risk. Moths were gently removed from the collection bucket using forceps and placed on a sterile surface under a dissecting microscope to swab for pollen. The proboscis and palps of the moth were swabbed with a mixture of glycerin jelly and fuschin dye (Jones 2012), which was then melted and mounted onto a microscope slide. Only the proboscis and palps of moths were swabbed to decrease the chance of inadvertent pollen contamination while inside the bucket. Once mounted, pollen grains on each slide were counted and identified using a compound light microscope (x400 magnification). Pollen grains were identified using a variety of print and online pollen identification manuals and reference photos (Print: Agashe and Caulton 2009, Harley et al. 2000, Online: Isaacs Lab at MSU Flickr Pollen Library - https://www.flickr.com/photos/161453633@N02/collections).

Results

A total of 189 moths (49 species) from three macromoth families were collected in 2017, along with 71 moths (26 species) in 2018. Of these, 89% of species, and 68% of individuals were carrying pollen. This included 15 of 17 (88%) of Erebidae species, 32 of 36 (89%) of Noctuid species, and 12 of 13 (92%) of Geometrid species. In terms of abundance, 112 of 167 (67%) noctuid moths were carrying pollen, along with 38 of 58 (66%) erebids and 27 of 36 (75%) geometrids. Some interactions were only observed within certain families (Figure 2.1). The Noctuidae moths carried a greater diversity of pollen grains than the Erebidae and Geometridae moths, and Poaceae and Pinaceae pollen seemed to be the most widespread across families. While we provide a general overview of these relationships (Figure 2.1), a network analysis of moth-pollen interactions is outside the scope of this present paper.

In all, 88 species of plant from 41 families were represented in our samples (Figure 2.1). The most common pollen grains identified were those in the plant families Pinaceae and Poaceae, the pine and grass family, respectively. Other families with a high number of interactions were Fabaceae, Caryophyllaceae, Asteraceae, Solanaceae, Euphorbiaceae, and Apiaceae. On average, moths carried 3.2 types of pollen, with 1.7 grains each, which was consistent across the three moth families observed. We attribute this to our conservative sampling method, focusing only on the palps and proboscis of the moth.

Discussion

The majority of moths collected in the study area carried pollen. Of the 65 species collected over the two-year study, 89% of moth species were found to carry pollen. The few species detected that did not carry pollen were often singletons that are likely not representative of their group. Our expectation was that because adult moths in the collected macromoth families (Erebidae, Geometridae, Noctuidae) depend on floral nectar for energy, they may also inadvertently transport pollen. It seems this prediction was supported, with 68% of individual moths carrying pollen.

These results align with some previous studies that have been done. A survey of pollen presence on moths in the Dolomite Glades in Alabama found that over half of the species they surveyed carried pollen, with Erebidae, Geometridae, and Noctuidae standing out as frequent pollen carriers (LeCroy et al. 2013). Another survey done in Florida sandhills found that 66% of individuals carried pollen (Atwater 2013). These researchers also found that moths tended to frequent plants in the Asteraceae and Fabaceae families, similar to our findings.

The highest proportion of interactions detected were between moths and plants in the Pinaceae and Poaceae families. Pine trees and grasses are predominantly pollinated by wind, so it is unlikely that these plants are dependent on moths for pollination assistance, and it is possible moths obtained these grains from the air or other surfaces. However, the next most common families found to interact with moths, Fabaceae, Caryophyllaceae, Asteraceae, Solanaceae, Euphorbiaceae, and Apiaceae, are all known to benefit from animal pollination. Visitation, which is what was recorded in this survey, is not direct evidence for pollination (King et al. 2013), so further research would need to be done in order to confirm that the moths we detected visiting plants in this survey were true pollinators.

Overall, evidence collected in this two-year survey indicates that moths in urban gardens are frequent, generalist plant visitors. In disturbed habitats, such as urban gardens, plants that are visited by more than one pollinator are more resilient to disturbance (Blüthgen and Klein 2011). Therefore, these interactions may be important for habitat stability. More work will need to be done to show that moths are truly carrying out pollination services, but as of now, it seems that moths are frequently interacting with a diversity of plants in urban gardens.

Acknowledgements

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APPENDIX A: RECORD OF DEPOSITION OF VOUCHER SPECIMENS

FORM 1
RECORD OF DEPOSITION OF VOUCHER SPECIMENS

The specimens listed below have been deposited in the named museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number have been attached or included in fluid preserved specimens.

Voucher Number: 2023-02

Author and Title of thesis:
Nicole Wonderlin
ECOLOGY OF MOTH POLLINATORS IN URBAN ENVRIONMENTS

Museum(s) where deposited:
Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Specimens:

Family	Genus species	Life Stage	Quantity	Preservation
Erebidae	Apantesis phalerata	Adult	2	Pinned
Erebidae	Bleptina caradrinalis	Adult	2	Pinned
Erebidae	Caenurgina erechtea	Adult	2	Pinned
Erebidae	Catocaia grynea	Adult	1	Pinned
Erebidae	Cisseps fulvicollis	Adult	2	Pinned
Erebidae	Ctenchua virginica	Adult	2	Pinned
Erebidae	Cycnia oregonensis	Adult	2	Pinned
Erebidae	Cycnia tenera	Adult	2	Pinned
Erebidae	Euxoa sinelinea	Adult	1	Pinned
Erebidae	Grammia virgo	Adult	2	Pinned
Erebidae	Halysidota tessellaris	Adult	1	Pinned
Erebidae	Haploa lecontei	Adult	2	Pinned
Erebidae	Lophocampa caryae	Adult	2	Pinned
Erebidae	Pyrrharctia isabella	Adult	2	Pinned
Erebidae	Renia discoloralis	Adult	1	Pinned
Erebidae	Spilosoma latipennis	Adult	1	Pinned
Erebidae	Spilosoma virginica	Adult	2	Pinned
Geometridae	Campaea perlata	Adult	1	Pinned
Geometridae	Cleora crepuscularia	Adult	1	Pinned
Geometridae	Ectropis crepuscularia	Adult	2	Pinned

Geometridae	Eugonobapta nivosaria	Adult	1	Pinned
Geometridae	Iridopsis humaria	Adult	2	Pinned
Geometridae	Lomographa glomeraria	Adult	1	Pinned
Geometridae	Metanema inatomaria	Adult	1	Pinned
Geometridae	Nematocampa resistaria	Adult	2	Pinned
Geometridae	Pero ancetaria	Adult	2	Pinned
Geometridae	Protoboarmia porcelaria indicataria	Adult	2	Pinned
Geometridae	Scopula limboundata	Adult	2	Pinned
Geometridae	Speranza pustularia	Adult	2	Pinned
Noctuidae	Agriopodes fallax	Adult	1	Pinned
Noctuidae	Agrotis ipsilon	Adult	2	Pinned
Noctuidae	Anagrapha falcifera	Adult	2	Pinned
Noctuidae	Apamea apamiformis	Adult	1	Pinned
Noctuidae	Apamea nigrior	Adult	2	Pinned
Noctuidae	Bellura gortynoides	Adult	1	Pinned
Noctuidae	Colocasia propinquilinea	Adult	1	Pinned
Noctuidae	Cosmia calami	Adult	1	Pinned
Noctuidae	Eudryas grata	Adult	1	Pinned
Noctuidae	Euxoa intrita	Adult	1	Pinned
Noctuidae	Feltia herilis	Adult	2	Pinned
Noctuidae	Hydraecia micacea	Adult	1	Pinned
Noctuidae	Lacinipolia lorea	Adult	2	Pinned
Noctuidae	Lacinipolia renigera	Adult	2	Pinned
Noctuidae	Lasionycta anthracina	Adult	2	Pinned
Noctuidae	Lasionycta phoca	Adult	2	Pinned
Noctuidae	Leucania phragmitidicola	Adult	1	Pinned
Noctuidae	Leucania pseudargyria	Adult	1	Pinned
Noctuidae	Leucania Ursula	Adult	2	Pinned
Noctuidae	Leuconycta diphteroides	Adult	1	Pinned
Noctuidae	Mythimna unipuncta	Adult	2	Pinned
Noctuidae	Noctua pronuba	Adult	2	Pinned
Noctuidae	Ochropleura implecta	Adult	1	Pinned
Noctuidae	Oligia minuscula	Adult	2	Pinned
Noctuidae	Orthodes cynica	Adult	2	Pinned
Noctuidae	Orthodes detracta	Adult	1	Pinned
Noctuidae	Orthodes majuscula	Adult	2	Pinned
Noctuidae	Panopoda rufimargo	Adult	1	Pinned
Noctuidae	Peridroma saucia	Adult	2	Pinned
Noctuidae	Photedes inops	Adult	1	Pinned
Noctuidae	Plusia venusta	Adult	1	Pinned

Noctuidae	Raphia frater	Adult	1	Pinned
Noctuidae	Striacosta albicosta	Adult	2	Pinned
Noctuidae	Ulolonche modesta	Adult	1	Pinned
Noctuidae	Xestia c-nigrum	Adult	2	Pinned
Noctuidae	Xylomoia chagnoni	Adult	2	Pinned

