DIVERSITY OF WINTER-FLYING MOTHS IN THE MARYVILLE COLLEGE WOODS

A Report of a Senior Study

by

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ABSTRACT

Lepidopterans, commonly referred to as butterflies and moths, are some of the most widely studied flying insects. Heterocera, or moths, are valuable to ecological and conservational research due to their diversity and geographical range. Their sensitivity to environmental shifts makes them a key indicator species for a variety of climates and habitat types. The goal of this study was to sample the moth population of the Maryville College Woods, a 0.56 km^2, mixed-mesophytic forest area in Maryville, Tennessee. Over the course of a three-month winter sampling period, thirty-two species from families Crambidae, Erebidae, Gracillariidae (unknown species), Gelechiidae, Geometridae, Noctuidae and Tortricidae were captured and preserved for identification. The most active temperature range for moths was 8.9 to 12.8˚C, and the most active flight time was between 19:00 and 20:00, when 65.2% of specimens were caught. The null hypothesis that neither temperature ($P<0.0001$) nor time of day ($P<0.0001$) would have an effect on the flight of moths over the course of the study was rejected. Several species not found in the Great Smoky Mountains National Park were documented in this study, including undescribed or unusual species, and many ecologically significant pests. With continued sampling and documentation of Lepidopteran species in the Maryville College Woods, this study provides a valuable tool to monitor species and ecosystem function in a fragmented and isolated habitat.

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CHAPTER I

INTRODUCTION

The Order Lepidoptera includes all butterflies (Suborder Rhopalocera), skippers, and moths (Suborder Heterocera), and is the second largest clade of insects (Superclass Hexipoda, class Insecta) aside from Order Coleoptera (beetles). Lepidopterans are characterized by the presence of four membranous, overlapping wings, fully or partially covered in scales, a long, coiled proboscis, and a caterpillar-type larval form. The Rhopalocera are generally more brightly colored, engage in day-flight, and have a conspicuous, fluttering flight pattern. Butterflies are more easily accessible for study given that they are most active during the day (diurnal), but are less abundant and diverse than their primarily nocturnal relatives, the Heterocera. Commonly called moths, they comprise the majority of the Lepidopterans with an estimated 160,000 species including both microlepidoptera and macrolepidoptera. Butterflies and moths can be identified by observing their antennae. In North America, only butterflies have straight, club-tipped antennae, while moths have simple (threadlike), pectinate (comblike), bipectinate (featherlike) or otherwise modified antennae (Covell 1984). Another identifying factor among the two Suborders is wing position when immobile. Rhopalocera typically hold their wings upright while most Heterocera hold their wings horizontally, at least partially covering their abdomen.

Insects are widely utilized as indicator species to analyze changes in the environment due to their abundance, short generation time, high number of offspring, ease of sampling, and diversity. They are also highly sensitive to perturbation, allowing scientists to compare the success of invertebrates and insects in a given area and explore new or better possibilities for environmental management. Heterocerans are highly diverse with an extensive geographical range, making them ideal for studies on environmental health in a given area. Their diverse roles as pollinators, herbivores, detritivores, and prey for bats, rodents, and other creatures makes them valuable for ecological and conservational research, especially in temperate and tropical areas (Choi 2011). Lepidopterans have an extensive habitat range, inhabiting every continent except Antarctica. With this range comes a set of highly varied body types, feeding habits, and behaviors within Families; the most variation is seen among moths.

The bodies of Lepidopterans are divided into three basic sections: the head, thorax, and abdomen. The muscles designated for flight are concentrated in the thorax, which consists of three segments: the prothorax, the mesothorax, and the metathorax. The forelegs attach to the prothorax, which is narrow at the top. The middle legs and forewings attach to the mesothorax (generally the largest segment of the thorax). The metathorax holds the hindlegs/hindwings and is more narrow. The "tympana" are commonly located near the lower edges on each side of the metathorax (Covell 1984). The flight system of Lepidopterans is neurogenic, or controlled by the nervous system. The two major groups involved with flight are the dorsal longitudinal muscles, which serve as wing depressors, and the dorsoventral muscles, which are the wing elevators. These muscles contract alternately during flight when wing movements typically have a large amplitude. During the warm-up period before flight, wing movements are usually of smaller or medium amplitude and most often occur at a higher frequency than that of the flight frequency. The alternation between depressors and elevators during this period varies from species to species. The elevators and depressors, which contract synchronously during warm-up, function separately from one another during flight. The transition from warm-up to flight in some species, such as the hawkmoth *Mimas tilae,* is gradual. The Saturniid moth, *Sanria Cynthia*, has an abrupt transition which occurs within one wing-beat cycle (Hanegan 1970). The thoracic muscles responsible for wing movement, and therefore flight, must maintain a delicate balance between having the necessary energy to promote movement and overheating. While these muscles are contracting to produce heat, a countercurrent heat exchange between the thorax and the abdomen draws cool blood from the abdomen through the aorta, pulling heat from the thoracic muscles. As the cool blood ascends through the aorta, heat is recovered by the ascending loop passage directly adjacent to it rather than allowing all heat to be shunted to the head (Heinrich 1986). In some families of moths, such as Sphingidae, the internal (thoracic) temperature during flight is kept between 40 and 41ºC, regardless of air temperature. This excludes the temperature ranges at which flight is not possible (Schmidt-Nielsen 1997).

Moth wings in most species are well developed and are supported by a network of modified tracheae (air tubes) called veins, and the venation patterns formed by these networks can aid in identification. Differences in wing form and angles between the costal margin (leading edge, ending at the apex), outer margin (extending from the apex to the anal angle), and inner margin (extending from the base to the anal angle) can be useful in identifying families and in some cases classification to species. In order to move as a unit, the forewings and hindwings of most moth species have a frenulum on the base of the hindwing, which catches a retinaculum on the underside of the forewings to hold the wings together during flight (Covell 1984).

Moth predation by bats (Order Chiroptera) is believed by many to be a defining factor in how nocturnal and diurnal moths' physiology (e.g., thermoregulation) and behavior (e.g., flight) has evolved. Tympanic organs which can detect ultrasonic echolocating bats, and non-tympanic organs which detect bisonar frequencies become evident in the fossil record in the late Eocene and early Oligocene. The tympanum's first appearance coincides with the early radiation of bats in the early Eocene. This event is thought to have placed selective pressure on moths favoring those which could avoid predation by detecting bisonar frequencies and subsequently taking evasive action, or by taking on rapid and erratic flight patterns (Rydell et al. 2000). Heteroceran morphologies including wing loading and body size as well as physiological body temperature during flight seem to have been shaped in part by bat predation, as bird predation has shaped the evolution of the Rhopalocera. Moths lacking tympanate organs, and therefore an "early warning system," must put forth a higher amount of energy during flight as they engage in erratic flight patterns to evade predators. This higher energy expenditure accompanies a faster metabolic rate, higher thoracic temperatures during flight, as well as some evolutionary repercussions. Non-tympanate moths may have shorter adult life spans and need to feed much more regularly than tympanate moths. As a result of these factors non-tympanate moths have a relatively low species diversity, reflecting their low radiation into the environment.

The physiological and behavioral adaptations that evolved with tympanic organs may have facilitated winter-flight in moths. With an "early warning system" to sense when a predator is near, tympanate moths can fly at much slower speeds and maintain a much lower thoracic temperature (Rydell et al. 2000). In short, thermoregulation of moths without tympanate organs developed with the need to maintain erratic, rapid flight patterns to avoid echolocating bats. Tympanate moths were able to keep thoracic temperature closer to the ambient temperature and expend less energy for flight, allowing them to efficiently evolve and radiate into numerous and expansive habitats.

