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LOCAL IMPACTS OF WHITE-NOSE SYNDROME ON THE FORAGING  
ECOLOGY OF INSECTIVOROUS BATS

By

Shelby Ann Fulton

Thesis Approved:



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Chair, Advisory Committee



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Member, Advisory Committee



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Member, Advisory Committee



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Dean, Graduate School

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June 7<sup>th</sup>, 2017

LOCAL IMPACTS OF WHITE-NOSE SYNDROME ON THE FORAGING ECOLOGY OF INSECTIVOROUS BATS

By

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Bachelor of Science  
University of Kentucky  
Lexington, Kentucky  
2015

Submitted to the Faculty of the Graduate School of  
Eastern Kentucky University  
in partial fulfillment of the requirements  
for the degree of  
MASTER OF SCIENCE  
August, 2017

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DEDICATION

For my parents.

#### ACKNOWLEDGEMENTS

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## ABSTRACT

Lepidoptera are a core resource for many of North America's insectivorous bats. These predators consume Lepidoptera of varying sizes, and some bat species remove the wings prior to consumption. Selection of larger prey and subsequent wing removal may allow bats to optimize the energetic value afforded by Lepidoptera. In Chapter 1, I explore the relationships between caloric yield, body size, and wing presence. Laboratory-reared *Trichoplusia ni* moths were grouped into large and small size classes, and wings were removed from half the moths in each size class. Bomb calorimetry was used to determine the gross heat (cal/g) of moths in each treatment. To account for potential differences in energetic value among species, specimens of *Malacosoma americanum*, *Halysidota tessellaris*, and *Iridopsis* sp. moths were also combusted. Larvae of *M. americanum* were field-collected in April 2012 and reared in the laboratory. Adult *H. tessellaris* and *Iridopsis* sp. moths were wild-caught using an illuminated substrate at Mammoth Cave National Park in June – July 2015. No energetic differences were detected for size class or wing condition of *T. ni*. Additionally, no differences were detected in the caloric yields of the species analyzed, except between *Ma. americanum* and *Iridopsis* sp. ( $P = 0.03$ ). These results suggest that Lepidoptera of various species and sizes may be of similar prey quality, and that the removal of wings by bats may be unrelated to caloric yield. Even so, I believe the lack of differences detected in this study indicate that my approach was likely too coarse of a method to capture subtle energetic differences.

Recent advances in high-throughput gene-sequencing technology have provided the opportunity for bat dietary studies to be conducted with high resolution; in Chapter 2, I describe methods for refining PCR parameters with the intent to maximize amplicon yield. Fecal pellets were collected in May and August of 2011 and 2016 from a maternity colony of *Corynorhinus rafinesquii* and stored in 95% ethanol at  $-80^{\circ}\text{C}$ . Insect DNA was extracted on a per-pellet basis and amplified by PCR; reaction parameters and reagent quantities were experimentally manipulated to determine optimal primer concentration, annealing temperature, and number of PCR cycles. Mean amplicon yield did not differ significantly across years, indicating that samples were preserved successfully and allowing future temporal comparisons to be made. Samples amplified with  $0.5\ \mu\text{M}$  primers had significantly higher mean DNA yield than those



amplified with 0.4  $\mu$ M primers ( $P = 0.02$ ). Mean amplicon yield differed significantly across annealing temperatures ranging from 50°C to 60°C in a gradient PCR ( $P = 0.008$ ). Number of PCR cycles was also significant ( $P = 0.0002$ ); samples amplified with 35 cycles had greater amplicon yield than those amplified with 30 cycles. These results suggest that optimal PCR conditions for bat dietary studies may include a 1:20 ratio of primer volume to total reaction volume, a 52°C annealing temperature, and 35 PCR cycles, although the optimal number of PCR cycles may be reagent-dependent.

White-nose Syndrome (WNS) has devastated the insectivorous bats of eastern North America, resulting in dramatic population declines and shifting foraging niches. In Chapter 3, I investigate the effects of WNS, as well as prescribed fire and insect availability, on bat assemblage diversity and composition. Acoustic bat surveys and concurrent insect sampling were conducted at Mammoth Cave National Park before and after the first on-site detection of WNS. Echolocation calls were classified by phonic group (low-, mid-, or *Myotis*-frequency). All insects were identified to order, and Lepidoptera were clustered into six classes defined by wingspan and characterized by mean dry weight and caloric values. Mean wingspan differed significantly across all size classes ( $P < 0.05$ ), suggesting that my classification was effective. Model selection determined that the best-fitting model for diversity of bat phonic groups included the relative abundance of dominant insect orders as well as WNS; WNS was the only significant term ( $P < 0.05$ ). A competing model included only WNS and was also significant ( $\Delta AICc = 1.22$ ,  $P < 0.05$ ). A distance-based redundancy analysis of the bat assemblage in relation to the relative abundances of dominant insect orders, burn history, and WNS was significant ( $P < 0.05$ , 999 permutations). Model selection found that the best-fitting model for Lepidoptera size class distribution included only WNS ( $P < 0.05$ ). My results implicate WNS as the primary driver of bat assemblage composition, but the magnitude of WNS masks more subtle processes. The indirect effects of WNS on Lepidoptera remain unclear, but my research suggests shifts in the composition of this assemblage following the arrival of WNS at Mammoth Cave National Park.

