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**HAWKMOTH – FLOWER INTERACTIONS IN THE URBAN LANDSCAPE:
SPHINGIDAE ECOLOGY, WITH A FOCUS ON THE GENUS *HEMARIS***

By

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ABSTRACT OF THE DISSERTATION

Hawkmoth-Flower Interactions in the Urban Landscape: Sphingidae Ecology, With a

Focus on the Genus *Hemaris*

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In this dissertation I examined the ecology of moths of the family Sphingidae in New Jersey and elucidated some previously unknown aspects of their behavior as floral visitors. In Chapter 2, I investigated differences in moth abundance and diversity between urban and suburban habitat types. Suburban sites have higher moth abundance and diversity than urban sites. I compared nighttime light intensities across all sites to correlate increased nighttime light intensity with moth abundance and diversity. Urban sites had significantly higher nighttime light intensity, a factor that has been shown to negatively affect the behavior of moths. I analyzed moths' diets based on pollen grains swabbed from the moths' bodies. These data were inconclusive due to insufficient sample sizes. In Chapter 3, I examined similar questions regarding diurnal Sphingidae of the genus *Hemaris* and found that suburban sites had higher moth abundances and diversities than urban sites. I also examined the nectar diets and flight distances of *Hemaris* moth populations. Pollen grains from purple flowers were significantly more abundant on moths' bodies across all sites, suggesting a preference for this corolla color. Flight data indicate that *Hemaris* are vagrants and seldom return to the same patch to feed. In Chapter 4, I examined the foraging behavior of *Hemaris* compared to the *Bombus* spp.

that they mimic and their Lepidopteran relatives, *Papilio glaucus* and *Manduca rustica*. I observed foraging by *Hemaris* sp., *Bombus* sp., and *P. glaucus* at *Cirsium discolor*, a thistle native to New Jersey. *Hemaris* individuals visited significantly fewer *C. discolor* inflorescences and probed significantly fewer *C. discolor* florets than *Bombus* or *Papilio glaucus*. *Hemaris* do forage more similarly to the related *M. rustica* than to the other two foragers. Finally, in Chapter 5, I explored *Hemaris*'s visitation to the native *Cirsium discolor* and non-native *Centaurea* spp. During the co-blooming period of *C. discolor* and *Centaurea*, *Hemaris* visited significantly more *C. discolor* inflorescences. *Hemaris* revert to visiting *Centaurea* after *C. discolor*'s bloom period ends. *C. discolor* nectar has a significantly higher sugar concentration than *Centaurea* nectar so this difference may partially account for *Hemaris*' higher visitation to *C. discolor*.

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Chapter I

Hawkmoth-Flower Interactions in the Urban Landscape: Sphingidae Ecology, with a Focus on the Genus *Hemaris*

INTRODUCTION TO THE DISSERTATION

Overview

Plant-pollinator relationships are one of the most ecologically important classes of animal-plant interaction. Without pollinators, many plants could not set viable seed to maintain their populations. In the absence of plants to provide pollen, nectar and other rewards, many animal populations would decline, with associated declines in other species. Because of the functional importance of pollination, recent evidence indicating declines in native pollinator abundance and diversity has generated international concern (Mayer *et al.*, 2011, Menz *et al.*, 2010). Most pollinator research has focused on bees as they are the most numerous pollinators in many ecosystems and are particularly instrumental in the pollination of food crops (Winfree *et al.*, 2011 and references therein). However, a multitude of animal groups act as important pollinators in habitats and ecosystems all over the world. Though moths are not major pollinators of crops, diverse pollinator communities contribute to plant reproductive success and enhance functional diversity of ecosystems (Albrecht *et al.*, 2012).

Biodiversity is undoubtedly an asset worthy of conservation in both natural as well as human dominated systems such as urban areas. Human activities in urban areas have drastically decreased the biodiversity and changed the ecology of these systems (Kazemi *et al.*, 2011). Understanding the consequences of these declines has developed

into a central focus of ecological studies in recent years (Albrecht *et al.*, 2012) As of 2006, nearly half of the world's human population lives in urban areas and these numbers are expected to increase, particularly in developed nations (United Nations, 2008). As urbanization increases in today's world, it becomes important for ecologists to assess ecosystem function within the context of the rapid changes occurring in the world's natural areas. Populations of organisms must be able to respond quickly and efficiently to urban stressors such as fragmentation in order to survive as a species and maintain biodiversity.

Urban areas provide a perfect opportunity to test ideas about the changing ecology of fragmented populations (McDonnell *et al.*, 1997). Urbanization has been positively correlated with increased ecological disturbance (Pyke and Knick, 2005) as well as increased habitat fragmentation (McDonnell *et al.*, 1997). Suitable habitats in urban and suburban landscapes generally exist as patches within a matrix of developed areas. This heterogeneous quality presents several problems for wildlife including reduced ability to disperse between patches resulting in detrimental genetic effects such as bottlenecks and decreased local diversity (Hilty *et al.*, 2006). Plant-pollinator interactions add an additional level of complexity to this problem since pollinators provide pollen dispersal services and reproductive assurance for plants. Any fragmentation affecting pollinators affects plant populations as well.

The science of restoration ecology develops and tests methods and techniques for recovering ecosystems that have been degraded, damaged, or destroyed (Society for Ecological Restoration International, 2004). Restoration ecology that focuses on urban areas is becoming an increasing concern as urban areas increase worldwide. Urban

restoration ecology aims to restore suitable, functioning habitats within the surrounding urban matrix. Habitat patches generally exist as fragments within a matrix of developed areas. This spatial heterogeneity presents several problems for pollinator and plant populations alike, including reduced dispersal ability among patches resulting in detrimental demographic and genetic effects (Hilty *et al.*, 2006).

In this dissertation I examine the role of sphingid moths as pollinators in the urban areas of New Jersey and elucidate some previously unknown aspects of their behavior as pollinators. The study of moth-plant interactions deserves attention for at least 4 reasons: (1) Moths are important pollinators in many ecosystems, notably the southwestern United States (Bawa *et al.*, 1985, Clinebell *et al.*, 2004, Ramirez 2004). (2) Plants that interact with diurnal pollinators may require nocturnal pollination to achieve maximum reproductive success (Dar *et al.*, 2006). (3) Moths, both as larvae and adults are an important food resource for birds (Robinson and Holmes, 1982), bats (Svensson *et al.*, 1999) shrews (Buckner 1969) and even bears (White *et al.*, 1998). If moths are not supported with nectar and larval food resources, this reduces an important food resource in the overall food network. (4) Moths are indicators of environmental change (Luff and Woiwod, 1995) and evidence from the United States (Wagner, 2012) and United Kingdom (Thomas 2005, Conrad *et al.*, 2006) suggests that moth populations are in decline.

STUDY ORGANISM

The Sphingidae is a family of moths that are found on every continent except Antarctica and were originally classified by Linnaeus who placed them all in the genus *Sphinx*

(Tuttle, 2007). Today, systematists recognize 3 subfamilies, approximately 200 genera and 1400 species of Sphingidae worldwide (Kawahara *et al.*, 2009; Kitching and Cadiou, 2000). Of these, all 3 subfamilies, and 38 species in 28 genera are known to occur in New Jersey with a small number of other species occasionally encountered as vagrants (Tuttle, 2007) (See Table 1).

Sphingids have been recorded as flower visitors in many habitats in the United States. Most species of adult hawkmoths feed on nectar, but are still effective pollinators of the plants they visit (Alarcon *et al.*, 2008). The vast majority of hawkmoths are active at night and are generally restricted to visiting flowers that produce large amounts of nectar (Haber and Frankie, 1989, Silva and Sazima, 1995) to supply energy for their adult reproductive phase. Hawkmoths can carry large pollen loads and are able to fly long distances. In contrast to the behavior of pollinators such as bees and hummingbirds, there is no evidence that hawkmoths forage in a home territory. This behavior, in addition to the potential for long flight distances (Linhart and Mendenhall, 1977), favors the outcrossing of widely spaced plant populations (Haber and Frankie, 1989), which has positive (increased genetic variation) as well as negative (outbreeding depression) implications for plant population genetics.

While the majority of Sphingidae are nocturnal, nineteen diurnal species exist worldwide. Three of these species – *Hemaris thysbe*, *Hemaris diffinis* and *Hemaris gracilis* occur in Eastern North America. These species are commonly known as clearwings. *Hemaris diffinis* closely mimics bumblebees, while *H. thysbe* and *H. gracilis* are hummingbird mimics (Kitching and Cadiou, 2000; Tuttle, 2007). Although they are

relatively common organisms, little is known of the behavior or function of *Hemaris* moths as pollinators.

Morphology

Adult sphingids are generally large moths (up to 200 mm wingspan) with prominent heads and eyes. The probosces of these moths are well developed and in some cases (most famously in *Xanthopan morganii praedicta*) are exceptionally long indicating that these moths sip nectar and pollinate flowers with long corolla tubes. However in some members of the Smerinthinae subfamily, the proboscis reduced to a length that is too short for nectaring at flowers although these moths may be able to sip water from leaves or puddles (Kitching and Cadiou, 2000; Tuttle, 2007).

One of the most salient characters of sphingids is their long narrow forewings which give them a distinctive “chevron” shape while at rest. Due to these narrow forewings, the spindle shaped abdomen and portions of the hindwings are visible when the wings are folded which is distinctive from most other moth families (Kitching and Cadiou, 2000; Tuttle, 2007).

Life history/ecology

Sphingids undergo complete metamorphosis, generally laying single eggs on appropriate larval host plants. Eggs hatch into first instar larvae in approximately one week. Larvae are characterized by the presence of a dorsal horn, giving them the common name “hornworms.” The larvae use camouflage as their main line of defense. Most are a leafy green color; however, some Macroglossinae larvae have evolved snakelike eyespots.

Many sphingid larvae rest with prolegs and claspers securing them to a twig while the rest of the body is lifted into a sphinx-like position. This distinctive posture gave rise to the common name Sphinx moth (Kitching and Cadiou, 2000; Tuttle, 2007).

Pupation occurs underground or in leaf litter. In the latter case, the moth may produce a silk cocoon. This stage may be as short as two weeks in multivoltine species. In temperate areas of the world, sphingids generally overwinter in this life history stage (Kitching and Cadiou, 2000; Tuttle, 2007).

Due to their long probosces, sphingids are able to drink both flower nectar and water, enabling them to live longer than most other species of moths that rely on stored fat reserves (Kitching and Cadiou, 2000; Tuttle, 2007). The need for sustenance also means that sphingids must possess the capacity to locate and remember the location of nectar and water resources.

Since they are long-lived, females are able to be choosy about males with which to mate, and males must “impress” females with courtship rituals involving pheromones and stridulation. Females also have the advantage of being selective about host plant selection and oviposition, and can exploit highly nutritious plants even though they may occur at low densities. Host plants are generally vines, shrubs or trees. Since sphingids can replenish their energy supplies by feeding, a female can continue to produce eggs throughout her lifespan (Kitching and Cadiou, 2000; Tuttle, 2007).

Once eggs are laid, larvae hatch out in approximately one week. Development is rapid due in part to the high nutritional value of sphingid host plants. Most Sphingidae are relatively specialized in host plant choice, feeding on a single genus or family (Kitching and Cadiou, 2000; Tuttle, 2007).

The suites of floral characteristics that attract certain pollinator types, referred to as pollination syndromes, have been well-studied. Lepidoptera as an order are attracted by certain floral morphologies, and the major groups of Lepidoptera – butterflies and moths, are each attracted to their own further-defined sets of floral morphologies. The majority of Lepidoptera share the characteristic of having a proboscis with which to drink nectar and proboscis length limits plants from which lepidopterans are able to take nectar. Most lepidopterans require dilute nectar because of their elongate probosces (Willmer, 2011). Hawkmoths are able to vary their nectar intake rate and achieve peak intake at 34% sucrose (Josens and Farina, 2001).

Butterfly- and moth-adapted flowers share some similar characteristics. Long corolla tubes (up to 15mm) with small apertures accommodate the long probosces of lepidopterans. Flowers such as *Asclepias syriaca*, *Lonicera*, *Saponaria* and *Silene* are commonly visited by butterflies during daytime hours and moths at night. Butterfly-adapted, or psychophilous, flowers are typically grouped into a flat inflorescence to provide a landing pad on which butterflies perch while feeding. They display exerted stamens and styles to deposit pollen on the head of the butterfly. Butterflies have acute color vision and are attracted to a wide array of colors, so the petals of psychophilous flowers are generally deep pink, blue, orange or red and often have a yellow center. Psychophilous flowers have mild, sweet scents and dilute nectar (Willmer, 2011).