The advantages of late-season flying moths capable of flying at near freezing temperatures could include avoiding bat predation altogether, due to winter bat hibernation. Svensson et al. (1999) had hypothesized that nocturnal activity in late-season moths was a function of avoiding predation by bats. Birds' diurnal flight makes them less of a factor after sunset, and bats' winter hibernation was thought to be an important reason for moth flight later in the season. Mating and flight in Geometrid "winter moths" (Order Geometridae, *Operophtera brumata*) were observed by Svensson et al. (1999) after dark, at times of rapidly dropping temperatures. In their study, if winter flight was a result of bat avoidance, the prediction was that these moths would exhibit degenerated predator defense systems due to alleviated selection pressure. The results of the study showed variance in peak activity at different months for different species of moths, from September to late November (19th). Bat activity coincided with a majority of the moth activity observed, including *Operophtera brumata* which flew latest in the season of all moths found. Moths and bats flew on the same nights and tended to be more active when the ambient temperature was slightly milder. The main difference in activity between the two was that when there was continuous rain, bats were not present. The bats were also not observed at temperatures less than 6ºC and moth flight was documented at 2ºC. Since these results showed that moths do not truly achieve isolation from bat predation by emerging and mating later in the season, this suggests the evolution of winter flight was not necessarily a result of bat predation. Predation pressure is still a factor in moth behavior, as males continued to exhibit sophisticated evasive responses when exposed to false echolocation in the field during this study. When exposed, moths either dropped quickly towards the ground or horizontally traveled away from the source of the ultrasonic frequencies. This observation was in keeping with the hypothesis that if bat predation was avoided successfully by flying during the winter, a physiological degeneration of the tympanum or other hearing organs of these moth species would have been evident. The males of tympanic moth species, as previously discussed, are physiologically able to maintain a lower thoracic temperature and flight speed. In many species the adult moths do not feed, making foraging irrelevant. Nocturnal flight allows the males to avoid diurnal predators altogether, and use their predation defense system based on sonic frequencies rather than advanced sight. An alternative hypothesis for nocturnal winter flight could be that it is meant to benefit the females of Geometrid cold-adapted species such as Operophtera and others. They are often cryptic and flightless, and can usually be found perched on a tree trunk or branch that matches their body and wing color/pattern. Females who remain immobile are far more susceptible to attack by visually-hunting, diurnal birds than they would be to echolocating bats. Bats typically need to locate their prey by sensing wing fluttering. Females can increase their fecundity by allocating all resources available to them to reproduction when flight is removed. This allows the space which could have been utilized for flight muscle and wing area as space for eggs. Overall body mass may also increase as they do not need to be aerodynamically compatible with flight. An additional advantage for cryptic females is the reduced abundance of non-flying invertebrates which may pose a threat during milder seasons. Moth predators such as spiders, beetles, centipedes, etc. experience a decline between the months of September and November, moving around and eating less as temperatures drop (Svensson et al. 1999). All of the above factors led to the conclusion that Geometrids are nocturnal because their tympanic organs provide them with an energy-efficient way to evade bat predation, and some are active at lower temperatures for seasonal avoidance of invertebrate predators.

Most of the peer reviewed literature on moths and cold season flight appear to focus on the mechanism and evolutionary causes of this flight at lower temperatures. Alternatives to flight during the night include hiding under leaf litter or other debris or perching on a tree or bush (Heinrich 1987). Moths face numerous obstacles as nocturnal insects, some of which include lower temperatures and highly specialized nocturnal predators (e.g., bats). Both endothermic and ectothermic moths may achieve flight during the late winter months using different biological tactics. Some ectothermic winter-flying microlepidoptera such as Geometrids have a particularly wide range of temperatures at which they can fly. Their typical temperature range is between -3ºC and 25ºC. This particular family of moths are thermoconformers, and have a low "wing-load," or mass to wing area ratio. The wingbeat frequency and therefore energy output for flight in species with this adaptation is significantly lowered (Marden 1995). Endothermic moths such as Noctuids of the subfamily Cuculiinae are also able to fly at low temperatures, by the employment of shivering in a pre-flight warm up, as well as heat produced during flight. Shivering is a very slight but powerful vibration of the moths' bodies, observed to occur at an amplitude of less than 1mm in Noctuid species. The pre-flight warm-ups have been recorded in laboratory settings ranging from 20-25 min at near 0°C to approximately 1 min at 20 °C, until a temperature which would allow flight was reached (Heinrich 1987). During warm-ups at 5°C, an estimated 82% of heat produced is lost through convection without actually heating the thorax, while in warm-ups from 20°C only 15-20% of the heat produced was lost in the same way. This heat loss accounts for the longer warm up time at lower temperatures. The rate of energy expenditure on the thorax leveled out at 0 at temperatures of -1 to -2°C, and was the lowest temperature at which warm-up was achieved by the Noctuids (Heinrich 1987). At higher air temperatures, excess heat is dissipated through the abdomen, given the larger surface area compared to the thorax and the general lack of external insulation. The thorax is commonly equipped with thicker, usually furry scales over its surface to reduce heat loss to the air. The countercurrent exchange system (control of bloodflow for the purpose of retaining heat) between the abdomen and the thorax, however, does not give winter-flying moths the ability to continue flight at high abdominal temperatures (Schmidt-Nielsen 1997). Unlike other insects such as bumblebees (Hymenoptera: Apidae), in which the countercurrent exchange is reversible pending the ambient temperature, moths cannot reverse their countercurrent exchange. As a result, winter-flying moths do not have the range of flight that other insects do for flight at higher abdominal/atmospheric temperatures. However, the ability to begin shivering at low temperatures and the ability to trap heat within the thorax are heightened in winter-flying moths, making them physiologically better equipped to warm up and fly than their summer-flying counterparts (Heinrich 1987).