APPENDIX B: CHAPTER TWO FIGURE

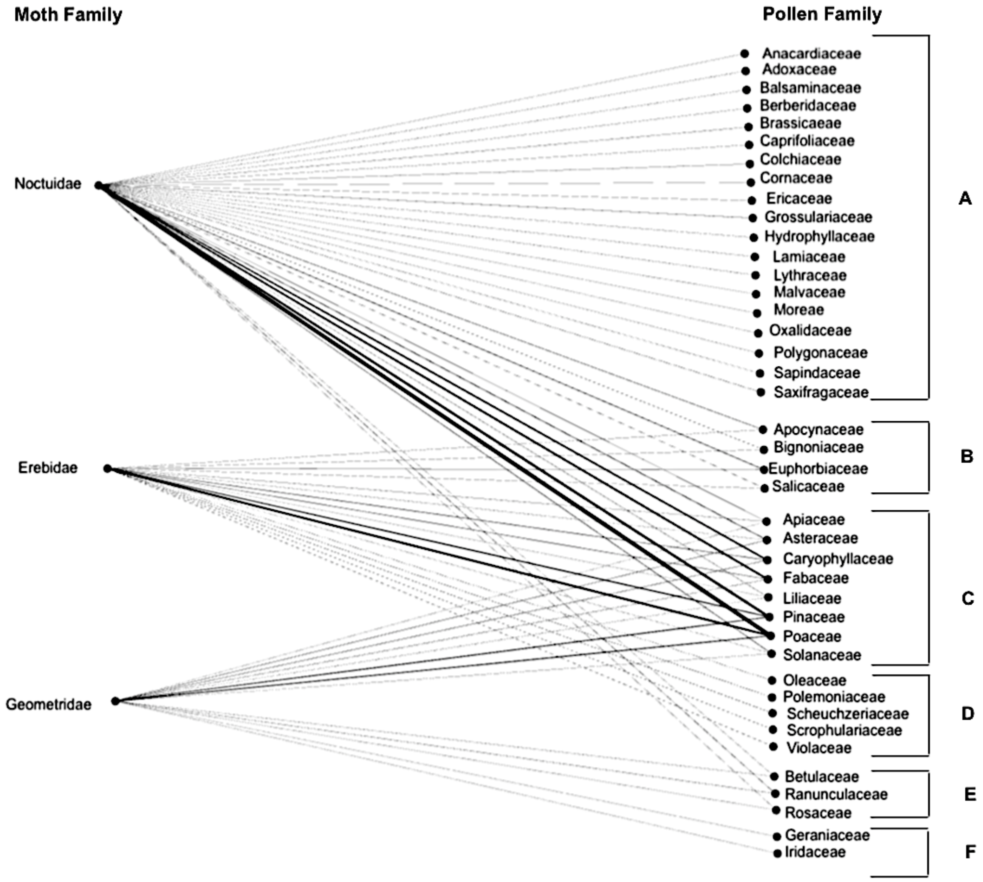

Figure 2.1. Interaction diagram of moth families and pollen families found to interact. Grouped by moth families that shared the interaction (A: Noctuidae only; B: Noctuidae and Erebidae; C: Noctuidae, Erebidae, Geometridae; D: Erebidae only; E: Noctuidae and Geometridae; F: Geometridae). Line thickness indicates the frequency of the interaction.

CHAPTER THREE

Distinct diurnal and nocturnal flower visitor communities provide pollination services in urban gardens

Abstract

Urban gardens are thought to be a key tool for mitigating biodiversity and plant-pollinator interaction loss due to their ubiquity in urban landscapes and the variety of resources they provide. To date, most pollination research in these habitats has focused on diurnal pollination, omitting a potentially important group of pollinators. To assess the diversity and pollination activity of both diurnal and nocturnal pollinators in urban gardens, I monitored all plant visitors to focal inflorescences of *Eupatorium perfoliatum*, a common Michigan-native species, for 24-hour cycles and calculated the frequency and duration of visitation. I also measured the contribution of day and night communities to pollination and plant fecundity using a pollinator exclusion experiment. On average, diurnal plant visitors tended to have higher visitation frequencies, but nocturnal visitors had significantly longer visit durations. Distinctly different arthropod communities engaged in daytime versus nighttime floral visitations. Plants open to only nocturnal pollinators produced larger seeds while plants open to only diurnal pollination trended towards producing more seeds, signaling a potential tradeoff between seed production and size among visitor communities. Differences in plant visitation and variable impacts on plant fecundity indicate that diurnal and nocturnal communities play unique roles in urban spaces.

Introduction

Pollination is an important function for persistence and maintenance of biodiversity in terrestrial ecosystems. Pollination also serves as a vital ecosystem service in agricultural systems, where 35% of global plant-based crops are pollinator dependent, and 75% experience improved production in conjunction with animal pollination (IPBES 2016). Environmentally, the role pollinators play in plant reproduction affects plant demography, population persistence, plant community structure, and overall ecosystem function (Bond 1994, Calvo and Horvitz 1993, Ishii and Masahiko 2001, Lennartsson 2002). Due to this importance, mounting evidence of pollinator decline has made pollinator conservation the target of international concern (IPBES 2016, Dicks et al. 2021, Potts et al. 2016). The implications of this decline can be of heightened consequence depending on pollinator group. For example, specialist pollinators, which typically occur in small, patchy populations, can be disproportionately affected by decline due to their dependence on specific interaction partners and their vulnerability to disturbance (Potts et al. 2010). Local loss of specialist pollinators creates more generalist, homogenized communities that are less biodiverse (Clavel et al. 2010). Given the potentially dynamic and consequential responses of pollinator groups to these changes, there is considerable interest in evaluating the threats to their persistence.

Land-use change plays a major role in pollinator decline, and urbanization is considered one of the most significant drivers of pollinator biodiversity change (Millard et al. 2021). Currently, more than 50% of the human population lives in urban areas, which is projected to increase to 68% by 2050 (UN 2019). Urbanization is associated with habitat fragmentation, loss of floral and nesting resources, altered plant communities, and increased air, noise, soil, and light pollution (Wenzel et al*.* 2020). Though these factors are considered negative in their effect on pollinator communities, studies have reported variable responses to anthropogenic change among taxa (Millard et al. 2021). In some cases, moderately urbanized cities that maintain beneficial habitats with forage and nesting resources such as gardens, parks, and remnant native habitat patches have displayed higher biodiversity than surrounding landscapes (Wenzel et al*.* 2020). A study on pollinator response to urbanization in the Tucson valley demonstrated this dichotomy among bees associated with the creosote bush (*Larrea tridentata*). Specialist, ground-nesting populations that solely depended on the study plant were diminished due to decreased availability of the bush in individual habitat fragments and the overall matrix. In contrast, cavity-nesting species had significantly higher abundance and diversity compared to the surrounding undisturbed desert, as the urban areas provided increased cavities in fencing, homes, and shade trees for nesting (Cane et al. 2006). Life history traits among pollinators can also influence their response to pollution. Along a pollution gradient originating at a nickel-copper smelter in north-western Russia, moth populations that fed externally on plants and hibernated as larvae were significantly diminished in proximity to the smelter, while internal plant feeders overwintering as pupae were unaffected by proximity to the pollution source (Kozlov et al. 2022). Changes in plant community composition can influence outcomes for pollinator groups in urban habitats. For example, high prevalence of exotic floral resources in cities compared to surrounding landscapes may favor exotic bee species, which have direct, negative influences on native bee populations (Aronson et al. 2014, Fitch et al. 2019, Goulson 2003, Pyšek 1998). Understanding these variable dynamics can help inform efforts to abate pollinator biodiversity loss.

Urban gardening is an area of emerging interest to mitigate the effects of anthropogenic change on biodiversity. Though individual gardens tend to be small, they can be numerous, contributing large proportions of the overall city green space (Gaston et al. 2005). For example, a comparison study of four urban areas in the United Kingdom estimated that residential garden space made up 24-36% of city space and contained 54-83% of the pollinators recorded in the four cities (Baldock et al. 2019). In a survey of 19 New York City community gardens, each averaging 900m^2 in size, researchers observed 13% of the recorded bee species for the state of New York (Matteson et al. 2008). One review of 87 articles related to bees in urban gardens and farms around the world reported that urban gardens, especially those with native plants, can support a high diversity of bee species (Rahimi et al. 2022). Increased prevalence of non-native plants in urban green spaces tends to favor higher proportions of generalist pollinators, often due to their ability to use a wider range of resources than specialists (Lowenstein et al. 2019). Despite cases of pollinator community composition change, urban gardens have been demonstrated to maintain the same functional diversity as surrounding, intact landscapes, highlighting their potential to promote pollinator community resiliency through functional redundancy (Vielella-Arnizaut et al. 2022). In addition to providing habitat to local pollinators, urban gardens can also be designed to benefit migratory species, like Monarch butterflies (*Danaus plexippus*), which benefit from habitat patches that connect their migratory pathways (Lewis et al. 2019). Urban gardens also provide a myriad of benefits to humans such as education opportunities, access to fresh produce, connection with nature, and opportunities to build community (Lin et al. 2018).

A key gap in our understanding of pollination and the pollinator communities in urban gardens is that most research on urban spaces has focused on diurnal insects (Maruyama et al. 2022, Salisbury et al. 2015, Silva et al 2020). This is a shortcoming in our understanding of urban garden pollinators because both diurnal and nocturnal pollinators are likely to be affected by urbanization, though potentially in different ways. As a virtue of being nocturnal, many night-active pollinators depend on olfactory cues when seeking floral resources (Balkenius et al. 2006, Stöckl et al. 2016). Air pollution, like ozone produced as a result of car exhaust and manufacturing practices, can interfere with floral scent cues, which decreases floral attractiveness to pollinators (Cook et al. 2020, Farré-Armengol et al. 2016). Nocturnal pollinators also face light pollution, which has been implicated in affecting predation risk, life history, and mortality for many species (Macgregor et al. 2015). There is evidence that some taxa may be able to subsist despite these pressures, for example, exhibiting reduced flight-to-light behavior in populations found in high light pollution habitats (Altermatt and Ebert 2016). This indicates that for some taxa, nocturnal pollinators may demonstrate resilience to the effects of urbanization. Better understanding nocturnal pollinator communities could help to identify which populations may be more vulnerable to the effects of anthropogenic change.