The syndrome of moth pollination is referred to as phalaenophily and flowers that are specifically pollinated by hawkmoths are termed sphingophilous (Haber and Frankie, 1989). Sphingophilous flowers are generally white or light in color making them highly visible at night, and have a strong, sweet or musky scent (Raguso *et al.* 2003). Moths may

also visit pale pink or yellow flowers at dusk, but visit only white or cream colored flowers as night becomes darker. Sphingophilous flowers are commonly radially symmetrical, with large trumpet shaped flowers to aid in night-time visibility. *Datura*, *Convolvulus*, *Lonicera*, *Nicotiana*, *Nerium*, *Mirabilis*, and *Plumeria* are all “typical” sphingophilous flowers (Willmer, 2011). Common Northeast sphingophilous wildflowers include *Oenothera biennis*, *Convolvulus* sp., *Lonicera japonica*, *Saponaria officinalis*, *Silene vulgaris*, and garden plants such as *Cleome hassleriana*, *Petunia x hybrida* and *Nicotiana* sp. Most of these species are visited by diurnal pollinators during the day as well as moths at night. Nighttime pollinator visitation in added to diurnal visitation may have an additive positive effect on the reproductive biology of these plant species.

Moths of the genus Hemaris

Chapters 3, 4 and 5 of this dissertation focus on one genus in the Sphingidae, *Hemaris*, which are diurnal moths. Nineteen *Hemaris* species exist worldwide and three of these – *Hemaris thysbe*, *H. diffinis* and *H. gracilis* occur in Eastern North America. These species are commonly known as clearwings. *Hemaris diffinis* closely mimics bumblebees, while *H. thysbe* and *H. gracilis* are hummingbird mimics (Kitching and Cadiou, 2000; Tuttle, 2007). Although they are relatively common organisms, little is known of the behavior or function of *Hemaris* moths as pollinators.

As pollinators, the nocturnal Sphingidae tend to visit flowers with certain morphological characteristics (Grant, 1983, Raguso *et al.*, 2003). These flowers are generally white or light in color making them highly visible at night, have long corolla tubes that can accommodate the long probosces of the moths and have a strong, sweet or

musky scent to attract pollinators in the dark. This suite of floral characters is referred to specifically as sphingophily (Haber and Frankie 1989). Nocturnal sphingids are restricted in their nectar diet to flowers with these characteristics. *Hemaris* have many more floral resources open and available to them due to their diurnal lifestyle. They are not restricted to flowers that are detectable and open at night and in general, the vast majority of flowers bloom during the day, so *Hemaris*, in theory should be able to utilize many more floral resources than their nocturnal counterparts. However, it is unknown whether *Hemaris* retain the diet preferences of nocturnal sphingids since their nectar diets have remained largely unstudied.

Little is known about flight distance of sphingid moths in general and even less is known about the flight distances of *Hemaris*. Records for nocturnal Sphingidae from a 1977 study by Linhart and Mendenhall were up to 400 m and some estimate that moths may fly up to 10 km between floral resources in search of nectar (Janzen, 1984).

This dissertation aims to answer some fundamental, previously unexplored aspects of Sphingidae, biology, pollination, and foraging behavior in northeastern North America. I also aim to address some of the limits to restoring target communities and determine whether plant-pollinator interactions are a “broken link” between degraded, pre-restoration habitats and restored, fully functioning communities. To restore ecosystem function we must not only focus on general interactions but on all types of interactions. Plant-pollinator interactions are essential to conservation and restoration practice since they represent a useful indicator for determining whether a restoration project has indeed become a functioning ecosystem. Sphingid pollination interactions represent a higher level of complexity than generalized ones. Very little plant pollinator

research has examined hawkmoth-plant interactions in the eastern United States (ex. Grant, 1983) and even less has been done in fragmented urban landscapes, which have become a major habitat type worldwide.

OUTLINE OF DISSERTATION

My dissertation focuses on mutualistic interactions in urban habitat fragments, with an emphasis on specialized plant-pollinator interactions. I first examine these interactions by quantifying hawkmoth abundance and pollination in urban and suburban habitat fragments around the New Jersey - New York metropolitan region. I then focus on an in-depth study of the behavior and pollination of one Sphingidae genus, *Hemaris*, and its role in the urban ecosystem of New Jersey.

Objectives and Questions

In Chapter 2, I investigate nocturnal sphingids in urban and suburban habitats, testing whether there is a difference in population abundance and diversity between urban and suburban systems in New Jersey and New York.

In Chapter 3, I examine similar questions regarding diurnal Sphingidae of the genus *Hemaris*. For this chapter I also include experiments on *Hemaris* flight range and nectar diets.

In Chapter 4, I delve into the foraging behavior of *Hemaris* as compared to other pollinators in the system, in particular the *Bombus* spp. that they mimic and their Lepidopteran relatives, *Papilio glaucus* and *Manduca rustica*.

Finally, Chapter 5 explores *Hemaris*'s preferences for a native Asteraceae, *Cirsium discolor*, over the non-native *Centaurea* spp. present at Hutcheson Memorial Forest in Somerset, NJ.

Study Sites

I conducted the field research for this dissertation at five sites (see Map 1):

Duke Farms, Hillsborough, New Jersey: Duke Farms is a 1080-ha former estate that is being restored to native forest and meadow areas. The site features patches of floral meadow resources within a mature upland hardwood forest matrix.

GPS coordinates: 40°33'18"N, 74°36'59"W

Hutcheson Memorial Forest, Somerset, New Jersey (HMF): HMF is a 226-ha tract of property owned by Rutgers University that contains some of the only remaining old growth forest on the east coast. The site features patches of floral meadow resources within a mature upland hardwood forest matrix.

GPS coordinates: 40°30'04"N, 73°33'34"W

Fresh Kills Landfill, Staten Island, New York: Fresh Kills Landfill is an 880-ha capped landfill on Staten Island, New York. The landfill features mainly turfgrass with a few weedy annual and perennial plants present and small portions of the landfill have been restored to native upland forest.

GPS coordinates: 40°33'24"N, 74°10'25"W

Meadowlands Harrier Marsh Meadow, Lyndhurst, New Jersey: Harrier Marsh Meadow is a 28-ha marsh restoration site within the larger 3360-ha New Jersey Meadowlands

ecosystem. Located in Bergen County New Jersey, Harrier Meadow features a mix of wetlands, hardwood forest and meadow plant species.

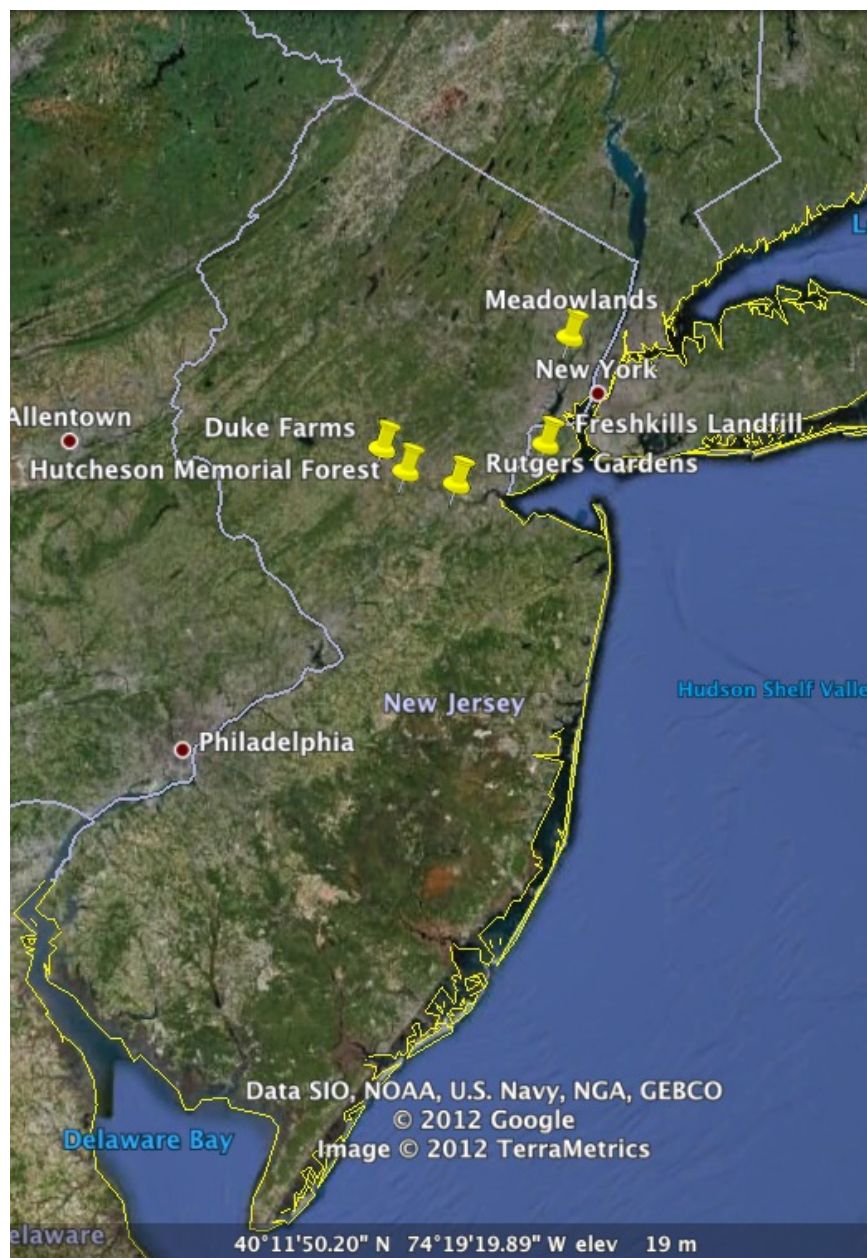
GPS coordinates: 40°47'04"N, 74°06'05"W

Rutgers Gardens, East Brunswick, New Jersey: Rutgers Gardens consists of a series of horticultural gardens spread over approximately 60 hectares. It is part of Rutgers University and is surrounded by the city of East Brunswick in Middlesex County, New Jersey.

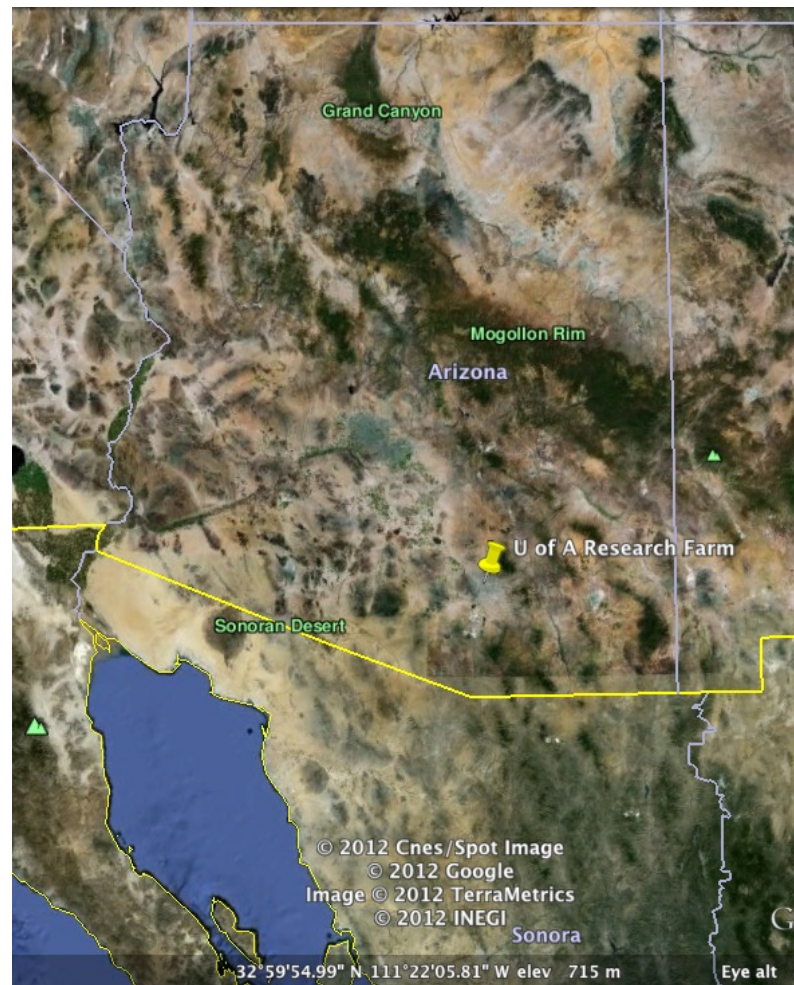
GPS coordinates: 40°26'25"N, 74°26'24"W

Arizona State University Experimental Farm, Tucson Arizona: The experimental farm is located on the northwest outskirts of Tucson, Arizona (see Map 2). This small, approximately 200-ha research farm is bordered on the south side by the city of Tucson and on the north side by the foothills of the Catalina Mountains.