The Great Smoky Mountains National Park is the most visited National Park in the United States, with approximately 10, 712,674 visitors in 2015 alone (NPS 2015). The Park comprises of 800 square miles and ranges in elevation from 875 – 6643 feet. The variety of habitats by elevation causes a distribution resulting in northern and boreal moth species reaching their peak density in higher elevation forests. The latest attempt at a comprehensive list of the Lepidopterans of the Great Smoky Mountains National Park was in 2007, the results of which involved DNA barcoding of 4156 specimens and 940 species. This number included only those species which were easily identifiable. The broad scale of taxonomic studies in habitats threatened by fragmentation, urbanization, and other issues yields valuable information pertaining to species of conservational concern. These may include endemic species or those whose host flora may be threatened with habitat loss or consumption by invasive species. Sampling efforts within the park have added only a few new taxa of macrolepidoptera, suggesting that at the time of the study 95-100% of these groups had been previously documented (e.g. Sphingoidea, Geometroidea, Noctuoidea, and others). Many microlepidoptera groups (e.g. Pyraloidea, Tortricoidea, Zygaenoidea) were sufficiently sampled due to involvement of experts, the relatively average size of the moths, and the wealth of recorded information on their taxonomy. Less common groups were still lacking in inventory. The absence of involvement of experts to the same degree as in other families could have had a role in this, or the baiting methods may need to be specialized for these species (e.g. pheromone trapping, sugar baiting). The absence of certain species at a light could be a simple indicator that other methods must be employed to attract them rather than the absence of the organism in the environment. It was estimated that the total number of Lepidoptera species in the National Park was between 1948 and 2164 although the microlepidoptera inventory was estimated at only 80-88% complete. Missing or inadequately represented species are associated with emergent aquatic vegetation, sandy soils, flood plains, expansive barrens, highly disturbed habitats, acidic wetlands, and large grasslands. These habitat types are poorly represented in the park, therefore individual sampling areas with these characteristics would be needed for an accurate estimate of underrepresented species. For the most part, however, the Lepidoptera of the GSMNP are dominated by species known to inhabit most eastern deciduous forests, especially cove forests. One Geometrid species known from only two locations in the park is the first recorded of its genus and tribe (Abraxini) in North America. The host plant for these moths is *Euonymus obovatus* Nuttall, an endemic species characteristic of mid-elevation fields. Lower elevation cove forests are home to another undescribed Crambid (Crambidae) moth with a wider distribution in the middle and southern Appalachians. There are at least three endemic species of moths at high elevations in spruce and fir dominated forests, all of which are limited in distribution to the middle to southern Appalachian Mountains. Two species within the families Hepialidae (ghost moths) and Noctuidae (owlet moths) comprise two of these endemics, while the third is an undescribed species of Agriphila (Crambidae) found in open habitats (e.g. roadsides, balds). These high-elevation species are especially vulnerable as spruce/fir habits are gradually infringed by invasive insect species (e.g. balsam woolly adelgid, *Adelges piceae*) and global climate change. Active conservation efforts and/or monitoring may be necessary in the future for the survival of these endemic species in the GSMNP (Sholtens and Wagner 2007).

Global biodiversity is threatened with rising temperatures and ozone levels as well as a continued rapid deforestation/urbanization phenomenon across the world since the Industrial Revolution. The actual shift in climate is projected by the Intergovernmental Panel on Climate Change (IPCC) to be rapid on an evolutionary time scale; mean global air temperature is likely to increase by 1.4ºC to 5.8 ºC by 2100, with continental (inland) and higher latitudes expected to experience more of an upward shift in temperature than that of coastal and tropical regions (Harvell 2002). As the continental Southeastern US specifically experiences continued climate change, the ease of winter flight may decrease significantly in endothermic moths. The GSMNP faces local ecological issues including both terrestrial and aquatic invasive species, high deposits of nitrogen and sulfur, rising ozone levels, and fragmentation of natural areas as a result of human development (Pogue 2005).

In close proximity to GSMNP is a small (0.56 km^2) woodlot on the campus of Maryville College (Maryville, TN), founded in 1819. Its location, as well as the similarity of flora populations (mixed mesophytic), suggest the Lepidopteran communities may be similar between the two localities. Moths are valuable to ecological and conservational research due to their diversity and geographical range, as well as their sensitivity to environmental shifts. Therefore, gaining an understanding of the diversity of rare, winter flying moths in a fragmented region is of value given the threat of habitat loss and urbanization. The objectives of this study were to observe the diversity of cold-adapted moths at a single, temperate locality during winter months, and to compare this to the Lepidopteran populations of Appalachia. The Lepidopteran Families active during the winter months will provide a glimpse into the Lepidopteran community of a disjunctive, previously unsampled habitat. Our null hypothesis was that neither temperature nor time of day would have an effect on the diversity of the observed species of Heterocera flying in the winter months.

CHAPTER II

MATERIALS AND METHODS

Collection

The study was performed in the Maryville College Woods, a temperate, mixed mesophytic forest area, spanning approximately 0.56 kilometers^2. The woods sit within the Maryville College campus, which is approximately 30.6 km north of the Great Smoky Mountains National Park. The collection site was chosen based on access to a power source, while maintaining a viable distance from any extraneous light sources which could interfere with nocturnal moths' attraction to the light source. A 12.2-meter rope was tied between two trees approximately 4.6 m apart, at a height of approximately 1.8 m. A standard, white, cotton sheet was folded over the upper section of rope such that one vertical edge (preferably the thick-hemmed side) was folded over the rope and pinned there with 3 heavy-duty diaper pins. Two pins were placed near the bottom of the rope, one on each side. To place these, the sheet was pulled tight such that the bottom corner was at a 90-degree angle with the ground (with about 0.6 m extended limp on the ground in the direction of the lower rope section, facing the lamp and the collector), and the pins were pushed through approximately 15.4 cm above the ground. These pins were for the placement of two stakes, which held the sheet taut after being hammered into the ground, using the pins as anchors. The cord of the 150-watt mercury vapor lamp (Damar Worldwide, 805 Carnation, Aurora, MO 65605) was looped twice around the lower section of rope in front of the collection sheet. The lamp's base was situated directly below the lower section of the rope. Once the sheet and lamp were set up, collecting began shortly after sunset (15 to 30 minutes). The light was used in conjunction with sweet wines either red or white (Roscato, Moscato), and mixed with brown sugar in a 1:3 (sugar:wine) ratio. A 5 cm paintbrush was used to "paint" the sugar bait onto several trees between 1 and 18 m from the collection site approximately one hour before sunset.

The jars for collection and transport of the moths were saturated for two days each with ethyl acetate, after which the excess was poured off into the original container. Two jars were dedicated to collection, and these jars were not lined with cotton. The two jars designated to "dumping" of moths after the loss of motor function in the collection jars were lined with cotton such that the moths' wings were not damaged. For collection of the moths, the lid of a collecting jar was removed, and each moth was individually collected by placing the mouth of the jar near the abdomen, with the lid raised off the mouth of the jar such that it was in front of the moth's antennae. When moving the lid down towards the mouth of the jar, the moths flew directly into the collection jar. After securing the lid, each moth was transferred to a cotton-lined jar after approximately 30 seconds or after cessation of movement. Collection of moths was performed continually throughout each hour because they often landed on the sheet and flew away after a minute or less. The temperature was recorded at the start of every hour. Each group of moths were kept in separate containers, labeled with the time and date they were collected. After collection was completed, the moths were taken to the lab and held in the freezer until they were pinned.

Pinning Procedure

Pinning materials were provided by the Mississippi Entomological Museum, at Mississippi State University in Starkville, MS. Prior to pinning, the moths were placed into a “relaxing” container. This was a simple plastic container lined interiorly with a layer of wet paper towels, a centimeter-thick layer of Styrofoam, and finally a layer of cotton. This allowed the moths’ wings to relax in the higher humidity while being kept separate from the wet paper towels. Their wings could not be pinned if wet. Any excess moisture on the interior sides and top of the container were wiped off. The moths were allowed to relax for approximately three hours before they could be pinned. The pinning board used was variable depending on the size of the moths. Each moth was fitted based on thorax size and wingspan to an appropriate pinning board. Moths were gently handled with forceps to keep the wing pattern as intact as possible. To pin the moths, each moth was placed gently between the thumb and point finger of the non-dominant hand of the pinner, using forceps. A fresh pin was used for each thorax, each pushed at a 90-degree angle through the highest point of the thorax such that the moth’s body was horizontal and straight. Any angling left or right of the thorax could cause complications with spreading the wings. Each moth was pushed up the pin with the pointer finger and thumb such that it rested approximately 1/3 of the length of the pin from the top. Each pinned moth was pushed into the notch of the pinning board until the wings could be spread at a 90-degree angle and lie flat on the surface of the pinning board. A pin was used to gently pull the moth’s forewing out at a 90-degree angle, stopping once the tip of the wing was approximately level with the antennae. A pin was placed into the forewing as close to the notch edge of the pinning board as possible. Using one pin to hold the side of the thorax in place, the hindwing was pulled out such that the top edge of the hindwing rested under the bottom edge of the forewing. Several moths were pinned onto one board at a time. 2.5 cm by 20 cm sections of tracing paper were placed over the wings of the moths. While applying pressure to the paper such that it was taut around the wings, a pin was placed above the forewing, another to the side between the fore and hindwings, and one behind the hindwing (just before the forewing of the next moth). After the tracing paper was in place (such that the wings would not shift) the pins next to the notch which held the wings in place were removed. The pinning boards were then placed into a large plastic container to allow the moths to dry for at least one week, after which they were removed and pinned by family into a storage drawer with labels. The labels included the date of collection, time of collection, collection site coordinates, temperature at the time of collection, and collector name. The family and species identifications were determined at the end of the study by Dr. Richard Brown (Director, Mississippi Entomological Museum). General data on time, temperature, and barometric pressure were compiled in Microsoft Excel using the total catch before identifications were completed. After positive identifications were established, the specimens were divided by family, species, time of capture, and temperature at the time of capture. The data were statistically analyzed and graphically represented using Excel such that the families found and the species within that family could be represented at each temperature.