Nocturnal pollinators as a group are diverse, but under-studied. Moths (Order Lepidoptera) are one of the better described nocturnal pollinator groups, though the emphasis of this work has been primarily on co-evolved, specialized interactions such as those between Sphingidae moths and plants, often from Orchidaceae (Macgregor and Scott-Brown 2020). Studies on non-Sphingid moths as pollinators are scarce on a global scale, and generally omitted from agricultural settings (Buxton et al. 2021). As adults, most moths are nectivorous, generalist plant visitors. Though significantly less explored than their diurnal counterparts, moths at the community level have been documented carrying a variety of pollen types (e.g. Atwater 2013, Banza et al*.* 2015, Devoto et al*.* 2011, LeCroy et al*.* 2013, Wonderlin et al*.* 2019). Recently, a handful of studies have reported moths pollinating crop species such as apples (Robertson et al*.* 2021), gourds (Lu et al*.* 2021), and avocados (Buxton et al*.* 2021). In North America, nocturnal bees (Order Hymenoptera) in the families *Peponapis* and *Xenoglossa* are considered significant pollinators of multiple *Cucurbita* species (Family Cucurbitaceae) (Cordeiro et al*.* 2021). There are also records of various nocturnal specialist interactions such as the fly *Megommata* sp. (Order Diptera) pollinating the plant *Kadsura longipedunculata* (Family Schisandraceae) or the beetle *Cyclocephala* sp. (Order Coleoptera) pollinating the fruit tree *Annona coriacea* (Family Annonaceae). A variety of organisms are noted for nocturnal pollination activity, there are insects such as ants, flies, thrips, grasshoppers, wasps, caddisflies, and cockroaches, and vertebrates such as bats, lemurs, civets, possums, and rodents (Buxton et al*.* 2022). Just like diurnal pollinators, there is quite a bit of variety among nocturnal pollinators—specialization, life history, mobility, resource use, and so on. Therefore, there is likely to be a varied response to urbanization among nocturnal pollinator groups, in addition to the unique urbanization pressures associated with being active at night.

In this study, I aim to improve our understanding of urban gardens' role as refugia for pollinator biodiversity and function by characterizing diurnal and nocturnal pollinator communities in two urban gardens in Lansing, Michigan. First, I report the results of a video monitoring study of the frequency and duration of diurnal and nocturnal flower visitation. Second, I report the results of an experiment that excluded pollinators during the day, night, both, or neither in order to determine the pollination capacity of diurnal and nocturnal pollinators and their interactions. I hypothesized that diurnal and nocturnal plant visitor communities would differ, with fewer Hymenopterans and more Lepidopterans at night, but that both diurnal and nocturnal communities would contribute to pollination. Characterizing diurnal and nocturnal plant visitor communities and quantifying their effects on plant fecundity demonstrates the diversity of pollinators being supported by these urban gardens, as well as the capacity at which they are providing pollination services. Additionally, contrasting floral visitation behaviors and plant fecundity outputs between diurnal and nocturnal pollinators improves our understanding of the differences between these two pollinating communities.

Materials and Methods

Study Sites

This study took place in Ingham County, Michigan in two public community gardens (site 1: 9,634 m^2, 42.78°N, 84.57°W and site 2: 3,827 m^2, 42.67°N, 84.55°W) with 12.6 km between them. The gardens primarily consisted of fruits, vegetables, herbs, cut flowers, and weedy vegetation. For both the video monitoring of plant visitors and the pollinator exclusion experiment, I focused on *Eupatorium perfoliatum* L. (Common Boneset, Asteraceae), a self-incompatible native perennial plant that both nocturnal and diurnal pollinators have been previously documented visiting (Byers 1995, Grabas and Laverty 1999, Wonderlin et al*.* 2019). *E. perfoliatum* was selected because it produces dense, white inflorescences with high floral area and accessible nectar, traits that are considered attractive to both diurnal (high floral area) and nocturnal (light floral color) visitors (Baker 1961, Russo et al. 2013). Plants were supplied by

Wildtype Nursery in Mason, Michigan and kept in 20 cm plastic pots that were watered as needed.

Video monitoring of plant visitors

I characterized the community of diurnal and nocturnal *E. perfoliatum* visitors in both garden sites in summer 2022 by recording *E. perfoliatum* inflorescences over twelve 24-hour cycles from late July through the end of August. Due to phenological and bloom duration variability, 6-7 blooming *E. perfoliatum* plants were kept at both garden sites for the duration of the recording months to maintain consistent attractiveness. During each monitoring cycle, a security camera connected to a DVR and 12V 14AH sealed lead-acid rechargeable battery was focused on a single blooming inflorescence (Figure S1). The cameras used were equipped with infrared lights, which do not typically alter insect behavior (Marchioro and Faccoli 2021), that allowed for continuous day and nighttime recording.

Plant-insect interactions were documented by reviewing videos for plant visitation. To avoid counting arthropods just passing through, only arthropods that interacted directly with the reproductive parts of the inflorescence for greater than two seconds were counted as a visitation. Frequency and duration of each individual visit was recorded. Plant visitors were identified to the lowest possible taxonomic group, typically order.

Pollinator exclusion experiment

To assess the relative pollination contribution of both diurnal and nocturnal pollinators, a floral bagging experiment was conducted in summer 2019. One blooming inflorescence per plant was covered using bridal mesh tied shut around the stem at different times of day to control which plant visitors had access. Bridal mesh has been shown to effectively prevent plant visitation while minimally altering the microclimate around the inflorescence when compared to other materials (Wyatt et al. 1992). Plants (n = 114) were divided evenly between garden sites and assigned one of four treatments: (1) inflorescence bagged during the day to prevent visitation from diurnal plant visitors (n = 30), (2) inflorescence bagged during the night to prevent visitation from nocturnal plant visitors (n = 30), (3) inflorescence not bagged at all (n = 30), and (4) inflorescence bagged continuously through both night and day for the duration of the experiment (n = 24). For diurnal plants, bags were removed 30 minutes before sunrise each morning and replaced 30 minutes before sunset. For nocturnal plants, bags were removed 30 minutes before sunset and replaced 30 minutes before sunrise. All insects were removed from the inflorescences before they were covered. All plants were kept in 20 cm plastic pots and watered as needed.

When blooming was complete, I dissected individual flowers, harvested and counted seeds, and recorded whether they had developed or not. Seed mass was collected by weighing 10 developed seeds randomly selected from each individual plant. I determined seed viability using a Tetrazolium test on up to 12 randomly selected seeds per individual (Peters 2000). A 0.5% Tetrazolium (TZ) solution was created using 0.5 g of 2,3,5-Triphenyltetrazolium chloride (T8877 Sigma-Aldrich ≥98.0% HPLC) in 100 mL distilled water. Developed seeds were soaked in deionized water for 24 hours, scarified using a scalpel, and then incubated in the TZ solution for 24 hours at 30°C. Seeds were observed at 100x and those that displayed red stain, a sign of metabolically active tissue, were considered viable.

Statistical analysis

Video monitoring of plant visitors analysis. Visitation behaviors were compared between *day* and *night* treatments, as well as across the various types of floral visitors. Frequency of visitation based on time of day was assessed with a negative binomial linear mixed-effects model using the R package *MASS* (Venables and Ripley 2002). Differences in visit duration were compared using a linear mixed-effects model with the R package *lme4* (Bates et al. 2015). For both visit frequency and visit duration, a model with day versus night as a fixed effect and sampling date as a random effect was compared to a null model containing only the random effect with an ANOVA. A model comparison approach with AIC was used to look at visitation behavior differences based on the identity of the floral visitor. When assessing the visitor community, the order Hymenoptera was divided into “Hymenoptera-ant” and “Hymenoptera-nonant” due to the abundance of ants observed and the differential functions carried out by ants and non-ant Hymenopterans. Duration of visits across types of visitors was assessed with linear mixed-effects models and frequency of visitation across type of visitors was assessed with negative binomial linear mixed-effects models. The fixed effects of interest were type of visitor and day versus night, with sampling date as a random factor. AIC values were compared using the R package *AICcmodavg* (Mazerolle 2020). An NMDS ordination was used to compare overall visitor communities between *day* and *night* using the R package *vegan* (Oksanen et al. 2022). A PERMANOVA was used to assess differences between the *day* and *night* communities. Environmental factors were fit as vectors onto the NMDS plot, with time of day being the variable of interest, and site and sample date as potential confounding effects on community based on spatial or temporal differences.

Pollinator exclusion experiment analysis. Plant reproductive success was determined using seed mass, seed count, and seed viability. Seed mass was assessed using a linear mixed effects model. Seed counts were assessed using a negative binomial generalized linear model to account for the high prevalence of zeros in the right-skewed data and generalized linear mixed-effects model with a binomial distribution was used to assess seed viability. In all models, the fixed effects were the treatments *night* and *day* and the interaction between them, and plant individual was treated as a random effect. Models with the variables of interest were compared to a null model containing only the random effect with a likelihood ratio test. Post-hoc comparisons between groups were done with estimated marginal means using the R package *emmeans* (Lenth 2022). All analyses were completed using R 4.2.1 (R Core Development Team 2022).

Results

Pollinator community from video monitoring. In total, 496 plant-visitor interactions were recorded during the day, and 270 plant-visitor interactions were recorded at night over the course of twelve 24-hour cycles. Visit duration was significantly higher at night (χ^2=14.85, df=1, p<0.01), averaging 318±47 seconds on the focal plant at night and 127±20 seconds during the day (Figure 1B). Visitation frequency tended to be higher during the day, with an average of 41±5 visits to the focal plant per 24-hour cycle in daytime and 23±13 visits per 24-hour cycle at nighttime (Figure 1A), though this difference was not statistically significant (χ^2=1.25, df=1, p=0.26).

Seven arthropod orders were recorded visiting during the day and 11 arthropod orders at night. All orders recorded during day also occurred at night (Table S1). The most common daytime visitors were from the orders Hymenoptera, both ant and non-ant, and Diptera (Figure 2A). At night, the most common visitors were ant Hymenopterans. Dermaptera were the second most common arthropod order to visit plants at night. These visitor communities were distinct (PERMANOVA, $F_{1,21}$=8.73, R^2=0.3, p=0.001). A fit of environmental factors onto the NMDS ordination determined that time of day, but not location or sample date affected the community groupings (time p=0.001, location p=0.318, date p=0.331). This indicates that at the same location, on the same date, these distinct communities of visitors were visiting the study plant at different times of day (Figure 2B).