GPS Coordinates: 32°16'54"N, 110°56'51"W



Map 1: NJ and NY Field Sites



Map 2: University of Arizona Research Farm

Table 1: List of the Sphingidae of New Jersey (from Kitching and Cadiou 2000)

Subfamily	Genus	Species
Macroglossinae	<i>Amphion</i>	<i>floridensis</i>
Macroglossinae	<i>Darapsa</i>	<i>choerilus</i>
Macroglossinae	<i>Darapsa</i>	<i>myron</i>
Macroglossinae	<i>Darapsa</i>	<i>versicolor</i>
Macroglossinae	<i>Deidamia</i>	<i>inscriptum</i>
Macroglossinae	<i>Eumorpha</i>	<i>achemon</i>
Macroglossinae	<i>Eumorpha</i>	<i>pandorus</i>
Macroglossinae	<i>Hemaris</i>	<i>diffinis</i>
Macroglossinae	<i>Hemaris</i>	<i>gracilis</i>
Macroglossinae	<i>Hemaris</i>	<i>thysbe</i>
Macroglossinae	<i>Hyles</i>	<i>gallii</i>
Macroglossinae	<i>Hyles</i>	<i>lineata</i>
Macroglossinae	<i>Sphecodina</i>	<i>abbottii</i>
Macroglossinae	<i>Xylophanes</i>	<i>tersa</i>
Smerinthinae	<i>Amorpha</i>	<i>juglandis</i>
Smerinthinae	<i>Pachysphinx</i>	<i>modesta</i>
Smerinthinae	<i>Paonias</i>	<i>astylus</i>
Smerinthinae	<i>Paonias</i>	<i>exaecatus</i>
Smerinthinae	<i>Paonias</i>	<i>myops</i>
Smerinthinae	<i>Smerinthus</i>	<i>jamaciensis</i>
Sphinginae	<i>Agrius</i>	<i>cingulata</i>
Sphinginae	<i>Ceratomia</i>	<i>amyntor</i>
Sphinginae	<i>Ceratomia</i>	<i>catalpae</i>
Sphinginae	<i>Ceratomia</i>	<i>undulosa</i>
Sphinginae	<i>Dolba</i>	<i>hyloeus</i>
Sphinginae	<i>Lapara</i>	<i>bombycoides</i>
Sphinginae	<i>Lapara</i>	<i>coniferarum</i>
Sphinginae	<i>Lintneria</i>	<i>eremitus</i>
Sphinginae	<i>Manduca</i>	<i>jasminearum</i>
Sphinginae	<i>Manduca</i>	<i>quinquemaculatus</i>
Sphinginae	<i>Manduca</i>	<i>sexta</i>
Sphinginae	<i>Paratrea</i>	<i>plebeja</i>
Sphinginae	<i>Sphinx</i>	<i>chersis</i>
Sphinginae	<i>Sphinx</i>	<i>drupiferarum</i>
Sphinginae	<i>Sphinx</i>	<i>franckii</i>
Sphinginae	<i>Sphinx</i>	<i>gordius</i>
Sphinginae	<i>Sphinx</i>	<i>kalmiae</i>
Sphinginae	<i>Sphinx</i>	<i>luscitiosa</i>

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Chapter II

ABUNDANCE AND DIVERSITY OF NOCTURNAL SPHINGIDAE IN FRAGMENTED LANDSCAPES

ABSTRACT

Moths of the family Sphingidae are important pollinators in many ecosystems across the United States; however their abundance, diversity and contributions to pollination have not been well studied in the Northeast. We compared abundance and diversity of sphingid moth populations between urban and suburban sites in the New Jersey – New York metropolitan region and found significant differences in these parameters, with suburban sites having both higher moth abundances and diversities than urban sites. We compared nighttime light intensities across all sites to correlate increased nighttime light intensity with moth abundance and diversity. Urban sites had significantly higher nighttime light intensity, a factor that has been shown to negatively affect the behavior of nocturnal organisms. We analyzed moths' pollen diets based on pollen grains swabbed from the moths' bodies to examine the contribution of Sphingidae to pollination in these habitat types. These data were inconclusive due to insufficient sample sizes.

INTRODUCTION

Plant-pollinator relationships are arguably the most ecologically important class of animal-plant interactions. Without pollinators, many plants could not set viable seed to maintain their populations. In the absence of plants to provide pollen, nectar and other rewards, many animal populations would decline, with consequent declines in other species. Because of the functional importance of pollination, recent evidence indicating declines in native pollinator abundance and diversity has generated international concern (Mayer *et al.*, 2011, Menz *et al.*, 2010). Most pollinator research has focused on bees as they are the most numerous pollinators in many ecosystems and are particularly instrumental in the pollination of food crops (Winfree *et al.*, 2011 and references therein). However, many animal groups act as important pollinators in habitats and ecosystems all over the world.

Biodiversity is undoubtedly a critical asset to conserve in both natural as well as human dominated systems such as urban areas. Human activities in urban areas have drastically decreased the biodiversity and changed the ecology of these systems (Kazemi *et al.*, 2011). As of 2006, nearly half of the world's human population lives in urban areas and these numbers are expected to increase, particularly in developed nations (United Nations, 2008). As urbanization increases in today's world, it becomes increasingly important for ecologists to assess ecosystem function within the context of the rapid changes occurring in the world's natural areas. Populations of organisms must be able to respond quickly and efficiently to urban stressors such as fragmentation to survive as a species and maintain biodiversity.

Urban areas provide a perfect opportunity to test ideas about the changing ecology of fragmented populations (Grimm *et al.*, 2008, McDonnell *et al.*, 1997). The degree of urbanization in a habitat has been positively correlated with increased ecological disturbance (Pyke and Knick, 2005) as well as increased habitat fragmentation (McDonnell *et al.*, 1997). Suitable habitats in urban and suburban landscapes generally exist as patches within a matrix of developed areas. This heterogeneous quality presents several problems for wildlife including reduced ability to disperse between patches, resulting in detrimental genetic effects such as bottlenecks and decreased local diversity (Hilty *et al.*, 2006). Plant-pollinator interactions add an additional level of complexity to this problem since pollinators provide pollen dispersal services and reproductive assurance for plants. Any fragmentation affecting pollinators affects plant populations as well.

The study of moth-plant interactions deserves attention for at least 4 reasons: Moths are important pollinators in many ecosystems, notably the southwestern United States (Bawa *et al.*, 1985, Clinebell *et al.*, 2004, Ramirez 2004). Plants that interact with diurnal pollinators may require nocturnal pollination to achieve maximum reproductive success (Dar *et al.*, 2006). Moths, both as larvae and adults are an important food resource for birds (Robinson and Holmes, 1982), bats (Svensson *et al.*, 1999) shrews (Buckner, 1969) and even bears (White *et al.*, 1998). If moths are not supported with nectar and larval food resources, this reduces an important food resource in the overall food network. Moths are indicators of environmental change (Luff and Woiwod, 1995) and evidence from the US and UK suggests that moth populations are in decline (Thomas, 2005, Conrad *et al.*, 2006, Wagner, 2012).

Study Organism

This chapter focuses on the abundance and diversity of nocturnal moths of the family Sphingidae. For a description of the organisms, please see Chapter 1 of this dissertation (Tartaglia, 2013).

Questions

In this study, I investigated nocturnal sphingids in urban and suburban habitats, testing whether there is a difference in population abundance and diversity between urban and suburban systems in New Jersey and New York. I aimed to answer the following questions. (1) Are there differences in sphingid abundance and diversity between the urban and suburban habitats sampled in this study? (2) Do the nectar diets of moths change between urban and suburban habitats and if so, do invasive species, generally more abundant in unrestored fragments “subsidize” moth populations in these areas?

METHODS

Field Sites

Two sites, Duke Farms and Hutcheson Memorial Forest (HMF) are in Somerset County, New Jersey and served as my suburban systems. Duke Farms is a 1080-ha former estate that is being restored to native forest and meadow areas. HMF is a 226-ha tract of property owned by Rutgers University that contains some of the only remaining old growth forest on the east coast. Both sites feature patches of floral meadow resources within a mature upland hardwood forest matrix.

Fresh Kills Landfill and the NJ Meadowlands Harrier Meadow represented my urban sites. Fresh Kills Landfill is an 880-ha capped landfill in Staten Island, New York. The landfill features mainly turf grass with a few weedy annual and perennial plants present and small portions of the landfill have been restored to native upland forest. Harrier Meadow is a 28-ha marsh restoration site within the larger 3360-ha New Jersey Meadowlands ecosystem. Located in Bergen County New Jersey, Harrier Meadow features a mix of wetlands, hardwood forest and meadow plant species.

Site Classification

To establish a criteria for determining whether a site should be considered urban or suburban, individual sites were evaluated for local patterns of land-use using four, 2.5 km line transects running in all cardinal directions from the center of each site. I chose 2.5 km as my scale due to distances that hawkmoths have been known to fly. For this study, I considered sites with greater than 50% developed land as “urban”. Sites with less than 50% developed land I considered suburban, rather than “rural” since they still had at least some degree of developed land within 2.5 km.

Using Google Earth, we obtained an aerial view of each site and drew and four transects using the straight-line ruler from the Google Earth toolbar (Google, 2012). We classified landscape types intersected by each line as forest, field, water, or developed area. We measured the distance each line ran through a specific landscape type and converted this distance a percent value then averaged percent values for each landscape type from all four lines to produce landscape percent values for each site (methods from Duchak and Holzapfel, 2011). Since only forested and field areas – presuming they are

comprised of nectar species rather than turf grass – constitute suitable sphingid habitat, we classified landscape types into “suitable” for moths and “unsuitable” for moths. Forested areas and meadow-type fields represented “suitable” habitat and developed areas, turf lawns and wetlands represented “unsuitable” moth habitat (Table 1).

The urban sites, Freshkills Landfill and Meadowlands Harrier Marsh have a higher percentage of unsuitable moth habitat compared to the suburban sites. Freshkills has 12% forest, 39.2 % field, and 48.8% developed area. Since most of the “field” area at the landfill is mowed turf grass lawn, I classified field as unsuitable moth habitat for this site. As such, Freshkills has 12% suitable moth habitat and 88% unsuitable moth habitat. The other urban site, the Meadowlands had 4.5% forest, 21.9% field, 35.2% water and 38.4% developed area. Since water contains no resources beneficial to moths, we considered these areas unsuitable habitat. The Meadowlands has 26.4% suitable and 73.6% unsuitable moth habitat.

Suburban site Duke Farms has 40.8% forest, 30.9% field, and 28.3% developed area. Since fields at Duke consist of restored wildflower meadows, in this case it was classified as suitable moth habitat, so Duke consists of 71.7% suitable habitat and 28.3% unsuitable habitat. HMF had 31.4 % forest, 59.6% field, and 9% developed area. Again, fields at this site were classified as suitable habitat natural wildflower meadows, so HMF has 91% suitable habitat and 9% unsuitable habitat.

Abundance and Diversity

It is well-established that insects, particularly moths, are attracted to lights (Linhart and Mendenhall, 1977, Eisenbeis, 2006, Frank, 2006). To assess abundance and diversity of

moths in urban and non-urban areas, I employed a collecting set up consisting of a 175-watt mercury vapor blacklight and a large reflective collecting sheet. I collected moths from dusk until approximately 3am between June and September of 2009 at four field sites.

I rotated sampling at each site on a weekly basis, resulting in 270 total hours of black light sampling. When a Sphingid moth arrived at the collecting sheet, it was collected and stored for later analysis.

Diet Analysis

A second aspect of this study was an analysis of the diets of the Sphingidae collected in order to determine whether invasive species comprised a significant portion of the diet of Sphingidae in urban systems. To accomplish this, the probosces and heads of species of nectar feeding Sphingidae collected during nighttime field sampling were swabbed with a small cube of fuchsin-infused gelatin thus collecting and staining any pollen present on the moth (Kearns and Inouye, 1993). The gelatin cube was subsequently melted onto a slide so pollen could be observed under a microscope.