CHAPTER III

RESULTS

A total of 95 individual specimens were captured over the course of the collection period from January to March, during 9 successful trapping nights. There were representatives from seven families, including Crambidae, Erebidae, Gelechiidae, Geometridae, Gracillariidae, Noctuidae, and Tortricidae, with a total of 32 individual species. Only 89 out of the total 95 specimens could be positively identified. The only representative of Gracillariidae could not be identified with references at the Mississippi Entomological Museum, and is being held pending identification or naming. Geometridae showed the greatest diversity, comprising 9 species of the total 32 species caught and 27 individual specimens, 30.4% of the total identifiable catch. Thirty specimens were of Family Tortricidae, comprising 33.7% of the total identifiable catch (Appendix 1).

93.6% of the total moth catch was acquired between 767.3 and 767.6 mmHg, with few to no specimens caught between 754.4 and 765.2 mmHg and between 767.9 to 772.4 mmHg (Figure 1). 1.1% of the total catch was observed between the hours of 18:00 and 19:00. Approximately 65.2% of the total moth catch of 95 specimens was caught during the hour between 19:00 and 20:00, and 23.2% was caught between the hours of 20:00 and 21:00. The temperature between 21:00 and 22:00 was nearly always too low to allow for significant moth flight, therefore 10.5% of the total catch was observed for this time period (Figure 2).

The null hypothesis stating that time of day would have no effect on the activity and abundance of species was rejected (P<0.0001).

Moths of the family Crambidae were observed from 8.9˚C to 12.5˚C, Erebidae from 8.9˚C to 12.5˚C, Gelechiidae from 0˚C to 8.9˚C, Geometridae from 6.1˚C to 12.5˚C, Noctuidae from 0˚C to 9.4˚C, and Tortricidae from 1.1˚C to 12.5˚C (Figures 3 and 4). The total catch was greatest between 8.9 to 12.5˚C, and once the temperature dropped below 6.7˚C, activity dropped rapidly (Figure 5). Therefore, the null hypothesis that temperature would have no effect on the abundance of species was rejected (P<0.0001).

Table 1. Notable information for each sampling session. Includes lunar phase, hours of sampling, total individual catch, bait type used, initial temperature and end temperature in degrees Celsius, and average barometric (atmospheric) pressure. Collection from January to March 2017, Maryville College Woods, Maryville Tennessee (US).

Date	Moon Phase	Hours	Catch	Bait Type	Temp. Initial (˚C)	Temp. End (˚C)	Avg. Bar. Pressure (mmHg)
25-Jan	Wan. Crescent	5pm-7pm	N/A	Light only	16.1	16.1	754.4
28-Jan	New	5pm-10pm	1	Light only	8.3	6.1	759.2
30-Jan	Wax. Crescent	5pm-10pm	0	Light only	2.8	0.28	762.8
17-Feb	Last Quarter	5pm-10pm	1	Light only	17.2	4.2	760.5
25-Feb	New	5pm-10pm	0	Light only	3.9	-1.4	756.6
26-Feb	New	5pm-10pm	2	Light and sugar	4.2	1.1	765.2
27-Feb	New	5pm-10pm	37	Light and sugar	9.7	6.4	767.6
3-Mar	Wax. Crescent	5pm-10pm	0	Light and sugar	2.2	-3.4	772.4
6-Mar	First Quarter	5pm-10pm	52	Light and sugar	15.6	12.2	767.3
10-Mar	Wax. Gibbous	5pm-10pm	2	Light and sugar	4.4	-0.05	761.9
15-Mar	Full	5pm-10pm	0	Light and sugar	-3.05	-6.7	767.9

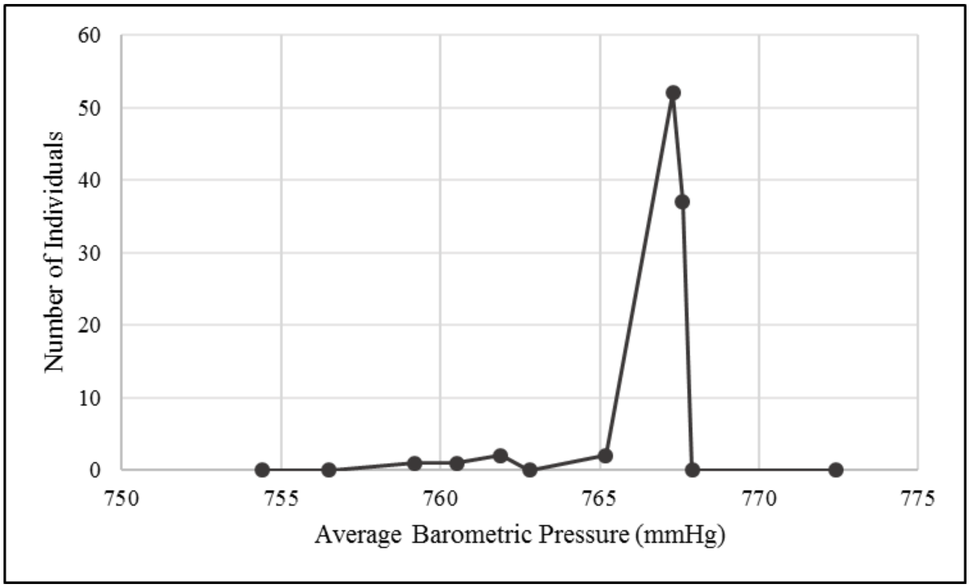

Fig. 1. Number of individual moths caught per average barometric pressure (mmHg). Collection period from January to March 2017, Maryville College Woods, Maryville Tennessee (US).