Pollinator exclusion experiment analysis. Average seed mass was significantly higher in the *night*-open treatment compared to *day*-open and *closed* treatment plants, with the *always*-open treatment falling in between (χ^2=11.02, df=3, p=0.01; Figure 3A). The *always*-open treatment had the highest percentage of viable seeds per plant, significantly higher than the *closed* treatment, with *day*-open and *night*-open plants between (χ^2=10.27, df=3, p=0.02; Figure 3C). For seed counts, *day*-open plants produced the most seeds on average, with a mean seed count of 375 seeds per plant (Figure 3A). *Always*-open plants averaged 273 seeds, *night*-open averaged 264 seeds, and *closed* treatment averaged 68 seeds per plant. However, this difference was not statistically significant (χ^2=5.35, df=3, p=0.15).

Discussion

The results of the video monitoring study and pollinator exclusion experiment indicated that floral visitor identities and behaviors differed substantially between day and night. During the day, visits were short, but there was a trend for them to be more frequent. Hymenopterans made the majority of daytime visits, 30% being from ants (Family Formicidae) and 34% being from non-ant Hymenopterans. The second most frequent order during the day was Diptera, making up 21% of total visits. At night, in contrast, there was a trend for there to be fewer overall visits, but the duration of those visits was significantly longer. Night visitation was dominated by ant Hymenopterans, 59% of visitations, followed by Dermaptera, 18% of visits. Of the floral visitors observed, Coleoptera, Diptera, Hymenoptera, and Lepidoptera have a fair amount of evidence of pollination behaviors within them (Bernhardt 2000, Hahn and Brühl 2016, Khalifa et al. 2021, Ssymank et al. 2008). Other floral visiting orders may carry out functions such as predation and herbivory, though to confirm individual visitor roles would require more precise taxonomic identification.

One hypothesis that follows from the finding of higher visit duration during the night than during the day is that a higher abundance of floral visitors leads to more interactions, some of which may be antagonistic. These interactions could cause visitors to leave prematurely, explaining the lower visit duration during the day. In contrast, at night with fewer floral visitors, visitors are able to interact with flowers for longer durations. Anecdotally, antagonistic interactions were observed between pollinator and non-pollinator groups (i.e., a spider presenting attack behavior when a moth attempts to land on the flower), and between different pollinator groups (i.e., a wasp presenting defensive behavior against a fly that has tried to simultaneously visit the flower). Previous work has demonstrated that predator presence on flowers can influence pollinator behavior and plant fitness as a result of modified pollination services (Gonçalves-Souza 2008, Antiqueira and Romero 2016). In one study, predatory crab spider (Family Thomisidae) presence on *Leucanthemum vulgare* (Asteraceae), in northern California led to a decrease in pollinator visitation rate by 40%, which in turn decreased seed set by 17% (Suttle 2003). Competition for floral resources among pollinators can also result in modified floral visitation behaviors, such as spending less time visiting flowers with depleted rewards. For example, bees have been demonstrated using scent cues to avoid flowers recently visited by other pollinators, both heterospecific and conspecific species (Stout et al. 2002; Williams 1998). Generally, the decreased floral visitation at night, nearly half as many as during the day, may have facilitated longer visit durations due to a decrease in antagonistic interactions. Previous diurnal versus nocturnal comparisons have demonstrated that in some cases, nocturnal visitors may be more effective per-visit, but diurnal pollinators have high pollination effectiveness due to their high abundance and frequency of floral visitation (Bertin et al 1980, Jennersten and Morse 1991). More floral visitors are often considered better for pollination. These results, however, suggest that high visitation rate may increase pollination, but also increase antagonistic interactions between floral visitor groups.

Ants, one of the most abundant visitors in this study, can significantly alter pollination success and floral visitor communities. Antibiotic secretions found on ant cuticles can render pollen grains inviable, meaning they rarely contribute to pollination (Beattie et al. 1985, Dutton and Frederickson 2012). Ant foraging behavior can also damage floral stigmas, which impedes floral reproduction (Galen and Cuba 2001). When it comes to the effect ants have on pollinators, they can both directly and indirectly repel them. When occupying a flower, ants can harass or attack visitors. A study looking at the effects of ant occupation on bumblebee behavior reported ants biting, grasping, and appearing to sting the bumblebees that attempted to visit. Generally, the bumblebees avoided flowers both occupied by ants and treated with ant scent (Cembrowski et al. 2014). In plants that produce extrafloral nectaries, which attract ant bodyguards, ant defensive behavior can significantly decrease pollinator interactions and have detrimental effects on plant fitness (Santos and Leal 2018, Villamil et al. 2022). However, ants deterring floral visitors does not always negatively affect plant fitness. The shrub *Melastoma malabathricum*, which is most effectively pollinated by carpenter bees (*Xylocopa spp.*), has been shown to attract ants that filter out less-effective pollinators, but do not deter the plants' larger primary pollinator (Gonzálvez et al. 2012). The effect of ant presence on flowers may be variable depending on the plant species involved.

Plant fecundity was significantly affected by the group of pollinators they were exposed to, indicating that diurnal and nocturnal pollinators differed in the pollination services they provided. The a*lways*-open treatment plants produced the largest proportion of viable seeds, significantly higher than the *closed* treatment, with *day* and *night*-open plants falling in the middle (Figure 3A). The low performance of plants with no access to pollinators indicates that *E. perfoliatum* is dependent on pollination services to reach full reproductive potential. Seeds produced by the *night*-open treatment had significantly higher mass than the *day*-open and *closed* treatment plants, with *always*-open seeds not significantly differing in mass from the other treatment groups (Figure 3C). There appeared to be a potential reproductive tradeoff between *day*-open and *night*-open plants. *Day*-open plants were smaller than those from other pollination treatments but tended to produce marginally the most seeds on average. In contrast, *night*-open plans produced seeds with higher mass than other treatments, but trended towards having fewer seeds on average. Seed number differences across treatments were marginally significant in this study, suggesting more research on this potential tradeoff is needed. Interestingly, the opposite trend was reported in a diurnal and nocturnal pollinator effectiveness study of *Silene alba*, which is generally considered to be a moth-pollinated species. Plants open to nocturnal pollinators produced more than twice the number of seeds than diurnal plants, but diurnal plants produced significantly larger seeds than their nocturnal counterparts (Young 2002). The author proposes that pollinator effectiveness could have been a factor in influencing the differential seed outputs between groups, with nocturnally open plants being saturated with pollen and setting seed after fewer visits than those open to diurnal pollinators. Here, the *day*-open plants tended to produce many small seeds and *night*-open plants tended to produce a few, larger seeds, which could signal a difference in visitation effectiveness between pollinator groups.

Having demonstrated that diurnal and nocturnal pollination services differ, there are a few broad characteristics that previous studies have found distinguish nocturnal pollinators as a group. Compared to diurnal pollinators, nocturnal pollinators are more likely to forage between patches, while diurnal pollinators typically spend more time foraging within a single patch (Barthelmess et al. 2005). Comparisons between moth and bee pollinators have found that moths will move pollen significantly further than bees (Miyake and Yahara 1998, Young 2002). The movement of pollen between patches and across great distances provides plants with greater interpopulation gene flow, which could be particularly important in isolated urban habitats. Several previous studies have found differences in pollinator effectiveness between nocturnal and diurnal pollinators, proposing that in some systems, nocturnal pollinators provide more effective per-visit pollination, but the high abundance of diurnal insects makes their overall pollination effectiveness equal or greater (Bertin and Willson 1980, Jennersten, O. and D. H. Morse 1991, Miyake and Yahara 1998). Differences in per-visit pollination effectiveness could be attributed, in part, to high pollen removal by many diurnal pollinators to provision young, which does not contribute to plant reproduction (Miyake and Yahara 1998).

In this study, nocturnal pollinator communities were distinct from diurnal pollinator communities, and produced reproductive output comparable to the other open to pollinator treatments. Given the emphasis on diurnal pollination activity in most studies, it is possible that some relevant plant-pollinator interaction information may be missed in cases where floral anthesis spans both day and nighttime. In a comparison of diurnal and nocturnal pollination in *Trifolium pratense*, nocturnal moth visitation had an additive impact on seed set in conjunction with diurnal pollinators (Alison et al. 2022). The authors note the importance of including nocturnal pollinators in their research, as previous day-focused work had found no relationship between diurnal pollinator visitation alone and seed set in *T. pratense* (Alison et al. 2022). In this study, nocturnal pollination significantly affected plant fecundity, and the community of floral visitors that were active at night were altogether distinct from those during the day, indicating that diurnal and nocturnal pollinator communities play unique roles in these urban spaces. Further examination of this distinction and inclusion of nocturnal pollinators in the assessment of urban gardens as key habitat for biodiversity maintenance will give a clearer picture of how urbanization is affecting pollinators and pollination services.

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APPENDIX

Table 3.S1. Summary of total duration and number of visits conducted by each floral visitor by order for both day and night observations.