Light intensity surveys

The final aspect of this study was an analysis of the nighttime light intensity at each of the four study sites. We took light meter readings at midnight for 10 nights at each field site in order to determine whether light intensity was significantly higher at the urban sites.

RESULTS

Abundance and diversity

Throughout the course of the summer 2009 field season, 38 Sphingid moths representing 6 of the 38 species known to be found in central New Jersey were collected. Of these 38 moths, 8 individuals representing 2 species were species that are known nectar-feeders. All 38 moths were collected at the non-urban sites with 22 individuals collected at HMF and 16 individuals collected at Duke Farms (See Table 2). No Sphingidae were collected at the urban sites, Harrier Meadow and Fresh Kills Landfill. These data represent a significant difference ($p < 0.05$) in the abundances of moths found at urban vs. non-urban sites. Moth abundance between Duke Farms and HMF did not significantly differ.

We compared community diversity using the Simpson Index. Fresh Kills and Harrier Meadow had diversity scores of zero, owing to the fact that we found no moths at either of these sites. DUK's diversity score was 0.62 and HMF's was 0.77. Across both suburban sites, the total diversity score was 0.81. When compared across communities, we found no significant difference in diversity between the two suburban sites.

Diet analysis

Since only 8 nectar-feeding individuals were collected, the results of the diet analysis are fairly inconclusive. From these 8 moths, I obtained 27 grains of pollen, 24 of which were from *Lonicera*. Since *Lonicera japonica* was the only species in the genus present at my sites, this suggests a trend toward an invasive species "subsidy" of moth populations, even at suburban sites

Light intensity

Across the 4 study sites, Harrier Meadow and Fresh Kills Landfill sites had significantly higher nighttime light intensity ($p < 0.01$) than Duke Farms or HMF (see Figure 1). The two urban sites did not significantly differ from one another, and the two suburban sites did not significantly differ from one another.

DISCUSSION

“Urban-ness” of habitats seems to play a role in sphingid abundance and diversity in New Jersey – New York metropolitan area. There are strong abundance similarities between the two urban sites and a lesser but not significantly different degree of similarity between the suburban sites. The small differences between the suburban sites were due to differences in relative abundance of different species found, rather than intrinsic differences between the habitats themselves since both suburban sites were similar with respect to percentage of suitable moth habitat available at sites.

Temporal population variability across seasons and years is a known phenomenon for a variety of insect species (Pimental, 1961, Gaston and Lawton, 1988, Boggs and Inouye, 2012) and moths are no exception (Holyoak *et al.*, 1997). The relatively low abundance and diversity of sphingids that I encountered could have been linked to the rainy, cool weather of that particular year, so additional field data would be necessary to make more generalized statements regarding moth abundance and diversity, particularly in urban areas. Anecdotal reports from sources such as the Lepidopterists’ Society’s seasonal summary data submissions do suggest an overall decline in sphingid populations and declines have been reported for other Northeast moth taxa (Wagner, 2012)

Different species relative abundances could be due to differences in the life histories of the most abundant moths at each site. The most abundant sphingid moth at HMF was *Paonias myops* while the most abundant sphingid at Duke was *Darapsa myron*. These species exhibit different life history characteristics in that *P. myops* is a non-nectar feeding moth as an adult while *D. myron* feeds on nectar (Tuttle, 2007). Since sites were assessed for adult nectar plants rather than presence of appropriate larval host plants, the differences may be due to the fact that the species require different larval host plants that may or not have been present at both Duke and HMF.

One of the major abiotic differences between the urban and suburban sites was the light intensity. There is growing concern over the ecological consequences of increased distribution, density and intensity of nighttime lighting in urban areas (Gaston *et al.*, 2012). Light pollution is increasing rapidly as development increases and is increasing in intensity as already-urbanized areas increase in density (Holker *et al.*, 2010). Wide-ranging ecological impacts of increased night-time light have been documented, including effects on movement, communication, foraging behavior, reproduction and mortality (Gaston *et al.*, 2012).

A few studies have been conducted indicating that moths are affected by high light levels such as those found in very urban areas. These studies indicate that moths may indeed avoid heavily light polluted areas. Fresh Kills Landfill and Harrier Meadow had significantly higher light intensity as compared to Duke Farms and HMF (though there were no significant differences in light intensity between the two urban sites and the two suburban sites).

Daily and Ehrlich (1996), for example performed population studies on geographically isolated habitats and found results suggesting that increased artificial light may affect moth species survival in highly fragmented habitats. However, light pollution typically exists in conjunction with several other environmental disturbances characteristic of urban areas so it is difficult to assess whether light alone affects moth abundance (Frank, 2006). My study suggests that some trend exists linking moth abundance to light levels in the field sites sampled.

Increased artificial light may be harmful to moths for a variety of reasons. Moths that fly to lights often land and remain inactive for the rest of the night. These hours of inactivity cost moths lost foraging time (Janzen, 1984). Moth vision is also affected by lighting, and a moth flying away from an intensely lit area to a darker area may be rendered functionally blind until their eyes re-adjust. Moths have compound eyes that adjust to light through the movement of pigments in the eye (Frank, 2006). After exposure to bright lighting, it may take up to 30 minutes for moth eyes to re-adjust to dark conditions (Bernhard and Ottoson, 1960). Flight to artificial light may also interfere with or override reproductive behaviors such as courtship (Delisle *et al.*, 1998, Hoffman *et al.*, 1966) and oviposition (Dirks, 1937).

The source of artificial light in fragmented habitats comes from the matrix surrounding habitat patches, which may disrupt moth dispersal and colonization and present serious problems for moths. Light can act as a barrier to disrupt the movement of moths between patches of suitable habitat (Frank, 2006) reducing immigration of moths from areas of higher diversity in less fragmented areas to low diversity fragments.

To restore ecosystem function we must not only focus on general interactions but on all types of interactions. Plant-pollinator interactions are essential to conservation and restoration practice since they represent a useful indicator for determining whether a restoration project has indeed become a functioning ecosystem. Hawkmoth pollination interactions represent a higher level of complexity than generalized ones. Very little plant pollinator research has examined hawkmoth-plant interactions in the eastern United States and even less has been done in fragmented urban landscapes, which have become a major habitat type worldwide.

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Site	% Forest	% Field	% Water	% Developed	% Suitable habitat	% Unsuitable habitat
DUK	40.8	30.9	0	28.3	71.7	28.3
HMF	31.4	59.6	0	9.0	91.0	9.0
FKL	12.0	39.2	0	48.8	12.0	88.0
MDL	4.5	21.9	35.2	38.4	26.4	73.6

Table 1: Site landscape classifications and percentages of suitable and unsuitable habitat at each site. DUK = Duke Farms, HMF = Hutcheson Memorial Forest, FKL= Freshkills Landfill, MDL = Meadowlands

Species	# Individuals	
	HMF	DUKE
<i>Darapsa choerilus</i>	1	0
<i>Darapsa myron</i>	8	3
<i>Eumorphia pandorus</i>	1	1
<i>Manduca jasminearum</i>	4	2
<i>Paonias exaecata</i>	1	9
<i>Paonias myops</i>	6	0

Table 2: Number of individuals of Sphingidae species collected at HMF and Duke Farms

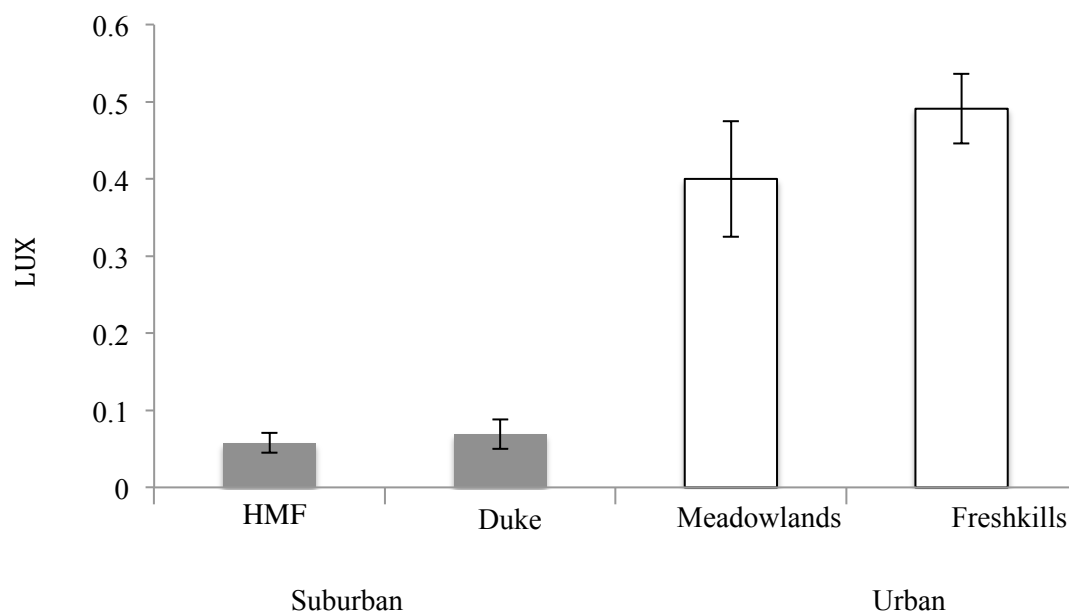


Figure 1: Nighttime light intensity was significantly higher at urban sites ($p < 0.01$)

CHAPTER III

ABUNDANCE, DIVERSITY, NECTAR DIETS AND FLIGHT RANGE OF

***HEMARIS* (SPHINGIDAE) IN FRAGMENTED LANDSCAPES**

ABSTRACT

Hemaris is a genus of Sphingidae, a family of moths that are important pollinators in many ecosystems across the United States. Their abundance, diversity and contributions to pollination have not been well studied in the northeastern United States. We compared abundance and diversity of *Hemaris* between urban and suburban sites in the New Jersey and found differences in these parameters, with suburban sites having both higher moth abundances and diversities than urban sites. I also examined the pollen diets and flight distances of *Hemaris* moth populations. Abundances were higher in suburban sites compared to urban sites, which correlated with the increased amount of suitable moth habitat at suburban sites. Diversity scores did not differ between urban and suburban sites. Pollen grains from purple flowers were significantly more abundant on moths' bodies across all sites, suggesting a preference for this corolla color. Flight distance data indicate that *Hemaris* are vagrants and seldom return to the same patch to feed.

INTRODUCTION

Plant-pollinator relationships are an ecologically critical class of animal-plant interactions. Without pollinators, many plants could not set viable seed to maintain their populations. In the absence of plants to provide pollen, nectar and other rewards, many animal populations would decline, with consequent declines in plant species. Because of the functional importance of pollination, recent evidence indicating declines in native pollinator abundance and diversity has generated international concern. Most pollinator research has focused on bees as they are the most numerous pollinators in many ecosystems and are particularly instrumental in the pollination of food crops (Winfree *et al.*, 2011 and references therein). However, many animal groups act as important pollinators in habitats and ecosystems all over the world.

Human activities have drastically decreased the biodiversity and changed the ecology of urban areas (Kazemi *et al.*, 2011). As of 2006, nearly half of the world's human population lived in urban areas and these numbers are increasing, particularly in developed nations (United Nations, 2008). As urbanization increases in today's world, it becomes important for ecologists to assess ecosystem function within the context of the rapid changes occurring in the world's natural areas. Populations of organisms must be able to respond quickly and efficiently to urban stressors such as fragmentation in order to survive as a species and maintain biodiversity.

Urban areas provide a perfect opportunity to test ideas about the changing ecology of fragmented populations (McDonnell *et al.*, 1997). Urbanization has been positively correlated with increased ecological disturbance (Pyke and Knick, 2005) as well as

increased habitat fragmentation (McDonnell *et al.*, 1997). Suitable habitats in urban and suburban landscapes generally exist as patches within a matrix of developed areas. This heterogeneous quality presents several problems for wildlife including reduced ability to disperse between patches resulting in detrimental genetic effects such as bottlenecks and decreased local diversity (Hilty *et al.*, 2006). Plant-pollinator interactions add an additional level of complexity to this problem since pollinators provide pollen dispersal services and reproductive assurance for plants. Any fragmentation affecting pollinators affects plant populations in turn. Habitat patches generally exist as fragments within a matrix of developed areas. This spatial heterogeneity presents several problems for pollinator and plant populations alike, including reduced dispersal ability among patches resulting in detrimental demographic and genetic effects (Hilty *et al.*, 2006).