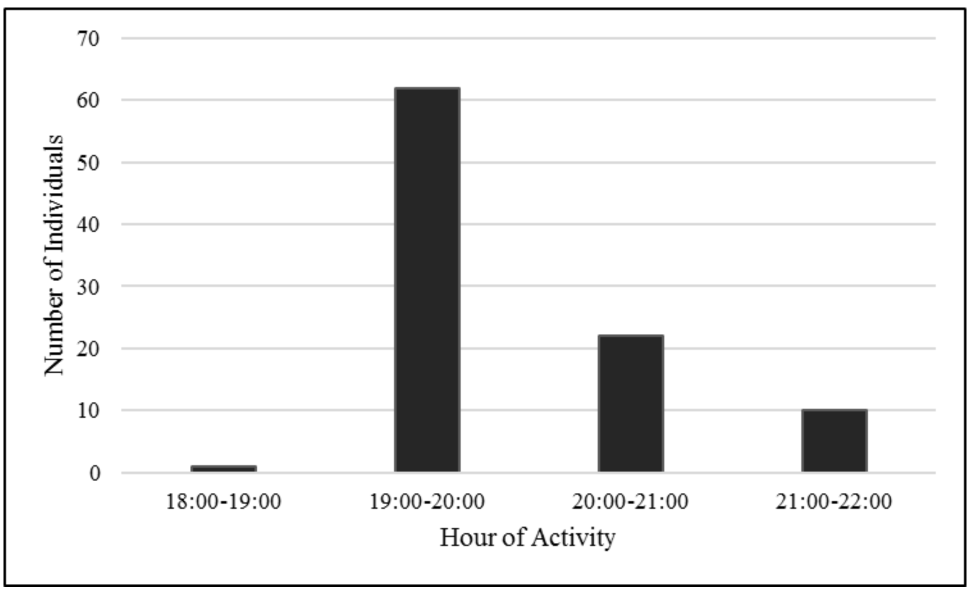

Fig. 2. Number of individuals caught during the hours of activity. Moths were captured continually over the course of each hour from 18:00 to 22:00. Collection period from January to March 2017, Maryville College Woods, Maryville Tennessee (US).

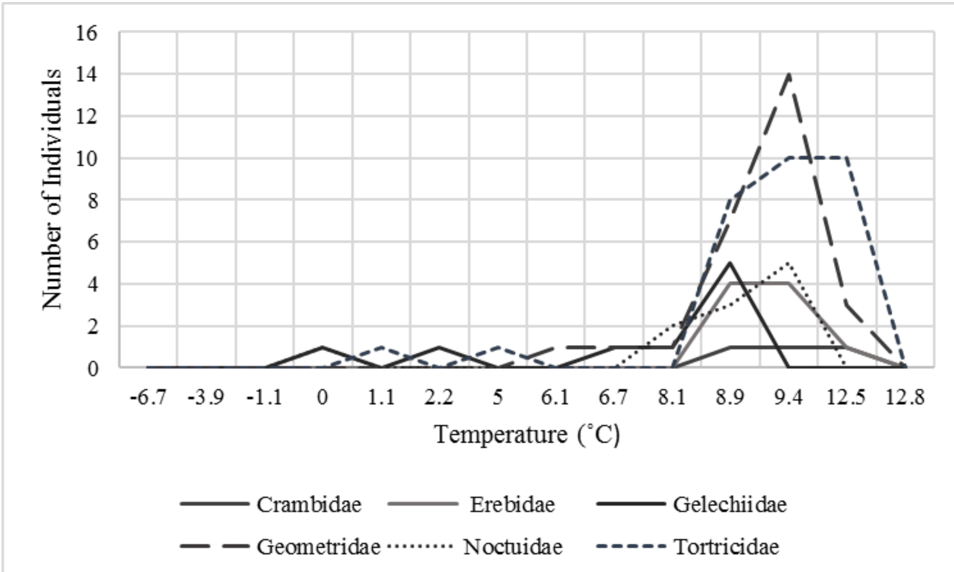

Figure 3. Number of individuals (by family) captured per temperature. Measured in degrees Celsius. Collection period from January to March 2017, Maryville College Woods, Maryville Tennessee (US).

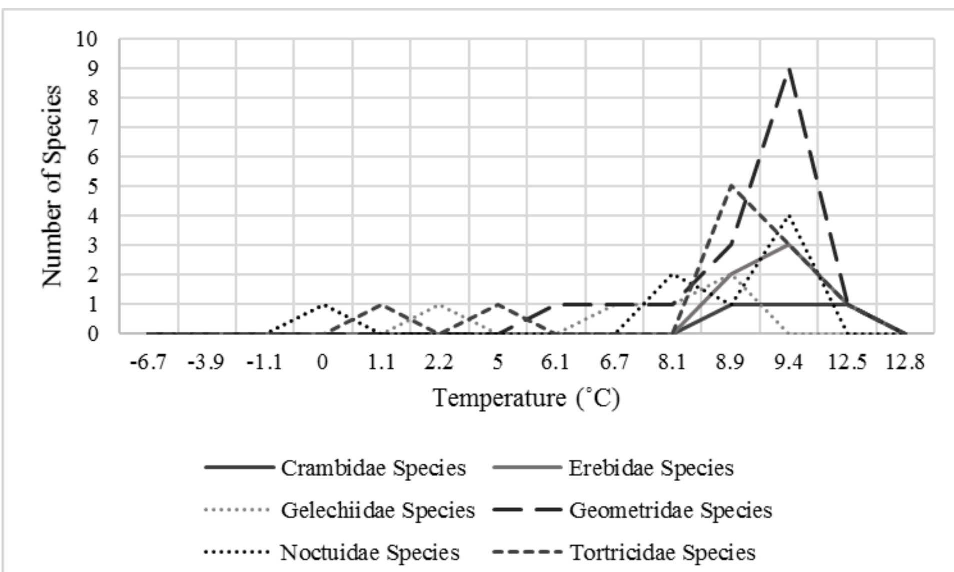

Figure 4. Number of species (by family) captured per temperature. Measured in degrees Celsius. Collection period from January to March 2017, Maryville College Woods, Maryville Tennessee (US).

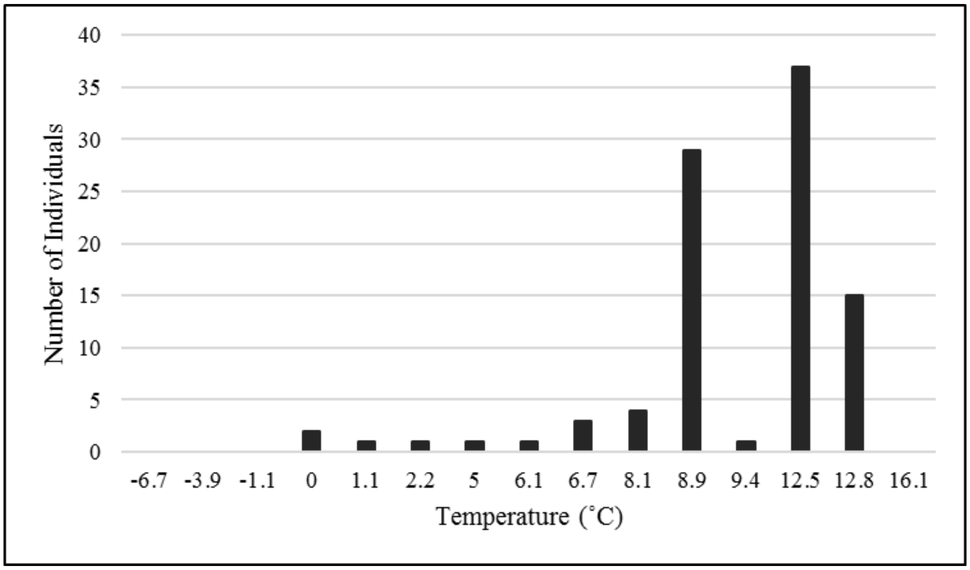

Figure 5. Number of individual moths captured by temperature. Measured in degrees Celsius. Collection period from January to March 2017, Maryville College Woods, Maryville Tennessee (US).