Order	Total day visits	Total night visits	Total day duration (s)	Total night duration (s)
Araneae	4	14	231	206.9
Coleoptera	28	6	3353.4	1145
Diptera	99	10	706.1	1603.9
Hemiptera	37	16	575.7	2159.1
Hymenoptera-ant	144	160	1590.3	2712.1
Hymenoptera-non-ant	164	1	957.2	16
Lepidoptera	1	11	1172	1981
Dermaptera	0	48	NA	2714.9
Neuroptera	0	1	NA	423
Opiliones	0	1	NA	20
Orthoptera	0	2	NA	21.5

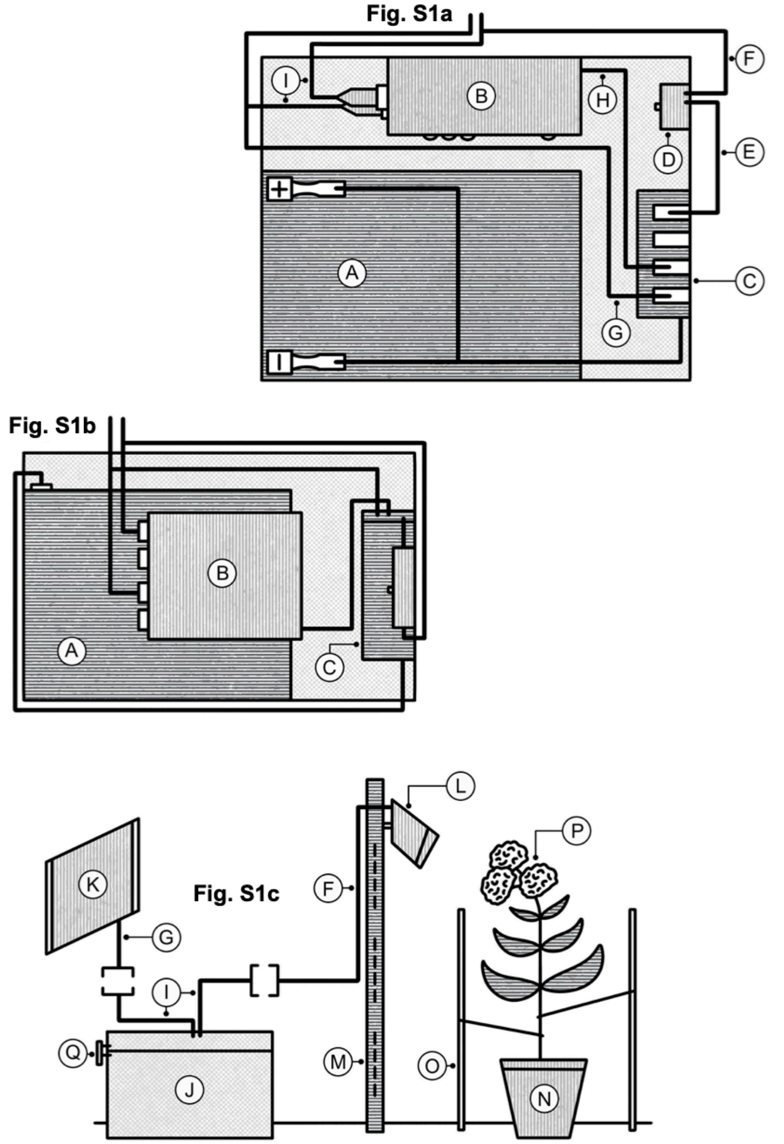

Figure 3.S1. Schematic of video monitoring apparatus. (a) Overhead view of the electronic configuration; (b) side view of the electronic configuration; (c) total video monitoring set-up. A 12V 14AH sealed lead-acid battery (A) powers a security camera (L), DVR (B), and LCD screen (K) all of which are routed through a 12V 24V to 5V 8A USB power adapter (C). From the battery, the security camera is connected to the power adapter with a USB extension cable male to female converter (E) which routes through a DC 5V to 12V USB voltage step up converter cable (D) with a 1A step-up transformer power regulator line (F) to the security camera which is

Figure 3.S1. (cont'd)

mounted on a steel u-post (M) using zip-ties. From the battery, the DVR is connected to the power adapter with a DC 5V to 12V USB voltage step up converter cable (H). The LCD screen is also connected to the power adapter with a DC 5 to 12V USB voltage step up converter cable (G). The video input and output (I) connect to the camera and LCD screen respectively. All electronic components are stored in a 45-caliber ammo box (J) for protection from the elements and secured with a combination padlock (Q). Boneset plants are planted in 20 cm plastic pots (N) and held in place using bamboo stakes (O) and twine. The blooming inflorescence of the focal plant (P) is placed directly in view of the camera.

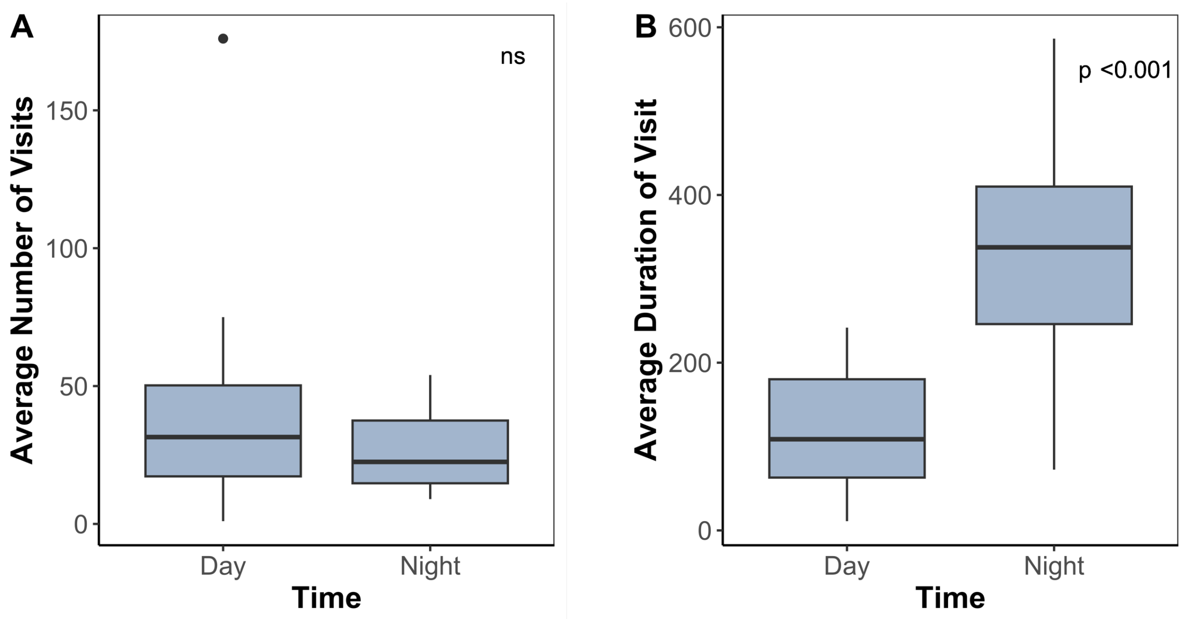

Figure 3.1. Plant visitation by time; (A) There were 43 visits on average during the day and 27 visits on average at night. This difference was not statistically significant (p=0.26); (B) On average, floral visits lasted significantly longer at night compared to during the day (χ^2=14.85, df=1, p<0.01).

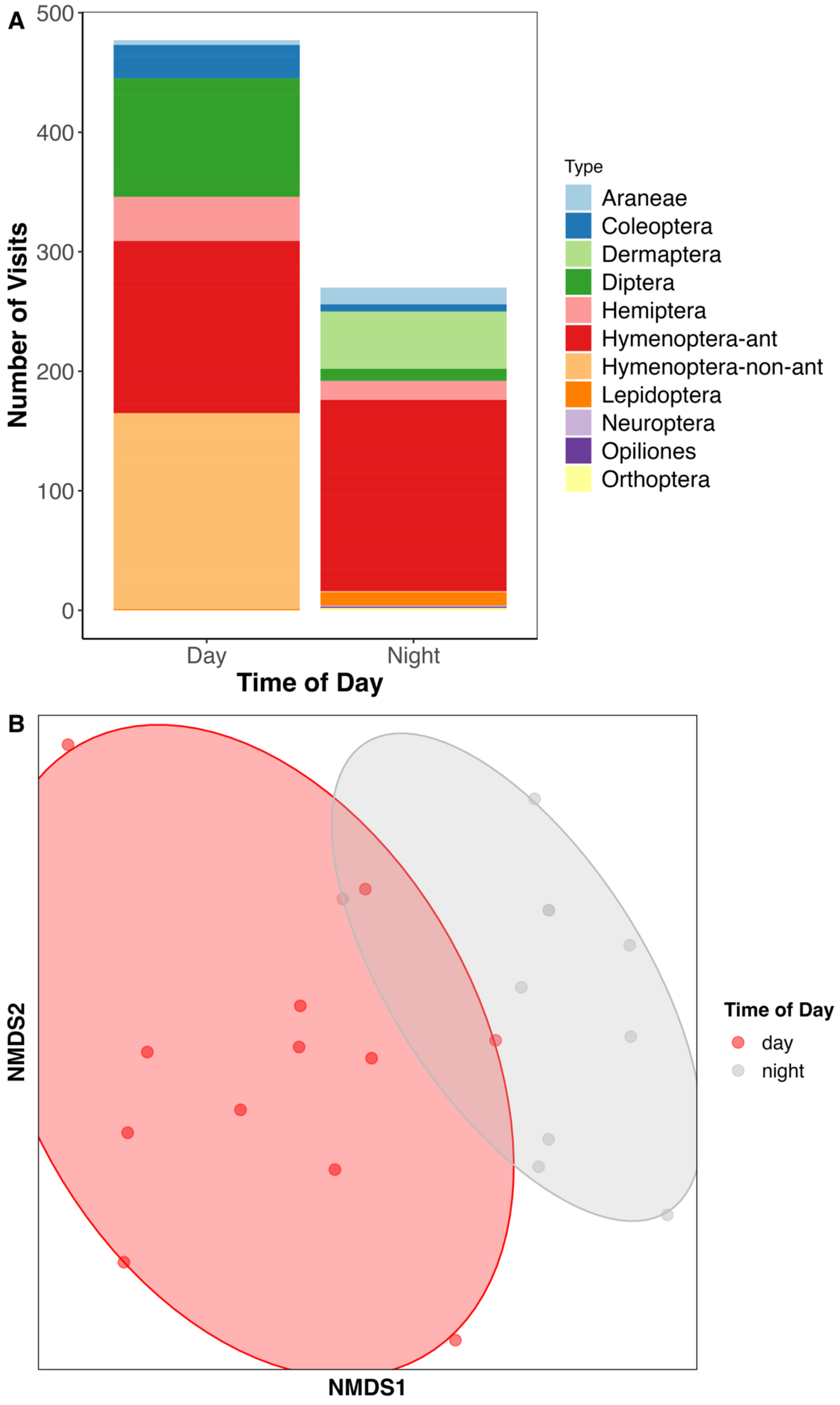

Figure 3.2. Comparison between *day* and *night* plant visitor communities; (A) Number of visits conducted by each type of arthropod between *day* and *night*; (B) NMDS plot comparing the communities of plant visitors during day and nighttime (Stress=0.13, PERMANOVA, $F_{1,21}$=8.73, R^2=0.3, p=0.001).