The study of moth-plant interactions deserves attention for several reasons. Moths are important pollinators in many ecosystems, notably the southwestern United States (Bawa *et al.*, 1985, Clinebell *et al.*, 2004, Ramirez, 2004). Moths, both as larvae and adults are an important food resource for birds (Robinson and Holmes, 1982), bats (Svensson *et al.*, 1999) shrews (Buckner, 1969) and are even eaten by bears (White *et al.*, 1998). If moths are not supported with nectar and larval food resources, an important invertebrate food resource in the overall food network is reduced. Finally, moths are indicators of environmental change (Luff and Woiwod, 1995) and evidence from the UK and US suggests that moth populations are in decline (Thomas 2005, Conrad *et al.*, 2006, Wagner, 2012).

Study Organism

This chapter focuses on the abundance and diversity of *Hemaris*, diurnal moths of the family Sphingidae. For a description of the organisms, please see Chapter 1 of this dissertation (Tartaglia, 2013).

Questions

This study addresses the following questions: (1) Are there differences in abundance and diversity of diurnal Sphingidae (genus *Hemaris*) between urban and suburban habitats? (2) What plant species comprise the nectar diets of the three *Hemaris* species? (3) Are there differences in pollen loads and/or number of pollen species carried by individual *Hemaris* moths and do these factors differ among the three *Hemaris* species native to the Northeast? (4) Do *Hemaris* moths demonstrate preference for any nectar species? (5) How far do *Hemaris* fly through a fragmented landscape to locate and exploit nectar resources?

METHODS

Site Classification

I sampled field sites that I classified as urban and suburban. The urban site was Rutgers Gardens, located in New Brunswick New Jersey. Rutgers Gardens consists of a series of horticultural gardens spread over approximately 60 hectares. It is part of Rutgers University and is surrounded by the city of New Brunswick in Middlesex County, New Jersey. Duke Farms and Hutcheson Memorial Forest (HMF), both in Somerset County,

served as my suburban sites. Duke Farms is a 1080-ha former estate that is being restored to native forest and meadow areas. HMF is a 226-ha property owned by Rutgers University that contains some of the only remaining old growth forest on the east coast (Monk 1961). Both sites feature patches of floral meadow resources within a mature upland hardwood forest matrix.

To establish a criteria for determining whether a site should be considered urban, individual sites were evaluated for local patterns of land-use using four, 2.5 km line transects running in each cardinal direction from the center of each field site. For this study, I considered sites with greater than 50% developed land as “urban”. Sites with less than 50% developed land I considered “suburban”, rather than “rural” since they still had at least some degree of developed land within 2.5 km.

Using Google Earth, I obtained an aerial view of each location and drew four transects using the straight-line ruler from the Google Earth toolbar (Google, 2012). I classified landscape types intersected by each line as forest, meadow, turf lawn, cultivated garden or developed area. I measured the distance each of the four lines crossed through a specific landscape type and converted this distance a percent value then averaged percent values for each landscape type (methods from Duchak and Holzapfel 2011). Since only forest, meadow and cultivated areas constitute suitable sphingid habitat, we classified these landscape types into “suitable” for moths. Developed areas and turf lawns represented “unsuitable” moth habitat (Table 1).

The urban site, Rutgers Gardens, higher a percentage of unsuitable moth habitat compared to the suburban sites. Rutgers Gardens has 17.7% forest, 0.5% cultivated

garden, 11.8% turf lawn and 70% developed area. Rutgers Gardens has 18.2% suitable moth habitat and 81.8% unsuitable moth habitat.

Suburban site Duke Farms has 40.8% forest, 30.9% meadow, and 28.3% developed area. Duke consists of 71.7% suitable habitat and 28.3% unsuitable habitat. HMF had 31.4 % forest, 59.6% meadow, and 9% developed area. HMF has 91% suitable habitat and 9% unsuitable habitat.

Abundance & Diversity Surveys

Since light trapping is not a viable option for collecting diurnal species, in order to conduct my studies on *Hemaris*, I used capture by hand netting along a transect. I netted moths on 10 meter transects through meadow areas at three sites between the hours of 10:30 am and 3 pm from mid-June to mid-August, 2010. Once netted, moths were cooled in a small, ice filled cooler until they were sluggish enough to be handled. I identified each individual to species and released the moths unharmed.

Nectar Diet Surveys

I netted moths on 10 meter transects through meadow areas at three sites between the hours of 10:30 am and 3 pm from July to mid-August 2011 days. Once netted, moths were cooled as above, and then identified each individual to species. I swabbed individuals' probosces and bodies with a fuchsin-infused 3-mm² gelatin cube to remove any pollen and melted the gelatin cubes on microscope slides for later pollen identification in the lab (Alarcon *et al*, 2008). I netted and swabbed 50 total individuals. Moths were released unharmed after a few minutes of warming. On each slide, I

identified 50 grains of pollen to the lowest possible taxonomic unit chosen from 10 random locations on the slide for a total of 3750 total pollen grains.

I also assessed the sites for floral resources available to moths to compare to the floral resources utilized by moths at the sites. At each site, I chose 3 locations in the field where I was netting moths and walked a 50 m transect at each location. I recorded the species of flowering plants available within 1 meter on either side of the transect and their corolla colors. I calculated relative abundances of each corolla color present based on the number of blooming stems of each plant species. I conducted these surveys 2x per week at each site throughout the 2011 field season, choosing different locations within the field for each survey.

Flight range study

To assess the minimum flight range of a *Hemaris* moth, I netted and tagged 75 individuals representing all three *Hemaris* species with small numbered tags glued to the dorsal surface of the thorax. Moths were collected during the month of July 2011. The moths were released at the site of their capture. I netted in four patches at varying distances from one another at Duke Farms (Map 1 and Table 2).

RESULTS

Abundance, Diversity & Community Similarity

In the 2010 field season, I netted a total of 90 *Hemaris* individuals representing all three species present in New Jersey. Of these, 45 individuals were netted at Duke Farms, 32 at

HMF and 13 at Rutgers Gardens (Table 3). The Simpson Diversity Index for each community was HMF 0.38, Duke Farms 0.61 and Rutgers Gardens 0.67.

Nectar Plant Diet

For this experiment, I netted moths directly from the plant species available at each site in the summer of 2011. At Duke, the moths were mostly netted on *Monarda fistulosa*. At HMF, moths were netted from *Cirsium discolor*, *Centaurea* sp. and *Phlox divaricata*. At Rutgers Gardens moths were netted from *Petunia x hybrida*, *Verbena bonariensis*, *Kalmia latifolia*, *Buddleija davidii* and *Syringa vulgaris*. Not all species of moth were netted from all plant species available at each site (Table 4).

H. thysbe individuals on average carried 4 species of pollen on their bodies, *H. gracilis* individuals carried 3 species on average and *H. diffinis* typically carried only one species of pollen. I also analyzed the relative abundance of each flower color of the pollen grains found on moths' bodies, which revealed differences between color most frequently found on moths' bodies (purple) and the relative abundances of flower colors in the field. Although purple/lavender flowers were the most abundant color at the field site, they were not significantly more abundant than the next most abundant color category ("other" comprising all non- purple, pink or white flowers) (Table 5). Nearly all of the pollen on an individual's body – 78% on average – was of the species of plant from which it was netted. 86% of the pollen on *H. thysbe* bodies came from purple colored flowers 47% from pink flowers, 13% from white flowers and 6% from other colors. 96% of the pollen on *H. gracilis* bodies came from purple colored flowers 3% from pink

flowers and 1% from other colors. 100% of pollen on *H. diffinis* bodies came from purple or lavender colored flowers (Figure 1).

Flight range

Of the 75 individuals netted and tagged at Duke farms, no tagged individuals were recaptured in the course of the study. I performed a small experiment to determine whether the tags remained on *Hemaris* after a period of flight. I captured 25 individuals and let them fly in a 24x24x72" flight cage for three days prior to release. Moths were able to fly as normal in the cage once tags had been attached. There seemed to be no physical hindrance to moths bearing tags. Tags remained on all but one individual.

DISCUSSION

Abundance/Diversity

Unlike the nocturnal sphingids, *Hemaris* are able to utilize resources in urban habitat patches, as evidenced by their presence and diversity at the urban site, Rutgers Gardens. Rutgers Gardens provides an abundance of floral resources for the moths as well as host plants in the small, forested area nearby.

HMF, one of the suburban sites, had the lowest diversity of the three sites, due to the high abundance of *H. diffinis* relative to the other species present at the site. *Hemaris* host plants, particularly honeysuckle, are extremely abundant at this site, but there is much overlap between the preferred host plants of all three *Hemaris* species (Wagner,

2005) so another factor may be at work contributing to the dominance of *H. diffinis* at HMF.

Diet

Although *Hemaris*' nocturnal counterparts are typically restricted to flowers that are easily located in the dark – white or light colored, heavily scented and available in the evening – being diurnal, *Hemaris* avoid the necessity of this restriction and can utilize a much wider array of available resources. Previous studies on *Macroglossum stellatarum*, a European diurnal sphingid, indicate that these diurnal moths show a color preference blue/indigo wavelengths (Kelber, 1997). My results indicate that *Hemaris* may seek out purple and lavender colored flowers, though small quantities of pollen from white, pink, and yellow flowers were also present on their bodies.

Flowers that the moths commonly nectared at also tended to be tubular in shape. *Monarda fistulosa*, *Buddleija davidii*, *Phlox divaricata*, *Petunia x hybrida*, *Syringa vulgaris*, and *Verbena bonariensis* are all generally purple or lavender and all possess tubular flowers or florets. The disk florets of *Cirsium discolor* and *Centaurea* sp. are tubular as well. *Hemaris*, like most other members of the family, drink nectar through long probosces and tubular flowers are best suited to this morphology. The seeming preference for purple and lavender flowers could be the result of innate preferences based on spectral receptors in the moths' eyes. Research on *Macroglossum stellatarum* (Kelber, 1997) and other Sphingidae such as *Deilephila elpenor* (Schwemer and Paulsen, 1973)

and *Manduca sexta* (Bennett and Brown, 1984) indicate that Sphingidae have three wavelength sensitivity peaks: 350 nm (ultraviolet), 450 nm (purple-blue) and 520 nm (yellow-green). However, based on this experiment, it is impossible to separate whether *Hemaris* is demonstrating an innate preference for flower color or a learned behavior based on rewards offered by flowers or signal strength of the flower colors in the system. These flowers may produce large quantities of nectar or high quality nectar, both of which could also potentially affect visitation rates to these plants.

Though there are many more floral resources available to them in the day, *Hemaris* still seem to be restricted in the plants that they visit for nectar. This may be due to floral morphology – an association between tubular flowers and purple and lavender colored flowers, or another, untested factor such as nectar quality or quantity present in the preferred nectar species.

Flight Range

None of the *Hemaris* in my experiment were recaptured, yet the tags do in fact remain on individuals, as seen in a flight cage. This result reveals a few previously unknown aspects of *Hemaris* behavior. *Hemaris*, like other Sphingidae are not central-place foragers like the bumblebees and other Hymenoptera pollinators with which they typically coexist (Heinrich, 1979). Since they have no need to return to a nest to tend young or provision colonies each day as bees do, *Hemaris* are vagrants – they can move throughout the landscape freely and travel longer distances without depleting energy needed for the return trip to their nest. This behavior can be beneficial to plant populations, particularly in newly restored communities like those found at Duke Farms. *Hemaris* will transport

more outcrossed pollen rather than facilitate inbreeding by pollinating plants with close (genetic and spatial) relatives. Increased outcrossing relative to bees has been demonstrated in other members of the Sphingidae (Brunet and Sweet, 2006) and these data support that *Hemaris* sharing this interaction.

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Site	% Forest	% Garden	% Meadow	% Lawn	% Devel	% Suitable	% Unsuitable
Duke Farms	40.83	0	30.92	0	28.25	71.7	28.3
HMF	31	0	60	0	9	91	9
RU Gardens	17.67	0.5	0	11.83	70%	18.17	81.83

Table 1: Landscape classifications at each field site and proportion of land classed as “suitable” and “unsuitable” moth habitat.

	Site	Distance
Conservatory Back Meadow	→ Hay Barn	415 m
Vista Lake South	→ Upper Foundation	450 m
Hay Barn	→ Upper Foundation	900 m
Hay Barn	→ Vista Lake South	1000 m
Conservatory Back Meadow	→ Upper Foundation	1200 m
Conservatory Back Meadow	→ Vista Lake South	1500 m

Table 2: Distances between flight range sampling sites at Duke Farms.