CHAPTER IV

DISCUSSION

Moth flight was observed during the winter months of 2017, from January to March. There was a wide range of temperatures over this period, with the highest observed temperature in the month of January at 16.1˚C at dusk on the 25th and the lowest temperature recorded for the study overall at -6.7˚C at the 22:00 reading on March 15^{th}. Moth activity is often the greatest at dusk or just after sunset, and during this study the greatest activity was noted approximately 30 minutes to 90 minutes after dark. Because it was still too bright for the mercury vapor bulb to attract moths, as well as the general lack of moth activity before dusk, the majority of the catch of moths occurred between the hours of 19:00 and 20:00. This finding is consistent with previous studies which found that male moth flight began within thirty minutes of the sunset and ended for the majority of specimens after approximately one hour of darkness (Kan 2002).

Changes in atmospheric pressure affect insect flight and duration, though its influence is not nearly as critical as temperature for moth flight specifically. When the barometric pressure is high, moth activity is often low, but when the barometric pressure is dropping or variation in pressure is recorded, moth activity rises. The tympanal organs most moths have are receptive to atmospheric pressure, and in many studies, "troughs" or drops in atmospheric pressure have been correlated to higher overall catch of moths, though the definitive causal factor could not be determined as atmospheric pressure (Spalding 2015). In the Maryville College Woods study, the vast majority of the total moth catch was acquired between 767.3 and 767.6 mmHg, with very few moths observed on either end of the range from 754.4 and 765.2 mmHg and from 767.9 to 772.4 mmHg. This concentration can be attributed partially to the fact that moth activity is often lower at very high barometric pressures, as well as to the majority of catches occurring on two sampling days. What is not readily explained is the absence of specimens below 765 mmHg, as pressure drops and precipitation have been linked to higher moth activity in some reports. February 27th and March 6th marked the two most productive catch days; February 28th brought storms, and it briefly showered before sampling on March 6th, with heavy rains on March 7th. The fluctuations, rather than static low levels, of barometric pressures on these days could have impacted the catch rate. There are contradictory reports, however, such as a study in which steady barometric pressure was correlated with larger catches, whereas dropping barometric pressure was correlated with low catch rates (Young 1997). Skuhravý (1981) provided no recorded influence of atmospheric pressure or precipitation on the total catch of moths. In alignment with the vast majority of reports, the definitive factor determining moth flight was temperature. The highest total catch of male *Lymantria monacha* L. was observed between 15 to 22 °C. Once the temperature dropped below 10 °C there was no recorded flight activity (Skuhravý 1981). Temperature is a critical factor in determining moth abundance and distribution of Lepidoptera, as it determines their larval development, flight patterns, and mating seasons (Spalding 2015).

In this study, it is important to note that even though moths were caught at temperatures ranging from 0 to 6.1˚C, there is possible error given that though the sheet was continually checked, some moths may have landed on the shaft of the lightbulb where they would not be noticed, and merely flew quickly to the sheet during or after the temperature dropped below their flight temperature range. This information could be of importance when considering outlier individuals, such as the two individuals (Noctuid and Gelechiid) observed at 0˚C over the course of the study.

Chill-coma temperatures are the temperatures at which activity in flight muscles ceases, and movement stops. Moths are known to “shiver” at temperatures just above their chill-coma temperatures as a means of warming their flight muscles. Previous research measured chill-coma temperatures for moths and found that they were between -2.0˚C and 0˚C. In this study, Noctuid moths were found in the range of 0˚C to 9.4˚C, consistent with previous studies. Previous research suggested that subfamily Cuculiinae could heat their flight muscles to temperatures above 30˚C for flight from ambient temperatures of 0˚C and slightly above freezing (Goller 1989). Moths observed within this subspecies in this study included *Eupsilia vinulenta*, *Lithophane bethunei*, and *Psaphida grandis*. Subfamily Hadeninae was the subject of a 2010 study across the GSMNP, in which *Mythimna unipuncta* and *Orthosia alurina* were both found. These two species were found in the Maryville College Woods and furthermore included in a comprehensive list of the Hadeninae of the Great Smoky Mountains National Park published in 1857. Larvae of *Mythimna unipuncta* and several other species of Tribe Leucaniini (9 species represented in the GSMNP) are grass feeders and significant agricultural pests (Pogue 2010). *Elaphria grata* was unique to this study, and not found in the original list of Hadeninae of the GSMNP or the study conducted by Pogue (2010). Moths of the subfamily Noctuinae were catalogued in a 2006 study of the taxa of the GSMNP. Forty-eight species of Noctuinae were collected in the National Park during this period, and according to calculations this total was approximately 91.4% of the total predicted species count for this subfamily in the park. Both *Anicla infecta* and *Cerastis tenebrifera*, the two species of Noctuinae documented in this study, were observed (Pogue 2006). Noctuids and Geometrids are some of the most widely studied families due to their flight ranges and endothermic behaviors. Prior to data collection in 2007, there were approximately 528 known species of Noctuid moths and 225 species of Geometrids in the National Park (Scholtens and Wagner 2007).

Geometridae was the most diverse family in this study, with 9 representatives out of a total 32 species. Geometrid moths are examples of thermoconformers, able to fly from -3˚C to approximately 25˚C. They were observed from 6.1˚C to 12.5˚C in the Maryville College Woods. Previous research has concluded that winter-flying Geometrids' ability to control body temperature is attributable to a morphological adaptation in which their thermal sensitivity to metabolic enzymes citrate synthase and pyruvate kinase were identical to that of winter and summer flying Noctuid and Sphingid moths, allowing their flight at low muscle temperatures (Marden 1995).

Family Erebidae, comprised of both large and smaller macrolepidoptera, was once part of Family Noctuidae. The species documented in a survey of the GSMNP in 1999 were likely tallied as Noctuids, as there was no family information in the full list of documented species (Scholtens and Wagner 2007). These moth species were observed from a range of 8.9˚C to 12.5˚C in the Maryville College Woods.

Crambidae was one of the more prevalent microlepidopteran families sampled in the comprehensive 1999 survey of the GSMNP, with 115 individual species found. Moths were documented by superfamily in the 2007 study, therefore there was no specific count for individual families and species (Scholtens and Wagner 2007). Members of this family observed in the Maryville College Woods were part of subfamily Pyraustinae and were observed at a temperature range of 8.9˚C to 12.5˚C.

Gelechiidae is one of the most abundant families within Order Lepidoptera, comprised of over 16,000 documented species. It has been estimated that a mere 25% of all Gelechiid species have been documented (Bucheli 2005). With 52 documented species in the GSMNP in 1999 and upcoming studies for the ongoing All Taxa Biodiversity Inventory project, it is likely that more species will be discovered. Moths were listed by superfamily in the 2007 survey, and there was no updated number beyond the 1999 survey (Scholtens and Wagner 2007). In the Maryville College Woods sample, both species of Gelechiids belonged to subfamily Gelechiinae and were found from 0˚C to 8.9˚C.

The microlepidopteran families tended to exhibit more limited temperature ranges, except that of family Tortricidae. This family had a range of 1.1˚C to 12.5˚C, the most variable range observed in this study. In 1999 there were 218 documented species of Tortricid moths in the GSMNP (Scholtens and Wagner 2007). There is no updated information on the species count of these organisms in the GSMNP, as the moths were listed by superfamily. One unknown species of family Gracillariidae was found in the Maryville College Woods, and is pending identification at the Mississippi Entomological Museum. In the 1999 survey of the GSMNP, there were 61 documented species of this family in the Park (Scholtens and Wagner 2007). Several species documented over the course of this study were undocumented in the GSMNP, such as *Elaphria Grata* and Gracillariidae sp., or are ecological pests such as *Mythimna unipuncta*.