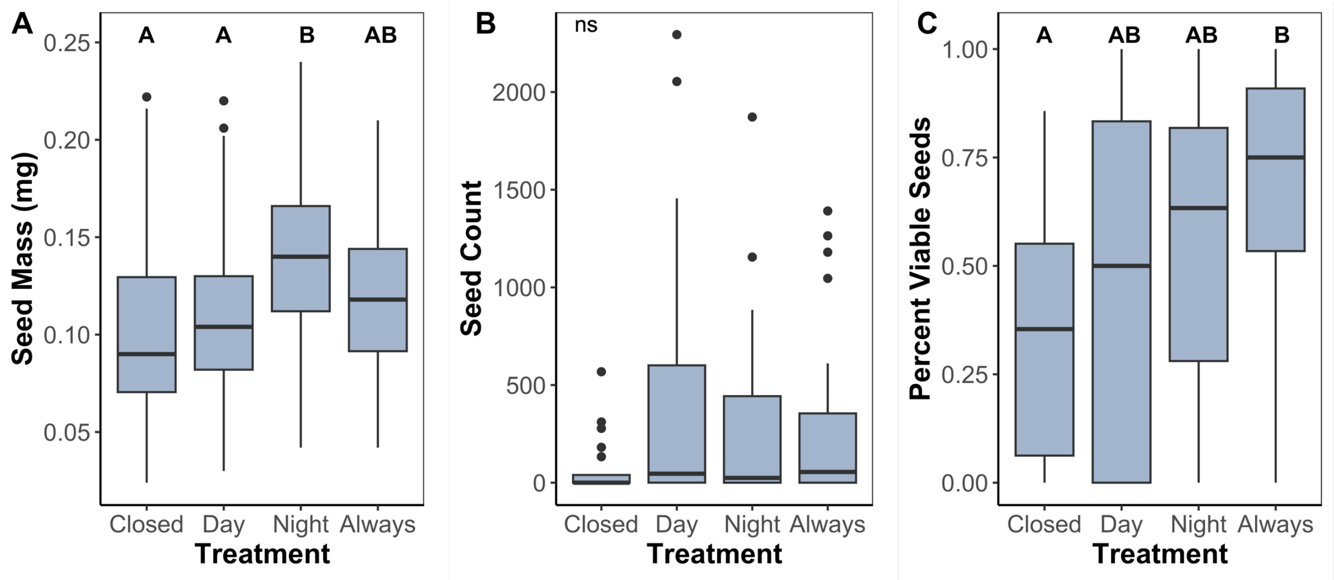

Figure 3.3. Plant fecundity by treatment; (A) Seed mass is significantly higher in *night*-open treatment compared to *day*-open and *closed* treatment plants with the *always*-open treatment falling in between (χ^2=11.02, df=3, p=0.01); (B) On average, *day*-open plants produced the most seeds (c*losed* average = 68, *day* average = 375, *night* average = 264, *always* average= 273), however, the difference in average seed count is not statistically significant (χ^2=5.35, df=3, p=0.15); (C) Plants in the *always*-open treatment had the highest percent of viable seeds, significantly differing from the *closed* treatment (χ^2=10.27, df=3, p=0.02). The *day*-open and *night*-open treatments fell in between, not significantly different from the other treatments.

CHAPTER FOUR

Habitats of urban moths: engaging elementary school students in the scientific process[2]

Abstract

Inquiry-driven teaching methods allow students to take on an active role in their own education. Through this framework, students are able to cultivate an understanding of scientific concepts and their connections while experimenting in the classroom. Our project applied this approach to the investigation of habitats of urban moths, which are abundant in most environments. Based on the students' hypotheses on where moths might be, home-made moth traps were placed either in a local nature preserve or in the school playground over the course of 2 nights. Overall, 27 moths were captured. Students then learned how to pin moth specimens and assessed what they could infer from how many moths were captured in each of the collection areas. This project created an environment for students to learn Next Generation Science Standards (NGSS) performance expectations about the diversity of life and how organisms interact with their environments.

Introduction

Inquiry-driven science teaching has recently increased in popularity as a way to combine learning with experimentation (Pedaste et al. 2015). With an inquiry-driven framework, students are encouraged to actively participate in the scientific process and take ownership of their learning by gaining knowledge through their work (Pedaste et al. 2012). Typically, students

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[2] Manuscript was published in The American Biology Teacher in 2022, Wonderlin, N. E., Lorenz-Reaves, A. R., and P. J. T. White (2022) Habitats of urban moths: Engaging elementary school students in the scientific process. *American Biology Teacher* 84(5) 284-289.

work through self-directed experiments in order to understand how variables are connected (Wilhelm and Beishuizen 2003). Rather than rote memorization, students are encouraged to learn about scientific ideas as they apply to the experiment in real time. This hands-on experience has been shown to help improve understanding and retention of scientific concepts (Minner et al. 2010). Additionally, students are able to develop their critical thinking and analytical skills by working to make connections on their own (Madhuri et al. 2012).

Community- or place-based learning emphasizes using the area students live in as a primary resource for education. Rooting education locally is thought to help students develop stronger ties to their community, enhance their appreciation for nature, and invoke a commitment to serve their community as a contributing member (Sobel 2004). In subject areas like biology and environmental science, one place-based learning option is studying local plants and animals. This can help students connect with nature in their local community while they learn broader scientific concepts like nutrient cycling, species diversity, or how anthropogenic activity impacts the environment (Vander Ark et al. 2020).

Insects, such as moths, are abundant in both urban and rural settings, making them an ideal taxonomic group for instructors who want to teach students about local biodiversity. Over the course of their life cycle, moths demonstrate a variety of ecological interactions. As caterpillars, moths are voracious herbivores, as adults, moths feed on nectar and act as pollinators, and at all life stages moths are food to birds, bats, and other predators (Bates et al. 2014). Because they are invertebrates, there are no restrictions on collecting non-endangered moths for research and education purposes. Additionally, their attraction to lights at night makes trapping moths relatively easy and low-cost (White et al. 2016).

These features make moths good candidates for teaching science in elementary school classrooms. For example, Next Generation Science Standards (NGSS) performance expectation 2-LS2-2 calls for students to understand reciprocal ecological relationships such as those between plants and their pollinators. There are many examples of moth-plant relationships in which they depend on each other for reproduction and survival. One example is the well-studied relationship between Yucca plants (*Yucca* sp.) and the Yucca moths (Family: Prodoxidae) that pollinate them. Adult Yucca moths use flowers for nectar and pollen and while doing so, they move pollen from plant to plant, helping Yucca plants produce seeds, some of which will be eaten by Yucca moth caterpillars (Pellmyr 2003).

The NGSS also call for students to make observations of plants and animals to compare the diversity of life in different habitats (PE 2-LS4-1). There are many factors that influence moth diversity in different habitats—a few of which are light at night, plants for caterpillars, nectar for adults, presence of potential mates, and presence of predators (Dulieu et al. 2007, Summerville and Crist 2008, White 2018). While these factors are well known, there is no general rule for what determines where moths prefer to be at night.

In this project, we asked students in a 2nd grade public elementary school classroom in a suburban town (pop. 26,065) of central Michigan to help us determine what habitat features may influence moth location at night. Students developed their own ideas, and we helped them construct low-cost traps and conduct moth trapping. We worked together to facilitate student projects over the course of 4 weeks late in the school year, from mid-May through early June in 2019. This project was reviewed by our university's Institutional Review Board and approved (IRB # STUDY00002563).

The overall goal of this project was to design and implement an inquiry-based science unit where students could explore the moth diversity in their local community. We engaged students in the scientific process as they surveyed moths in local habitats, constructed moth traps and handled moth specimens.

Methods and Results

Our project was implemented in a 2nd grade elementary school classroom in Michigan over the course of four weeks from the second week of May to the first week of June. The teaching team consisted of two faculty members and one graduate student member of Michigan State University Department of Entomology, one faculty member and one graduate student member of the Michigan State University department of Teacher Education, and two undergraduate students from the Lyman Briggs College at Michigan State University. During the course of the project, the teaching team spent an average of 45 minutes with the class of 19 students twice a week. The project was broken into four parts designed to model by the cycle of scientific inquiry: (1) observe and learn about moths; (2) ask questions and create hypotheses; (3) design and implement an experiment; (4) interpret results and ask more questions.

Part 1 – Observe and Learn

The first step was to survey students on what they already knew about moths. Prior to any instruction, students were asked to draw what they thought a moth looked like using pencil and paper. They were given 10 minutes to complete their drawing and any questions they asked were answered with simple encouragement ("just do your best") in order to reduce the risk of influencing the students' drawings in any way. This activity was repeated at the end of the project to gain a sense of how students' ideas about moths changed over the course of the lesson series (Figure 4.1).

Further, students were asked to share what they know about moths verbally. To facilitate this with 2nd grade students, the class was broken into groups of 3-4 students with a teaching team member assigned to each group. Students shared their thoughts while the teaching team member acted as the scribe. Next, one member of the teaching team stood at the front of the classroom, called on groups to share their ideas, and wrote answers on the board as students offered them. A few examples shared by students were, "they are a bit like butterflies but do different things", "they are furry on the bottom and scaly on the top", "they follow the moon to see where they are going at night", "when moth wings are wet, flying is difficult." Each idea shared was treated the same and no misconceptions were commented on. After hearing students' thoughts, we gave a short, image-based presentation on moths that focused on 3 key messages that we wanted students to retain and understand: (1) moths help flowers make seeds (shown with imagery of moths pollinating flowers); (2) moths are food for birds, bats, frogs, and other animals (shown with imagery of these animals eating moths); (3) some moths harm the environment (shown with imagery of herbivory damage in crops, forests). Though the intent of the project was primarily for students to learn through action, we incorporated this step as an opportunity to show imagery of a diversity of moths and habitats that otherwise might not be found during moth collection around their school.