	<i>H. thysbe</i>	<i>H. diffinis</i>	<i>H. gracilis</i>	Total
Duke Farms	16	23	6	45
HMF	25	4	3	32
RU Gardens	6	5	2	13
Total	47	32	11	90

Table 3: *Hemaris* abundances by species at each field site

Netted from	<i>H. thysbe</i>	<i>H. gracilis</i>	<i>H. diffinis</i>	Color
<i>Buddleija davidii</i>		X	X	white /purple
<i>Cirsium discolor</i>	X		X	pink
<i>Centaurea</i> sp	X	X	X	purple
<i>Kalmia latifolia</i>	X			white
<i>Monarda fistulosa</i>	X	X	X	lav
<i>Phlox divaricata</i>	X	X		pink
<i>Petunia x hybrida</i>	X			magenta/purple
<i>Syringa vulgaris</i>	X		X	lavender
<i>Verbena bonariensis</i>			X	purple

Table 4: Species and flower colors of plants from which *Hemaris* were netted.

Flower Color	Rel Abundance at Sites	Rel Abundance <i>H. thysbe</i>	Rel Abundance <i>H. gracilis</i>	Rel Abundanc <i>H. diffinis</i>
purple	0.46	0.87	0.98	1
pink	0.1	0.09	0.017	0
white	0.1	0.03	0	0
other	0.34	0.01	0.003	0

Table 5: Most abundant flower colors at field sites compared to most frequently carried pollen color on moths' bodies

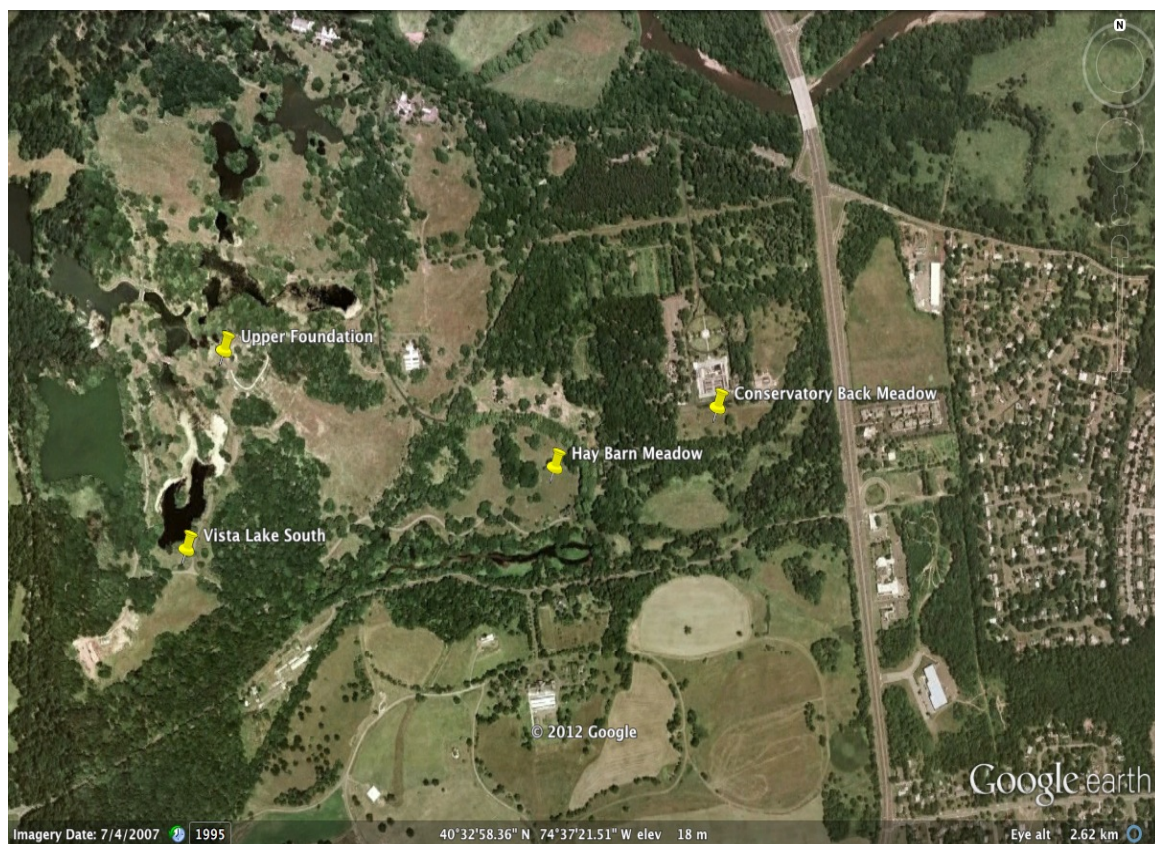


Figure 1: Flight range sampling sites at Duke Farms

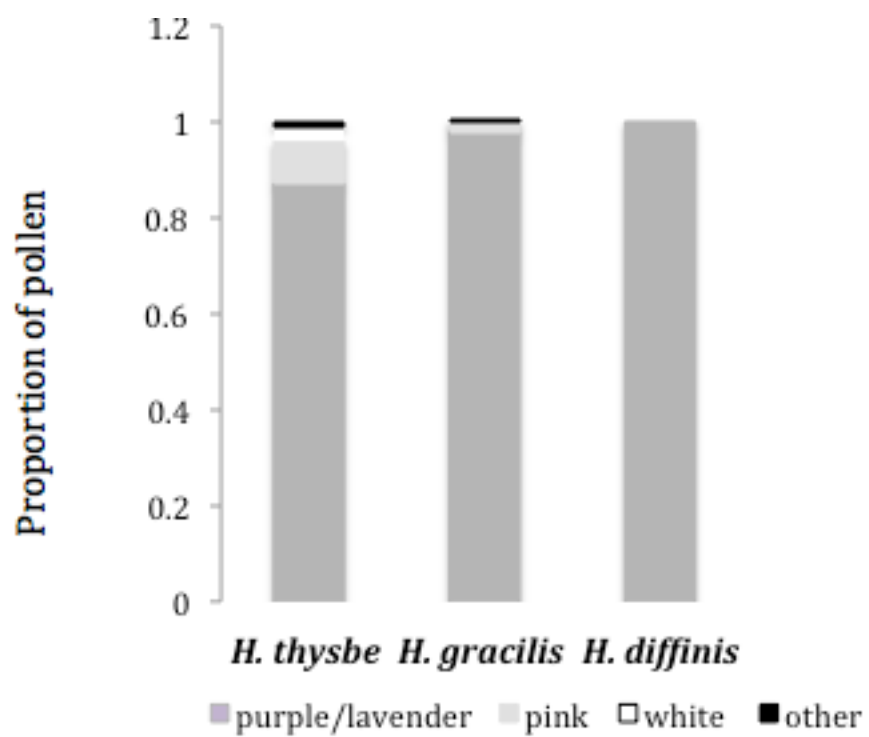


Figure 2: Proportion of pollen colors on *Hemaris* bodies

CHAPTER IV
**COMPARISON OF NECTAR FORAGING BEHAVIORS OF *HEMARIS*,
BOMBUS AND *PAPILIO* AT *CIRSIIUM DISCOLOR* INFLORESCENCES**

ABSTRACT

Foraging behavior has been well studied and documented for many organisms.

Lepidoptera are frequent flower visitors and many plants have specially adapted to accommodate these insects, however few studies address lepidopteran behavior and even fewer studies exist specifically examining moth foraging behavior. In this study I investigated three questions. (1) Do *Hemaris* forage differently at thistle than *Bombus* (model-mimic system) and *Papilio glaucus* (Lepidopteran relative)? (2) Do *Hemaris* forage similarly to the closely related *Manduca rustica*? (3) What might be driving differences in foraging behaviors? I observed foraging bouts by *Hemaris* sp., *Bombus* sp., and *P. glaucus* at *Cirsium discolor*, a thistle native to the study area in Somerset, NJ. *Hemaris* individuals visit significantly fewer *C. discolor* inflorescences and probe significantly fewer *C. discolor* florets per foraging bout than *Bombus* or *Papilio glaucus*. *Hemaris* do forage more similarly to the related *M. rustica* than to the other two foragers. Differences between *Hemaris* behavior and that of bumblebees may be attributed to their model-mimic system or may be due to a retained ancestral trait.

INTRODUCTION

Foraging behavior has been well studied and documented for many organisms. These behaviors may be observed and provide insight into animal behavior, and in the case of nectar foraging animals, increase our understanding of plant population dynamics as well. Among invertebrates, Hymenoptera, in particular, are well represented in foraging studies and many have focused specifically on bumblebees (*Bombus* spp.) (Heinrich, 1975, Pyke, 1978, Heinrich 1979 a,b).

Lepidoptera are also frequent flower visitors and many plants have specially adapted to accommodate these insects (Proctor *et al.*, 1996). Relatively few studies address Lepidoptera foraging behavior and even fewer studies exist specifically examining moth behavior.

The majority of moth-focused foraging studies concentrate on nocturnal Sphingidae, particularly *Manduca* sp. (Brantjes, 1978, Willis and Arbas, 1981, Raguso and Willis, 2002, Goyret *et al.*, 2007) and *Hyles lineata* (Waser, 1982, Hodges 1995, Brunet and Sweet, 2006). There are a number of studies on the foraging behavior of the diurnal *Macroglossum stellatarum*, a European native (Kelber, 1997, Kelber, 2010, Goyret and Kelber, 2011). One of the only studies regarding behavior of moths of the genus *Hemaris*, comes from Dreisig (1985). In this study, Dreisig examined the foraging patterns of *Hemaris fuciformis* at *Vicia vulgaris* inflorescences. Dreisig compared the direction *H. fuciformis* traveled after visiting an inflorescence to bumblebee directional flight after visitation. Both *H. fuciformis* and bumblebees tended to move in one direction from inflorescence to inflorescence and *H. fuciformis* also foraged in such a manner as to avoid already-visited florets, for example moving “forward” away from already visited

florets and “upward” from the base toward the top of the inflorescence, again avoiding already-visited florets. In this way, *H. fuciformis* maximized energy gain from foraging bouts.

Moths of the genus Hemaris

This chapter focuses on the behavior of *Hemaris*, diurnal moths of the family Sphingidae. For a description of the organisms, see Chapter 1 of this dissertation (Tartaglia, 2013).

Questions

In this study I test three questions. (1) Do *Hemaris* forage differently at thistle than *Bombus* (model-mimic system) (2) Do *Hemaris* forage differently at thistle than *Papilio glaucus* (Lepidopteran relative)? (3) Do *Hemaris* forage similarly to the closely related, but nocturnal, *Manduca rustica* (Sphingidae)?

METHODS

Study system

Hutcheson Memorial Forest (HMF), located in Franklin, Somerset County, New Jersey, is a 226 ha habitat consisting of several early successional meadows interspersed between forest patches of varying ages and species composition. HMF is surrounded by various matrix types including urban and suburban areas as well as being connected to a corridor network of open space throughout central NJ (Monk, 1957). I conducted my observations in one of HMF’s early-successional meadows. This meadow is permanently maintained

in an early successional sere and is surrounded by stands dominated by *Juniperus virginiana*.

I carried out observations from 14-26 August, 2010. At the time of observation, the most abundant blooming plant was *Cirsium discolor*, a thistle native to the northeast. I selected *C. discolor* due to the abundance of inflorescences as well as its attractiveness to all three types of pollinators targeted in this study. One *C. discolor* inflorescence consists of many tubular florets so it can accommodate *Hemaris* probosces and is frequently visited by all three of the pollinators we were observing in this experiment, *Bombus*, *Hemaris* and *Papilio*.

Additionally, I wanted to assess the foraging behavior of another Sphingidae species more closely related to *Hemaris* than the lepidopteran *Papilio glaucus*. Since sphingids are not abundant in the Northeast, I observed foraging of *Manduca rustica* on *Datura wrightii* at the University of Arizona experimental farm in Tucson, Arizona.

Data Collection

I selected a patch of approximately 50 *Cirsium discolor* inflorescences as the observation area. Each time a pollinator (*Hemaris* sp., *Bombus* sp., or *Papilio glaucus*) entered the selected patch, I recorded its identity as one of my three target pollinator types. I observed the pollinator's entire foraging bout, starting when the pollinator entered the patch, following it from inflorescence to inflorescence until it exited the patch. *C. discolor* is a composite flower and pollinators probe individual florets within a flower head. I was able to watch pollinators very closely without disturbing them to count the number of probes. *Hemaris* and *Papilio* have long probosces which are easily observed

when inserted into the *C. discolor* florets. *Bombus* individuals are generally unconcerned with close observation, so I was able to view these pollinators inserting their tongues into the florets. Though there are three species of *Hemaris* present at HMF, they showed no behavioral differences with regards to the data I collected.