As urbanization and habitat destruction become more prevalent, ecosystems and their endemic species can be threatened or altered with the addition of buildings, roads, highways, and other human made obstacles to continuous natural areas. Forest fragmentation specifically can influence diversity of insect populations and community-wide interactions. (Didham 1996). Though on a much smaller scale than studies conducted in the GSMNP, with further study and continued sampling, monitoring the species diversity of habitats like the Maryville College Woods can provide valuable insight into isolation and fragmentation-induced shifts in biodiversity and ecosystem function.

Taxonomic Descriptions of Observed Specimens

Family Crambidae

These "grass moths" belong to the superfamily Pyraloidea, and are often referred to as "snout moths." There are over 11,000 species worldwide within this family, with more than 800 species in North America. This family is highly variable in morphology and larval habits.

Subfamily Pyraustinae

Species in this subfamily include *Palpita magniferalis* and *Udea rubigalis*.

Family Erebidae

Members of the superfamily Noctuoidea, this family was previously a subfamily under family Noctuidae, but now includes many subfamilies which were previously in the noctuid category.

Subfamily Eribinae

Species in this subfamily include *Phoberia atmosana*, *Zale duplicata* and *Zale intenta*.

Subfamily Hypeninae

The cubitus of the hindwing appears to have four branches. The M2 is moderately curved and parallel to the M3. The eyes are lashed. Labial palps are very long, usually at least twice the size of the head. Members of this subfamily are typically blackish with dull patterns – at rest the wings form a triangle, and these moths are often referred to as "deltoids" for this reason. Species in this subfamily include *Hypena scabra*.

Family Gelechiidae

This diverse family is part of superfamily Gelechioidea, including small to very small moths, with wingspans of 0.7 to 2.5cm (average 1 to 2cm). The heads are tooth-scaled; the maxillary palps are segmented into four parts and folded over the base of the proboscis. Labial palps are long and curved upwards, with the third segment long and tapered. The hind tibia has long hair-scales. The forewings are narrowly rounded or pointed at the tips, the hindwings of most species are trapezoidal, with the outer margin concave below the apex. The larval habits vary widely within this family, including leaf miners, tiers, fruit and seed feeders, and stem gall makers; many pests which eat stored grain belong to this family.

Subfamily Gelechiinae

Species in this subfamily include *Chionodes* sp. and *Sinoe chambersi*.

Family Geometridae

This family is part of superfamily Geometroidea. Commonly referred to as inchworm or geometer moths, this group is comprised of small to medium-sized moths, with slender bodies and wide wingspans. Their wingspans are typically 1 to 6 centimeters, with wingless females in some species. Their labial palps are short and turned up, and they have unscaled proboscises. Males usually have bipectinate antennae, while females have simple antennae. Their tympanal cavities are located ventrolaterally at the base of the abdomen, opening anteriorly. Their wing venation involves a fusing of 1A and 2A veins to the forewing base. M_2 of the forewing is typically closer to M than to M_3. The forewing and hindwing often have similar coloration, with linear patterns continuing from the forewing to the hindwing. The larvae of these moths are usually twiglike. The first two to three pairs of abdominal prolegs will be absent. This causes the larvae to move by extending their front end as far as possible, then looping the rear of their bodies up to meet it, thus the common name of "inchworms." They feed externally on leaves, and pupate in leaf litter or soil in loose cocoons.

Subfamily Ennominae

This group is typically comprised of the "grays." This is the largest subfamily, with 751 known North American species. It contains many small to medium-sized species, and the largest inchworm moths. Colors and patterns vary, but the majority are gray to light brown. The M_2 of the hindwings of these moths is thinner than the M_1 and M_3, sometimes a simple fold in a membrane. Specimens within this subfamily include *Cleora sublunaria*, *Ectropis crepuscularia*, *Eutrapela clemataria*, *Ilexia intracta*, *Iridopisis defecta*, *Macaria aequiferaria* and *Melanolophia canadaria*.

Subfamily Larentiinae

This group is often referred to as the "carpets." The majority are small to medium-sized moths, with complex forewing patterns and simple hindwing patterns. This is the second largest subfamily, with 467 known North American species. Specimens within this subfamily include *Eupithecia miserulata* and *Eupithecia* sp.

Family Noctuidae

Members of superfamily Noctuoidea, this family is often referred to as the "owlet" or noctuid moths; it is the largest family in the Lepidoptera, with approximately 20,000 species globally and 2,900 in North America. Some members of this family are brightly colored, but most are gray to brown with complex patterns of spots and lines. The orbicular and reniform spots are usually visible, though in some species they may appear obscure. In most species the hindwing pattern is simpler than the forewing. When at rest, most noctuid moths hold their wings rooflike over their bodies, resembling arrowheads or triangles when viewed laterally. These moths are small to large, with wingspans of 1.2-17cm, the average moths in this family with wingspans falling between 2 and 4.5cm. Their bodies are thick, and usually hairy. The labial palps are long and upturned, with a well-developed proboscis. Their antennae are simple to bipectinate. The tympanum is on the side of the metathorax below the hindwing base and opens outward or toward the rear. The frenulum of these moths is always well developed. Noctuid moths pupate in cavities in the soil or in food plants, or in silk cocoons. Adults of most species are nocturnal, but may be active during the day.

Subfamily Cuculliinae

This subfamily has conspicuous lashes (rows of bristles) in front of and behind the eye. The cubitus (longitudinal wing vein between veins Media (M) and 1A, which normally ends in two branches) of the hindwing appears to be three-branched. Many adults are active in late fall, winter, and early spring. Species in this subfamily include *Eupsilia vinulenta*, *Lithophane bethunei*, and *Psaphida grandis*.

Subfamily Hadeninae

This is the only subfamily besides Pantheinae which has hairy eyes. The cubitus of the hindwing appears to have three branches. Species in this subfamily include *Elaphria grata*, *Mythimna unipuncta*, and *Orthosia alurina*.

Subfamily Noctuinae

The forewing of moths in this subfamily is usually brownish. The orbicular and reniform spots are often conspicuous. Spines are present on middle and (often) hind tibiae. The cubitus of the hindwing appears to have three branches. The eye is smooth. It is important to note that in many recent publications this subfamily is referred to as Agrotinae. Species in this subfamily include *Anicla infecta* and *Cerastis tenebrifera*.

Family Tortricidae

This family belongs to superfamily Tortricoidea, and is comprised of small to medium-small moths, with average wingspans of 1cm to 3.3cm. The head is usually rough-scaled. The proboscis is naked, with filiform (threadlike) antennae. The maxillary palps are small, and the labial palps usually project forward. The wings of these moths are moderately broad, and held like a flattened roof at rest, making the moths resemble small arrowheads. The larvae of this family are leaf rollers, leaf tiers, or borers in roots, stems, or fruits – for this reason many of them are voracious forest and orchard pests.

Subfamily Olethreutinae

This subfamily is sometimes considered its own separate family. They tend to be grayish to brownish with complex, obscure forewing mottling and lines. There is a fringe of long hair-scales along the base of the cubitus on the upper side of the hindwing. Species in this subfamily include *Chimoptesis pennsylvaniana*, *Chimoptesis* sp., *Epinotia vertumnana*, and *Gretchena bolliana*.