Next, we allowed students to observe moths in display cases brought in from Michigan State University. During this time, we asked students about their observations on what moths look like, what makes them different from other insects, and what distinguishes the different types of moths on display. Similar to their initial share-outs, this was facilitated by splitting the class into groups of 3-4 students per teaching team member. The teaching team member wrote down the students' ideas and ensured each student got an opportunity to share their thoughts. These activities were incorporated to as an opportunity for students to note the diversity of moths that occupy many habitats (NGSS 2-LS4-1).

Part 2 – Question and Hypothesize

Once students had some general information on moths, they were asked a mixture of open-ended and guiding questions to facilitate hypothesis formation. For example, "what would you like to learn about moths?" or more leading - "how do you think we collected these moths?" During this discussion we also asked students to imagine how we might answer some of their questions. For example, if we are wondering about where moths live, we could go out and attempt to collect moths from different areas we think they might be found in. Focusing on the concept that moths occupy many habitats, we took the students out on a walk around the grounds of their school, asking them to make predictions on where they thought moths might be found and why. This was an opportunity to use some of the knowledge they had learned during Phase 1—moths visit flowers, moths need to avoid predators, and moths eat leaves. While walking the grounds in groups of 3-4 students per teaching team member, students marked areas they predicted moths would be found with stake flags.

After marking their predictions in small groups, a teaching team member summarized students' predictions and reasoning on the board back in the classroom (Table 4.1). Concurrently with the share-out, we asked students to form hypotheses on why they thought moths might be found in a certain location. Their reasoning was both drawn from Phase 1, and knowledge they had from their own experiences with moths and other insects prior to beginning the project. Following class discussion, the students settled on two locations they wanted to compare—a well-lit and highly populated area near their school playground and a forested nature preserve next to the school that is relatively dark at night and doesn't experience much human activity.

Part 3 - Experiment

Students worked in small groups of 3-4 students and 1 teaching team member to build their own moth traps. The materials needed to build a trap were 1 cylindrical stake, 1 2-liter bottle, 1 binder clip, 1 piece of cardstock or construction paper, 1 LED light (5mm straw hat type), 1 coin cell battery (CR2477 battery 3 volt), scissors, and duct tape (Figure 4.2). The teaching team pre-cut the 2-liter bottles in half, a task that may be difficult for small hands. Once constructed, traps were deployed by the teaching team on two non-consecutive nights in areas chosen by students during Part 2. The teaching team set out the traps because they needed to be set out at dawn and dusk, outside of school hours. This also meant the teaching team members were the only ones to touch the pesticide strip placed in the collection bucket of the trap. We used Hot Shot brand No Pest Strips (https://www.hotshot.com/products/general-insect-control/no-pest-strip.aspx) cut into small pieces, the active ingredient of which is dichlorvos (2,2-dichlorovinyl dimethyl phosphate).

Collected moths were brought back to the classroom where students were taught how to pin and spread moth specimens (Figure 4.3). Overall, 25 moths were collected in the forested nature preserve and 2 moths were collected near the school playground. To pin moths, students used Bioquip brand insect pins, small pieces of Styrofoam to push their pins into, and strips of wax paper to hold moth wings into position. Students worked closely with members of the teaching team to ensure safety when using the sharp pins. It takes about 24 hours for a moth specimen to be fully dried and set in place after being pinned. Once students had pinned their moths, they were given moth identification guides to flip through and determine what moth species they had pinned (Beadle and Leckie 2012, Handfield 2011). In place of book guides, it would also be possible to use online resources such as bugguide.net or discoverlife.org.

Here we would like to address potential questions about the safety and ethics of insect collecting. Regarding safety, while the pesticide strips should not come into contact with eyes or mouths, placement in a well-ventilated area or outdoors allows vapors from the strips to disseminate safely (Hot Shot 2016). The strips used inside the insect traps are efficient and kill moths rapidly upon their entrance into the trap. These pesticide strips were only handled by the teaching team members placing out the traps and were removed from the traps before they were brought into the classroom. Regarding ethics, we note that there is a long history of enthusiastic discourse around the ethics of insect collection for hobby, education, and research purposes (Trietsch and Dean 2018, Drinkwater et al. 2019, Fischer and Larson 2019). There is no single “right” answer to this question, and different readers, educators, and students may feel differently about this practice. It is not our goal with this paper to present the arguments for or against using insects in this manner.

Pilot studies conducted by our teaching team in a middle school classroom (Stroupe et al. 2018) did not reveal student concerns about insect collection nor suggest that killing insects would be a barrier for student learning. If this is an area of concern or interest for an educator, we encourage them to discuss the ethics of insect collecting with their students prior to moth trapping, and to consider alternative activities if concerns arise. In the case of the project that we present here, students did not voice concern about the moths we collected. This could be in part because their introduction to moths was through pinned specimens, or perhaps due to the nocturnal nature of most moths, students were not observing and personifying moths in the wild before collecting them.

Part 4 – Interpret Results and Start again!

To help visualize what we had collected, all of the pinned moth specimens were organized onto a 'Biodiversity Board' (Figure 4.4). Using this display, students were asked to interpret what they had learned about moths. This opened a discussion on moth habitat preferences, how they fit into local ecosystems, and what we might do in their community if we wanted to help moths. Following this discussion, we asked students what new questions they had based on the results, explaining that the scientific process is continuous, and our research projects often lead to more questions. Lastly, we re-surveyed students by asking them to draw what they think of when they think of a moth (Figure 4.1B). Again, they were given 10 minutes to work independently with no feedback from the teaching team. Both the pre- and post-unit drawings were scored for various markers consistent with features discussed during the unit that separate moths from other animals (Figure 4.5).

Discussion

In total, the students collected 25 moths from the forested nature preserve and 2 moths from the well-lit area near their school playground over the course of 2 nights. Our project took place in Michigan from the second week of May to the first week of June. In this research area, moths generally fly from the end of May through the end of August, meaning students were catching some of the first moths emerging for the season. This may have limited the number of moths available for collection. For other institutions in warmer or more mild climates, this project could be conducted during a broader range of days within the school year.

Visualizing the collection using a ‘Biodiversity Board’ with all of their moths sorted by catch location helped students connect the traps placed in the two study locations and the moths they now had in front of them. While discussing results, students were asked to recall their initial predictions that led them to choose those two locations and reflect on why the forested nature preserve might have caught more moths than the well-lit area. One student suggested, “because [forested nature preserve] has more trees and leaves, that’s how moths can hide” noting our discussion on moths’ need to avoid predators.

There were consistent differences observed between the pre- and post-unit drawings created by students. Though not intended as a strict quantitative measure of students’ grasp of moth biology, a few interesting trends emerged when comparing drawings (Figure 4.5). For example, though students were given the same amount of time to work on their drawings before and after the project, the post-unit drawings often featured more structural detail such as the addition of antennae or a proboscis (moth tongue). In their post-unit drawings, 42% of students also added habitat features such as trees and flowers, connecting back to the experiment the students had conducted on moth location within a habitat.

During our final discussion as a class, we asked students what they had learned about moths through this experiment. Some students remarked on the experience itself, noting that moths can be tricky to pin. One student pointed out that moths can sometimes be bad for the earth because they eat so many leaves. Students also reflected on the diversity of moths and how that varies between habitats, noting that there are many moth species in general and that there were many more types of moths found in the forested nature preserve than there were at their school playground. We believe these reflections are an indication that the project created opportunities for students to form ecology-focused connections like those denoted by the Next Generation Science Standards.

Lastly, this project was created with elementary aged children in mind but could certainly be implemented for older students as well. In our case the students had lots of help when it came to facilitating discussion, writing down their thoughts, and with trap construction components that required more dexterity. To adjust the project for older students we believe they could be given even more agency during these activities to encourage independent development throughout the project. Additionally, in this project the entire class worked together to explore a single hypothesis, at higher levels, students could work in teams or pairs to address their own hypotheses, and then they could report their findings to the class in either a written or oral format.

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APPENDIX

Table 4.1. Suggestions from students on where to place traps in order to capture moths and the explanation they gave for their location.

Location	Reasoning
Well-lit areas	Lights attract moths
Forests	They have flowers, trees
Closets in homes	Some moths like clothing
Tree covered areas	There is no light
Below a tree	Moths eat leaves
Near a flower	Moths like flowers
Open field	No trees in the way of flight, many flowers
Nature reserve park	Lots of trees, few people

4.1A.

4.1B.

Figure 4.1 An assortment of examples of students' moth drawings comparing those drawn (A) at the start of the four-week project and (B) after finishing the 4-week unit.