I recorded the total number of inflorescences visited per foraging bout and the number of individual florets probed on each inflorescence. This allowed us to calculate the total number of florets probed during the entire foraging bout. Finally, I recorded the time each forager spent at a floret and the total time of the foraging bout. Over the course of the observational period, I recorded 1000 total foraging bouts by the three pollinator types.

To assess *Manduca rustica*'s foraging behavior, I employed the same procedure outlined above, observing foraging bouts at a patch of approximately 50 *D. wrightii* flowers. Though *D. wrightii* has a different floral morphology than *C. discolor*, it does have a corolla that is nearly completely divided into five nectar chambers at the base just above the ovary. As a result foraging sphingids often make multiple probes into one flower during foraging.

RESULTS

Hemaris compared to Bombus and Papilio

I observed 450 *Hemaris* foraging bouts, 443 *Bombus* foraging bouts and 116 *Papilio glaucus* foraging bouts.

ANOVAs revealed that *Hemaris* individuals visited significantly fewer ($p < 0.001$) *C. discolor* inflorescences per foraging bout than *Bombus* or *Papilio glaucus* in my

system. On average *Hemaris* visit 3 inflorescences per bout compared to 7 inflorescences visited by *Bombus* and 4 inflorescences visited by *Papilio glaucus* (Figure 1).

Hemaris also probe significantly fewer ($p < 0.001$) *C. discolor* florets per foraging bout. On average, *Hemaris* probe 12 florets per foraging bout compared to 116 florets probed by *Bombus* and 59 florets probed by *Papilio* (Figure 2).

Using these data, I also calculated the visitation rate and handling time (Herrera, 1989) for each pollinator type at *C. discolor*. Visitation rate (VR) is a measure of the number of florets visited by a pollinator during the total observation period (TT). In this case, I used the number of *C. discolor* florets probed (NF) divided by TT to calculate VR. To calculate TT, I added the total time each pollinator spent at a floret (TF) to the total flight time (TF – time in flight between flower visits). I calculated TF as $(TT - TF)/NF$. I also calculated handling time (HT – average time spent at a floret) for each pollinator. I recorded times in seconds and multiplied the final VR for each pollinator type by 60 to find the per minute visitation rate (Table 1).

Hemaris had the highest visitation rate of all three pollinator types, visiting an average of 10.92 *C. discolor* florets per minute. *Papilio glaucus* had a VR of 3.11 and *Bombus*'s VR was 2.98. The pollinators demonstrated a similar pattern of handling times. *Hemaris*'s HT was 4.07, *Papilio glaucus*'s was 15.56 and *Bombus*'s was 17.72.

Manduca rustica* foraging behavior on *Datura wrightii

On average *Manduca rustica* visited 3 *Datura wrightii* flowers per foraging bout and remained at each flower for an average of 3.8 seconds. As calculated by the methods above, their visitation rate at *D. wrightii* was 13.05 with a handling time of 2.78.

DISCUSSION

We often assume that animals forage “optimally” such that they maximize their net rates of energy intake and minimize energy expenditure (Macarthur and Pianka, 1966). A few studies have examined optimal foraging strategies for bumblebees (Pyke *et al.*, 1977; Pyke, 1984). However, it is questionable whether animals such as insects are able to “calculate” an optimal foraging strategy. It seems counter-intuitive to optimal foraging concepts for a *Hemaris* individual to depart from a patch of seemingly high-quality resource more quickly than the bumblebees and swallowtail butterflies with which they forage. Clearly there is plenty of nectar present, as both the bees and butterflies remain in the patch for extended periods. *Hemaris* spend significantly less time in the patch and visit significantly fewer *Cirsium* florets per bout.

Bumblebees forage differently and remain at inflorescences longer than *Hemaris*. Bumblebees are not capable of hovering flight, so they must land on inflorescences to drink nectar. Bumblebee tongues are shorter (Harder, 1982) than *Hemaris*’ probosces so they must reach further into florets to extract nectar. Additionally, while the bumblebees in this system seemed mainly to be taking nectar from the *Cirsium* inflorescences, bumblebees also collect pollen both to eat and to provision their nests. Collecting two resources from an inflorescence takes more time than collecting one resource. Bumblebees are central-place foragers and their foraging strategies have presumably come under selective pressure to optimize food returns to the colony (Heinrich, 1979a) and have been shown to do so on *Trifolium repens* (Heinrich, 1979b). Bumblebees may stay at a nectar-rich *C. discolor* inflorescence for a long period of time to maximize

energy intake from that source while decreasing their search time. Since bumblebees are spending long periods at thistle inflorescences, they are likely emptying, or nearly emptying, many florets of nectar. *Hemaris* may sense the presence of empty florets and as a result, move quickly to another inflorescence in the patch. Alternatively, they may leave the patch entirely if they sense, after probing a small sample of inflorescences, that they will not gain resources from inflorescences already emptied by bumblebees.

Hemaris may also attempt to avoid direct contact with bumblebees at inflorescences.

Since bumblebees are abundant in this system, it is likely that a *Hemaris* will encounter a bumblebee at a given thistle inflorescence and may quickly leave the inflorescence in the presence of a bumblebee.

Hemaris moths are mimics of bumblebees so we can also take model-mimic behavior into account when addressing *Hemaris*' foraging behaviors. The main predators of *Hemaris* and the other pollinators in my system are birds, praying mantises and crab spiders (personal observations). Bumblebees are well protected from predators due to their ability to sting. *Hemaris* on the other hand, are virtually unprotected (cannot sting or bite) except that they look like protected organisms and can fly quickly. In model-mimic systems, predators should not catch palatable (in this case, unprotected) mimics too frequently or they will learn that the mimics are palatable (Pasteur, 1982). The swift departure of *Hemaris* from nectar resource patches may be an adaptive response to avoid frequent predation and assist in upholding the model-mimic system.

Additionally, *Hemaris*' behavior was more similar to *Manduca rustica*'s foraging metrics as calculated above. This result is expected because the two species are more closely related to one another (sharing the same family) than either are to bumblebees or

swallowtail butterflies. Foraging movement may also be affected by predator avoidance, and several studies have examined predator avoidance movements in nocturnal moths in various families documenting zig-zagging and looping flights, dives and falls in response to bats and synthetic bat signals (Lee and Surlykke, 2001). Zig-zag movements by nocturnal moths during foraging has also been linked to avoidance of attack by ambush predators hidden in flowers (Kitching, 2002). In the nocturnal moth, short foraging bouts wherein the organism moves quickly from flower to flower could be a mechanism to avoid sonar detection by bats, or attack by ambush predators. Character evolution does not necessarily occur synchronously, so *Hemaris* may retain some ancestral behavior even though diurnal flight and morphological mimicry have evolved in this genus.

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Term	Calculation
TF	Total time at floret
TT	Total observation time (at floret + flight between inflorescences)
NF	Number of florets visited over observation period
VR	Visitation rate = florets/unit time = NF/TT
HT	Handling time = average time at each floret = TF/NF
FT	Flight time = $(TT-TF)/NF$

Table 1: Terms and calculations for foraging behaviors.

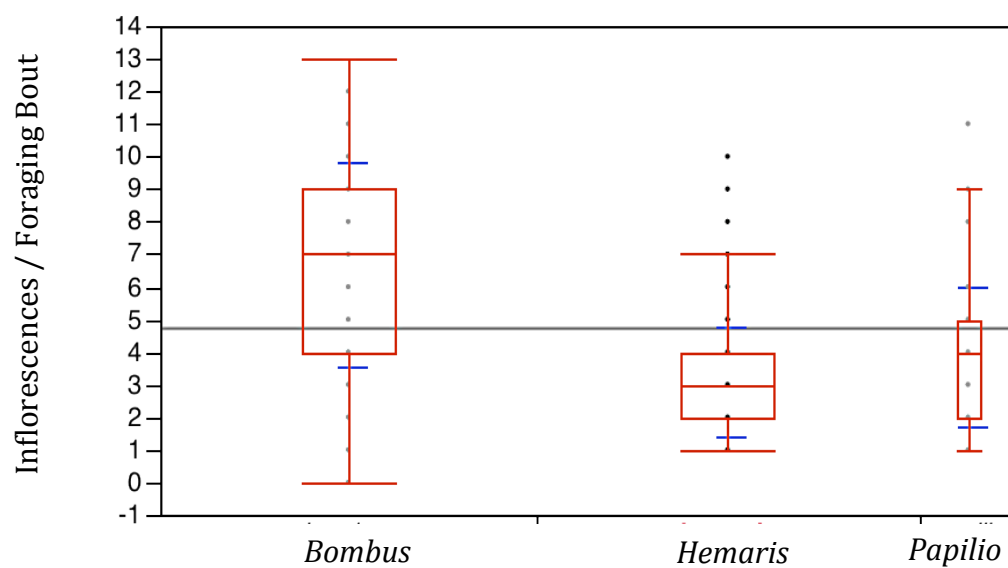


Figure 1: *Hemaris* visit significantly fewer *C. discolor* inflorescences per foraging bout than *Bombus* or *Papilio*.

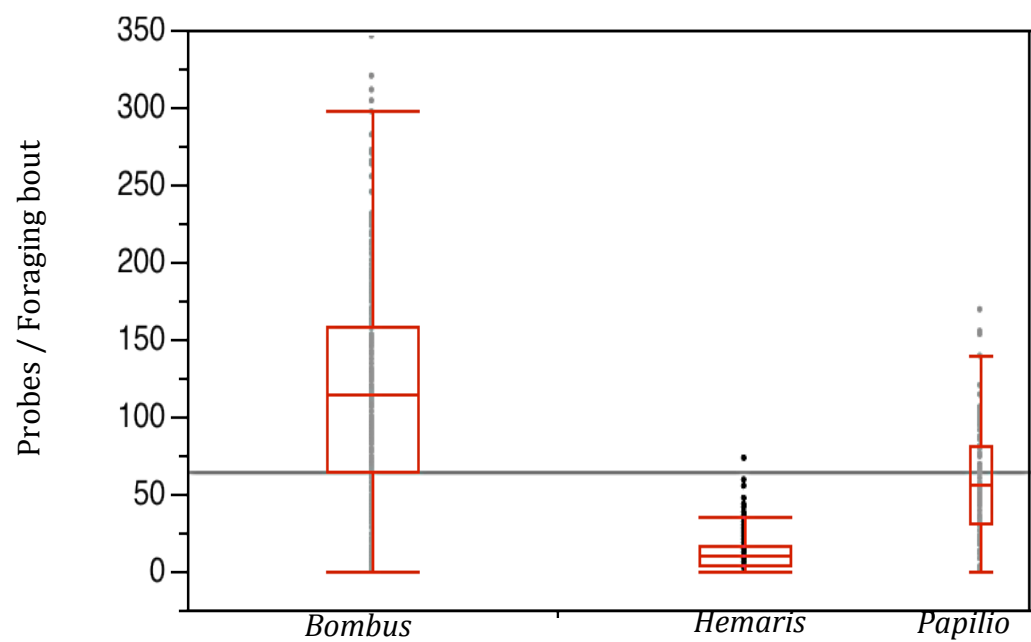


Figure 2: *Hemaris* probe significantly fewer *C. discolor* florets per foraging bout than *Bombus* or *Papilio*.

CHAPTER V
NECTAR PLANT PREFERENCES OF *HEMARIS* (SPHINGIDAE) MOTHS ON
CO-OCCURRING NATIVE *CIRSIIUM* AND NON-NATIVE *CENTAUREA*
(ASTERACEAE) INFLORESCENCES

ABSTRACT

Preferences for certain nectar plants by pollinators has been examined for a variety of organisms including bees, butterflies, birds and, more rarely, in moths. The relative abundances of floral resources can change throughout a pollinator's life, necessitating seasonal switches in nectar diets and many types of pollinators have displayed these nectar diet shifts. In this study I address the following questions: (1) Does *Hemaris* display a preference for foraging on the native swamp thistle, *Cirsium discolor*, over the non-native invasive knapweeds, *Centaurea* spp.? (2) What factors might be driving *Hemaris*' preferences? The bloom periods of *C. discolor* and *Centaurea* overlap in the northeastern United States, with *Centaurea* blooming from approximately June through September and *C. discolor* blooming for approximately the first two weeks of August. *Hemaris* typically eclose in the first week of July and in this system feed on *Centaurea*. During the co-blooming period of *C. discolor* and *Centaurea*, *Hemaris* visit significantly more *C. discolor* inflorescences, demonstrating a possible preference for this species. *Hemaris* revert to nectaring at *Centaurea* after *C. discolor*'s bloom period ends. *C. discolor* nectar has a significantly higher sugar concentration than *Centaurea* nectar so this difference may account for part of *Hemaris*' seeming preference for *C. discolor*.