Subfamily Tortricinae

Moths in this subfamily lack the fringe along the base of the cubitus and usually have a paler forewing; it can be reddish, yellowish or pale brown with a sharper pattern. Species in this subfamily include *Argyrotaenia floridana* and *Argyrotaenia velutinana*.

APPENDIX

List of Species

1. Anicla infecta (Ochs.)
2. Argyrotaenia floridana Obraztsove
3. Argyrotaenia velutinana (Walker)
4. Cerastis tenebrifera (Walker)
5. Chimoptesis pennsylvaniana (Kearfott)
6. Chimoptesis sp.
7. Chionodes sp.
8. Cleora sublunaria (Guenee)
9. Ectropis crepuscularia (Denis & Schiffermuller)
10. Elaphria grata Hubner
11. Epinotia vertumnana (Zeller)
12. Eupithecia miserulata Grote
13. Eupithecia sp.
14. Eupsilia vinulenta (Grote)
15. Eutrepela clemataria (J.E. Smith)
16. Gretchena bolliana (Slingerland)
17. Hypena scabra (Fabricius)
18. Ilexia intracta (Walker)
19. Iridopsis defectaria (Guenee)
20. Lithophane bethunei (Grote & Robinson)
21. Macaria aequiferaria Walker
22. Melanolophia canadaria choctawae Rindge
23. Mythimna unipuncta (Haworth)
24. Orthosia alurina (Smith)
25. Palpita magniferalis (Walker)
26. Phoberia atomaris Hubner
27. Psaphida grandis Smith
28. Sinoe chambersi Lee
29. Udea rubigalis (Gn.)
30. Zale duplicata (Bethune)
31. Zale intenta (Walker)
32. Unknown, Family Gracillariidae

REFERENCES

Bucheli, Sibyl Rae. Systematics of the megadiverse superfamily gelechioidea (Insecta: Lepidoptera). Diss. The Ohio State University, 2005.

Casey, Timothy M., and Barbara A. Joos. "Morphometrics, conductance, thoracic temperature, and flight energetics of noctuid and geometrid moths." Physiological Zoology 56.2 (1983): 160-173.

Choi, Sei-Woong. "Moth Diversity and Identification of Indicator Species in Temperate Forests of Southern South Korea." Annals of the Entomological Society of America 104(5):952-959. September 2011.

Covell, C. V. "Eastern moths." Peterson Field Guide. Houghton Mifflin Company, Boston (1984).

Covell, C.V., Jr. 2005. A field guide to moths of eastern North America. Virginia Museum of Natural History, Martinsville, VA.

Didham, Raphael K., et al. "Insects in fragmented forests: a functional approach." Trends in Ecology & Evolution 11.6 (1996): 255-260.

Esch, Harald. "The effects of temperature on flight muscle potentials in honeybees and cuculiinid winter moths." Journal of experimental biology 135.1 (1988): 109-117.

Goller, Franz, and Harald Esch. "Comparative study of chill-coma temperatures and muscle potentials in insect flight muscles." Journal of Experimental Biology 150.1 (1990): 221-231.

Hanegan, James L., and James Edward Heath. "Temperature dependence of the neural control of the moth flight system." Journal of Experimental Biology 53.3 (1970): 629-639.

Harvell, C. Drew, et al. "Climate warming and disease risks for terrestrial and marine biota." Science 296.5576 (2002): 2158-2162.

Heinrich, Bernd. "Thermoregulation by winter-flying endothermic moths." Journal of Experimental Biology 127.1 (1987): 313-332.

Kan, Eiko, et al. "Dusk mating flight in the swift moth, Endoclita excrescens (Butler)(Lepidoptera: Hepialidae)." Applied Entomology and Zoology 37.1 (2002): 147-153.

Lacey, Lawrence A., et al. "Entomopathogenic nematodes for control of codling moth (Lepidoptera: Tortricidae) in apple and pear orchards: Effect of nematode species and seasonal temperatures, adjuvants, application equipment, and post-application irrigation." Biological Control 37.2 (2006): 214-223.

Liu, Shu-sheng, et al. "Seasonal abundance of the parasitoid complex associated with the diamondback moth, Plutella xylostella (Lepidoptera: Plutellidae) in Hangzhou, China." Bulletin of entomological research 90.03 (2000): 221-231.

Marden, J. "Evolutionary adaptation of contractile performance in muscle of ectothermic winter-flying moths." Journal of experimental biology 198.10 (1995): 2087-2094.

National Park Service (NPS). “Great Smoky Mountains NP.” National Park Service Visitor Use Statistics. Web. 2015. < https://irma.nps.gov/Stats/Reports/Park/GRSM>

NOAA (National Oceanic and Atmospheric Administration). “State of the Climate.” (October, 2016). Web. 8 Nov. 2016. <http://www.ncdc.noaa.gov/sotc/>

Pogue, Michael G. "The Hadeninae (Lepidoptera: Noctuidae) of Great Smoky Mountains National Park, USA." Zootaxa 2380 (2010): 1-75.

Pogue, Michael G. “The Noctuinae (Lepidoptera: Noctuidae) of Great Smoky Mountains National Park, USA.” Magnolia Press, 2006.

Pogue, Michael G. "The Plusiinae (Lepidoptera: Noctuidae) of Great Smoky Mountains National Park." Zootaxa 1032 (2005): 1-28.

Rydell, Jens, and Winston C. Lancaster. "Flight and thermoregulation in moths were shaped by predation from bats." Oikos 88.1 (2000): 13-18.

Schmidt, B. C. "Taxonomic reassessment of Zale lunifera (Hiibner)(Erebidae, Erebinae)." Contributions to the Systematics of New World Macro-Moths II 39 (2010): 99.

Schmidt-Nielsen, Knut. Animal physiology: adaptation and environment. Cambridge University Press, 1997.

Scholtens, Brian G., and David L. Wagner. "Lepidoptera of Great Smoky Mountains National Park: methods and results of the inventory." Southeastern Naturalist 6.sp2 (2007): 193-206.

Shirai, Yoichi. "Seasonal changes and effects of temperature on flight ability of the diamondback moth, Plutella xylostella (L.)(Lepidoptera: Yponomeutidae)." Applied Entomology and Zoology 26.1 (1991): 107-115.

Skuhravý, V. and Zumr, Ing. V. (1981), Nocturnal and seasonal flight activity of the nun moth Lymantria monacha L. (Lepidoptera, Lymantriidae) as determined by pheromone and light traps. Zeitschrift für Angewandte Entomologie, 92: 315–319.

Spalding, Adrian. Loe Bar and the Sandhill Rustic Moth: The Biogeography, Ecology and History of a Coastal Shingle Bar. Brill, 2015.

Summerville, Keith S., and Thomas O. Crist. "Temporal patterns of species accumulation in a survey of Lepidoptera in a beech-maple forest." Biodiversity & Conservation 14.14 (2005): 3393-3406.

Svensson, Mats GE, Jens Rydell, and Richard Brown. "Bat predation and flight timing of winter moths, Epirrita and Operophtera species (Lepidoptera, Geometridae)." Oikos (1999): 193-198.

Visser, Marcel E., and Leonard JM Holleman. "Warmer springs disrupt the synchrony of oak and winter moth phenology." Proceedings of the Royal Society of London B: Biological Sciences 268.1464 (2001): 289-294.

Young, Mark. The Natural History of Moths. A&C Black, 1997.