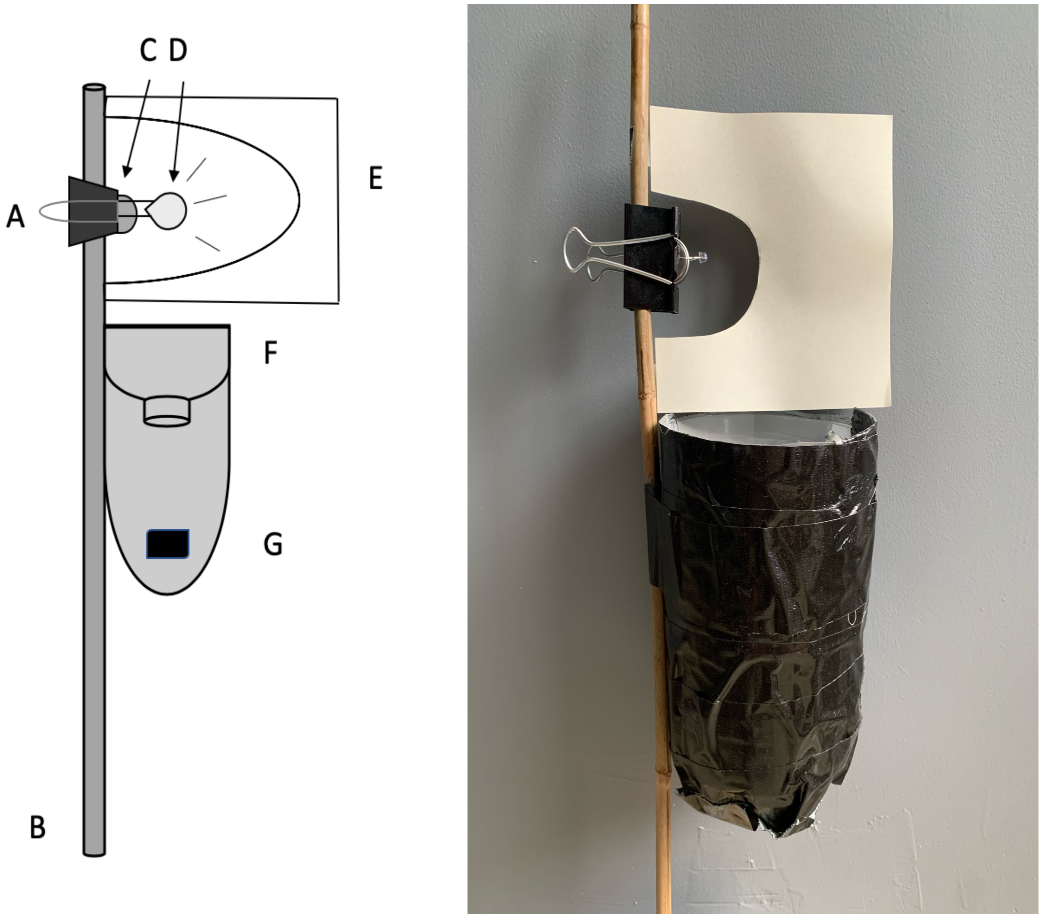
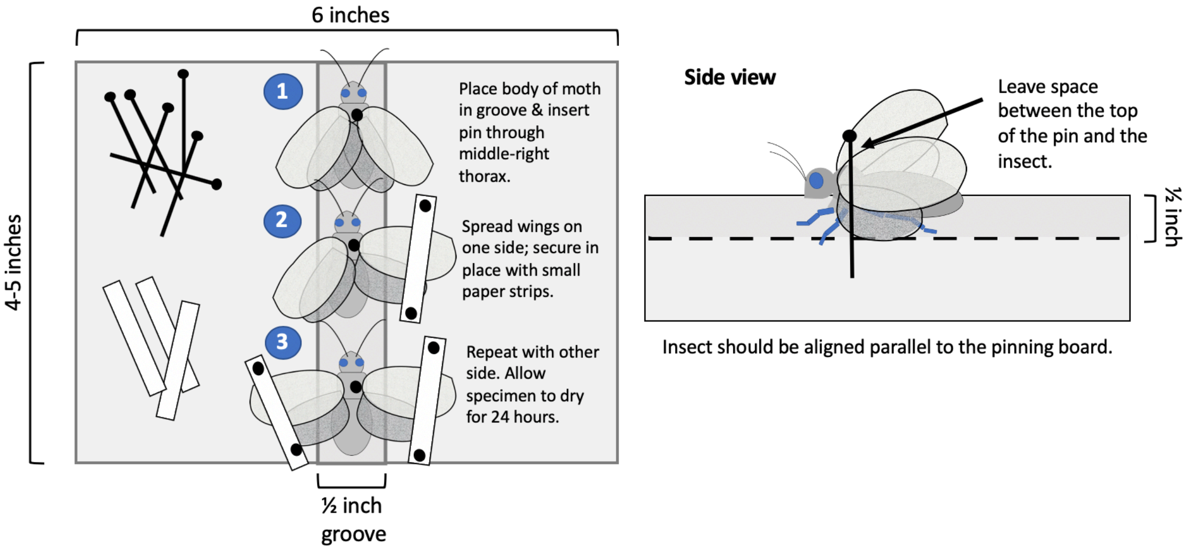


Figure 4.2. Trap used to capture moths. 2-liter bottle (2F) cut in half and top placed upside-down to allow moths entry but prevent escape. Binder clip (2A) holds coin cell battery (2C) to nodes of LED light (2D). Bamboo stake (2B) is taped onto the bottle and holds the binder clip. Paper with an opening cut in is affixed to stake with tape to knock moths into bottle. Pesticide strip (2G) is placed into bottle to incapacitate moths as they enter. Example student trap pictured on right side.



1. Place body of moth in groove & insert pin through middle-right thorax.
2. Spread wings on one side; secure in place with small paper strips.
3. Repeat with other side. Allow specimen to dry for 24 hours.

Leave space between the top of the pin and the insect.

Insect should be aligned parallel to the pinning board.

Figure 4.3. Diagram of how to pin a moth. Pinning board can be created by attaching pieces of Styrofoam together with a groove in the center for the moth body to be pinned into.

Figure 4.4. Students observing the Biodiversity Board with moths they have pinned and helped to identify.

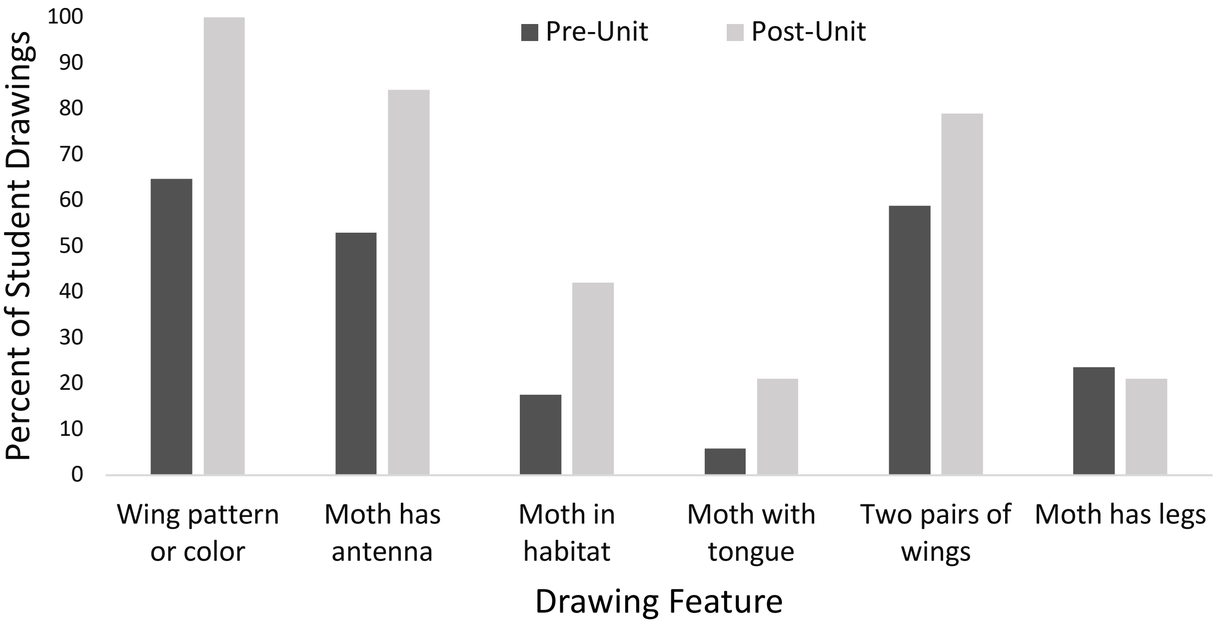


Figure 4.5. Pre- and post-unit drawings from students were scored for markers based on features discussed during the unit that make moths unique from other animals (n = 19).

CHAPTER 5: CONCLUSION

In this thesis I have expanded our knowledge on moths as pollinators, described how moths fit into larger communities of urban pollinators, explored the utility of urban gardens as mitigators of biodiversity loss due to anthropogenic change, and proposed bridges that can be built between the important work of ecologists and the broader community. In Chapter One, I introduce moths as a speciose, nectivorous, group that carries out many ecosystem functions. I explain the current status of moths and the unique threats that are thought to have contributed to their current decline, such as habitat loss and environmental pollutants like artificial light at night and insecticides. Pollination biology and urban ecology are introduced to explain how aspects of both, namely plant-pollinator network analysis and manipulation of urban green spaces like gardens, can be leveraged to inform conservation practices. In Chapter Two I use both of these concepts to investigate moth-pollen transport in 14 urban community gardens. Over a two-year survey, 89% of species and 68% of individual moths carried pollen on their mouthparts, interacting with a high diversity of plant species.

To put these interactions into a broader ecological context in Chapter Three, I investigate nocturnal and diurnal pollinator communities as a whole by using video monitoring to capture 24-hour cycles of plant visitation in urban gardens. When comparing plant visitor behavior, diurnal floral visitors tended to make frequent, short visits, while nocturnal visitors made less frequent but longer lasting visits. Despite these different behaviors, I show through a pollinator exclusion experiment that both nocturnal and diurnal pollinators contribute to plant reproduction in urban garden environments. Highlighting the broad diversity of pollinators that use urban gardens demonstrates their potential to act as refugia for urban pollinators within the larger urban matrix.

Urban gardens are not just important to pollinators, they are also very important to the humans who use them. They provide education opportunities, access to fresh produce, connection to nature, and opportunities to build community. As a community, scientists continue to create and grow connections with the larger public, sharing our exciting research, advancing conservation efforts, and educating future generations. In Chapter Four, I outline an opportunity to teach students about ecology and conservation through the lens of urban moths. I describe a project that uses low-cost, simple to make light traps that can be deployed in any habitat to collect moths at night. With this tool, students can ask questions about the diversity, distribution, and habitat use of moths by comparing the various places they collect from. Ubiquitous even in urban environments, this is an opportunity for students to engage with nature wherever their school may be.

Altogether, in an increasingly urbanized world, our understanding of these changing habitats becomes increasingly important as we try to mitigate the effects of anthropogenic change.