INTRODUCTION

Preferences for certain nectar plants by pollinators has been examined in bees (Wykes, 1952, Roubik and Buchmann, 1984, Leong and Thorp, 1999, Schemske and Bradshaw, 1999, Alm *et al.*, 1990), butterflies (Wiklund *et al.*, 1979, Alm *et al.*, 1990, Grundel *et al.*, 2000), birds (Bolten and Feinsinger, 1978, Roberts, 1996, Schondube and Del Rio, 2003) and, more rarely, in moths (Riffell *et al.*, 2008). The relative abundances of floral resources can change throughout a pollinator's life, necessitating seasonal switches in nectar diets and many types of pollinators have displayed these nectar diet shifts (Feinsinger and Swarm, 1982).

Food preference may also change based on a pollinator's capacity to learn and seasonal resource availability and ensuing shifts in diet are commonly described for a variety of organisms (e.g. Tinbergen, 1960, Persson and Hansson, 1999, Sydeman *et al.*, 2001) The mechanisms underlying diet shifts have not been frequently determined however. For pollinators such as bees, maximizing energy rewards has been cited as the main driver of diet shifts (Heinrich, 1979a, Heinrich, 1979b, Cartar, 1991) but the causes of diet shifts have been infrequently examined for other pollinator types.

Another emerging issue in ecology is the role of non-native species in the diets of native pollinators. Interactions between pollinators and non-native plants vary considerably among invaded systems (Parker and Haubensack, 2002, Mitchell *et al.*, 2009). In many cases non-natives have been shown to directly compete with natives and draw pollinators away from native plants thereby reducing native seed set (Brown and Mitchell, 2001, Brown *et al.*, 2002, Bell *et al.*, 2005, Kandori *et al.*, 2009) while in other

cases, the presence of non-natives has no effect on or may even facilitate native pollination (Moragues and Traveset, 2005, Bartomeus *et al.*, 2008).

Moths of the genus Hemaris

This chapter focuses on the behavior of *Hemaris*, diurnal moths of the family Sphingidae. For a description of the organisms, please see Chapter 1 of this dissertation (Tartaglia, 2013).

Questions

In this study I address the following questions: (1) Does *Hemaris* display a preference for foraging on the native swamp thistle, *Cirsium discolor*, over the non-native invasive knapweeds, *Centaurea* spp.? (2) What factors might be driving *Hemaris*' preferences?

METHODS

Study system

Hutcheson Memorial Forest (HMF), located in Franklin, Somerset County, New Jersey is a habitat consisting of several early successional meadows interspersed between forest patches of varying age and species composition. HMF consists of 226 ha of meadows and upland temperate forest surrounded by various landscape matrix types including urban and suburban areas as well as being connected to a corridor network of open space throughout central NJ. I conducted my observations in one of HMF's early-successional meadows. This meadow is permanently maintained in an early successional sere and is surrounded by stands of *Juniperus virginiana*.

I carried out observations from 16 July until 28 August, 2012. Throughout the study period, the most abundantly blooming plants were *Centaurea* sp, knapweeds native to Eurasia. There are two species of non-native *Centaurea* at HMF, *C. maculata* and *C. dubium*. As the two species are nearly indistinguishable, I did not differentiate between them in this study. *Cirsium discolor*, a thistle native to the northeast blooms abundantly for a short period of time during the summer, so the bloom periods of these plants overlaps for only approximately the first three weeks of August. Thistle grows to an average height of 1.8 m at HMF while knapweed is shorter (average height 1.2 m). Both plants belong to the Asteraceae family and have similar floral morphologies consisting of purple/lavender inflorescences of densely packed discoid florets. However, knapweed possesses ray florets, which are lacking in thistle. I had previously established that *Hemaris* are attracted to purple flowers over other colors (Tartaglia, Chapter 3 of dissertation, 2013). *C. discolor* and *Centaurea* inflorescences consist of large quantities of tubular florets so they can accommodate *Hemaris* probosces and are frequently visited by the moths.

Data Collection

I netted *Hemaris* of all three species on two 20 m unidirectional transects, one running through a patch of *Cirsium discolor* plants and one running through a patch of *Centaurea* plants. Upon capture, each moth was manually dusted with fluorescent dye powder (Shannon Luminous Materials, Inc. via BioQuip Products) to track which flowers they landed on. Care was taken to apply dye to both dorsal and ventral surfaces of the moths and to remove any powder that might obstruct their vision or antennae. Moths were

released immediately after dye application. *H. thysbe* individuals were dusted with orange dye powder, *H. diffinis* individuals were dusted with blue dye powder and *H. gracilis* individuals were dusted with yellow dye powder. At dusk, I returned to the site with a blacklight flashlight to track moth landings and recorded the number and species of inflorescences in the transects with orange, yellow or blue dye on them. I also examined other floral resources present in the field to determine whether *Hemaris* utilize species besides *C. discolor* and *Centaurea* to any significant degree, though these species are less abundant at HMF. Since the dye faded considerably over the course of the night in this system (particularly if rainfall occurred), I was able to distinguish newly-visited inflorescences (i.e. visited during the course of that day) as distinctly brighter than previously visited inflorescences (i.e. dye was very faint or had disappeared totally).

To determine whether sugar concentrations in nectar might be driving any observed preferences for thistle or knapweed, I sampled 20 disc florets from 10 inflorescences each for thistle and knapweed plants growing adjacent to my transect. I extracted nectar by separating individual disc florets, removing the bottom of the tube and squeezing nectar onto a Reichert 10431 hand refractometer surface. Nectar extracted from individual florets from separate inflorescences was pooled. I sampled nectar once at mid-day (between 1200 and 1300h) and once in afternoon (between 1500 and 1600h).

RESULTS

In the northeastern United States, the bloom times of knapweed and thistles coincide for only a few weeks (Figure 1). Knapweed blooms for nearly the entire summer (from June through September) and has a much longer bloom period than *Cirsium discolor*, which

blooms for approximately the first three weeks of August. Knapweed is also more abundant than thistle. During the overlapping bloom period, there were on average 45.3 thistle inflorescences (115 at peak) and 157 on average (175 at peak) knapweed inflorescences present in my transects. Prior to thistle blooming at the study site, *Hemaris* (n=50) were netted from knapweed and fluorescent dye tracking revealed that they nectared exclusively at knapweed during this time. When thistle bloom began, *Hemaris* (n=64) were netted from both thistle and knapweed and fluorescent dye tracking revealed that they nectared at both thistle and knapweed. However, the moths visited significantly more thistle inflorescences ($p < 0.01$) during overlapping bloom times, despite the difference in abundance between the two plant species at the site. During the co-blooming period, *Hemaris* made 351 total visits to *Cirsium* inflorescences vs. 78 visits to *Centaurea* inflorescences (Figure 1). When thistles ceased blooming, fluorescent dye tracking revealed that *Hemaris* (n=11) reverted to nectaring at knapweed inflorescences (58 visits).

Three *Hemaris* species are present at HMF. Of the 114 individuals dusted with fluorescent powder in this study, 65 were *H. diffinis*, 43 were *H. thysbe*, and 6 were *H. gracilis*. Among *Hemaris* species there were no significant differences in visitation to thistle and knapweed. Other floral resources (*Asclepias syriaca*, *Convolvulus* sp., *Erigeron philadelphicus*, *Leucanthemum vulgare*, *Penstemon hirsutus*, *Solidago* sp.) existed in the field but were ignored by the moths.

Refractometry to determine sugar concentration differences between the two preferred nectar resources revealed that thistle (56.2% sugar) has significantly ($p < 0.05$) more concentrated nectar than knapweed (47.1% sugar).

DISCUSSION

My results add to the growing body of literature regarding the role of non-native plant species in plant-pollinator mutualisms. It seems that the non-native *Centaurea* serves as a “place-holder” food resource for *Hemaris* until their preferred nectar source, *C. discolor*, blooms, creating an apparent sequential mutualism between *Hemaris*, the non-native *Centaurea*, and the native *C. discolor*. *Centaurea* may help sustain *Hemaris* populations, allowing sufficient numbers of *Hemaris* to survive until their preferred food source becomes available. (I have no data regarding the relative importance of different pollinator types on *C. discolor*, so I can’t draw any conclusions about whether *C. discolor* benefits as well). Waser and Real (1979) first introduced the concept that sequentially flowering species may sustain pollinator populations throughout seasons, ensuring reproductive success for both plants and pollinators though they argue that this is an unexpected result of divergence in flowering time rather than a specifically selected trait. My data support this concept.

No specific research has been done addressing color preference in *Hemaris* outside of this dissertation, but it has been established that naïve *Macroglossum stellatarum* are able to learn and retain visual color cues. Comparisons between diurnal and nocturnal Sphingidae have revealed that diurnal hawkmoths do rely more heavily on visual cues (color and light intensity) to detect resources, while nocturnal species relied on odor cues (Balkenius *et al.*, 2006) so color may indeed be a critical factor in *Hemaris*’ selection preferences. This is particularly true when moths are not naïve (Kelber, 1999), as in this study. *M. stellatarum* is able to learn to associate nectar rewards with particular colors (Kelber, 1999) but newly-eclosed naïve moths also display an innate preference

for 440 nm wavelengths (Kelber, 1997) lending more support to the notion that diurnal hawkmoths such as *Hemaris* may show both innate and learned preferences toward lavender colored flowers.

Though the reason why *Hemaris* seems to prefer *C. discolor* may be due to the higher sugar concentration in the native thistle, other factors may be influencing the differential attraction. Hawkmoths rely on multiple sensory inputs to detect nectar resources (Raguso, 2004, Balkenius *et al.*, 2006), and Sphingidae have keen olfactory capacities in addition to their visual capacities. In fact, switching in Sphingidae has been documented by Riffell *et al.* (2008). *Manduca* individuals switched from *Agave* flowers to *Datura*, though *Datura* flowers have much less nectar, due to an innate preference these flowers (Riffell *et al.*, 2008). Although the plants seem odorless to humans, *Hemaris* may be detecting different more- or less-attractive volatiles from the two plants. Additionally, *C. discolor* does not possess ray florets, so differences in ray floret reflectance may also drive differential visitation to the flowers. These factors may be tested in subsequent studies.

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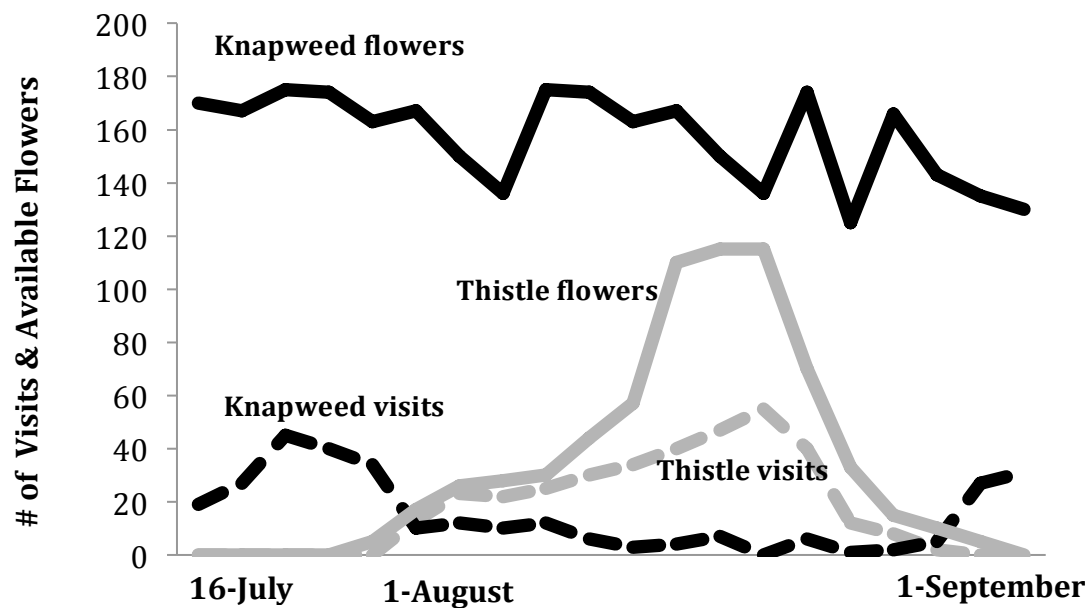


Figure 1: *Hemaris* visitation to thistle and knapweed flowers vs available thistle and knapweed blooms over the course of the study