## TABLE OF CONTENTS

CHAPTER	PAGE
1 Evaluating the energetic value of Lepidoptera using bomb calorimetry .....	1
Introduction .....	1
Methods.....	2
Results.....	4
Discussion .....	4
2 Laboratory methods for maximizing DNA yield from bat fecal pellets .....	6
Introduction .....	6
Methods.....	7
Results.....	9
Discussion .....	9
3 Understanding relationships between bats and their insect prey following the arrival of White-nose Syndrome to a fire-managed landscape.....	11
Introduction .....	11
Methods.....	13
Results.....	15
Discussion .....	16
IMPLICATIONS.....	19
LITERATURE CITED .....	20
APPENDICES .....	26
A Tables .....	27
B Figures .....	34
C List of Lepidoptera known to occur at Mammoth Cave National Park and corresponding size and energetic metrics. ....	47
D Percent of Lepidoptera species occurring at Mammoth Cave National Park in each of six size classes.....	64
E Percent composition of Lepidoptera size classes by family; the families Erebidae, Geometridae, and Noctuidae are highlighted due to their abundance and importance as prey resources for insectivorous bats. ....	66

LIST OF TABLES

TABLES	PAGE
1.1. Summary of <i>Trichoplusia ni</i> , <i>Malacosoma americanum</i> , <i>Halysidota tessellaris</i> , and <i>Iridopsis</i> sp. treatments.....	28
3.1. Size-based classification for Lepidoptera based on 541 species in 28 families collected at Mammoth Cave National Park, Kentucky. ....	29
3.2. Pre- and post-WNS compositions of bat assemblages (organized by phonic group), insect communities, and Lepidoptera assemblages at Mammoth Cave National Park, Kentucky based on 4,760 echolocation passes and collection of 125,445 insects. ....	30
3.3. Summary of support for candidate models for the diversity of bat phonic groups (low-, mid-, or <i>Myotis</i> -frequency) acoustically detected at Mammoth Cave National Park, Kentucky, calculated as the reciprocal of Simpson’s Diversity ( $1/D$ ). . . . .	31
3.4. Summary of the coefficients and significance of fixed effects in the best-fitting linear mixed models for bat phonic diversity at Mammoth Cave National Park, Kentucky, selected using an information theoretic approach. ....	32
3.5. Summary of support for candidate models for the diversity of Lepidoptera size classes (classification presented in this work) observed at Mammoth Cave National Park, Kentucky, calculated as the reciprocal of Simpson’s Diversity ( $1/D$ ). . . . .	33
C.1. List of Lepidoptera known to occur at Mammoth Cave National Park and corresponding size and energetic metrics. ....	48

LIST OF FIGURES

FIGURES	PAGE
1.1. Cotton sheet deployed at Mammoth Cave National Park to sample Lepidoptera, illuminated by 10-W black lights with electrical harnesses. ....	35
1.2. Mean ( $\pm$ standard error) gross heat (cal/g) generated by combustion of coarsely ground samples of <i>Malacosoma americanum</i> , <i>Trichoplusia ni</i> , <i>Halysidota tessellaris</i> , and <i>Iridopsis</i> sp. using bomb calorimetry. ....	36
1.3. Mean ( $\pm$ standard error) gross heat (cal/g) generated by combustion of coarsely ground <i>Malacosoma americanum</i> samples using bomb calorimetry. ....	37
1.4. Mean ( $\pm$ standard error) gross heat (cal/g) generated by combustion of coarsely ground <i>Trichoplusia ni</i> samples using bomb calorimetry.....	38
2.1. Mean ( $\pm$ standard error) amplicon concentration (nM) of insect DNA extracted and amplified from bat fecal pellets collected in 2011 ( $n = 55$ ) and 2016 ( $n = 55$ ) at Mammoth Cave National Park, Kentucky. ....	39
2.2. Mean ( $\pm$ standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at Mammoth Cave National Park, Kentucky and amplified with either 0.4 or 0.5 $\mu$ M forward and reverse primer.....	40
2.3. Mean ( $\pm$ standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at Mammoth Cave National Park, Kentucky and amplified with a gradient PCR procedure. ....	41
2.4. Mean ( $\pm$ standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at Mammoth Cave National Park, Kentucky and amplified with either 30 or 35 PCR cycles. ....	42
3.1. Graphical approach to selecting an ideal numbers of clusters for a size-based classification of 541 species of Lepidoptera collected at Mammoth Cave National Park, Kentucky.....	43
3.2. Empirically-determined relationship of Lepidoptera dry weight to wingspan, based on 47 species collected at Mammoth Cave National Park, Kentucky.....	44
3.3. Mean ( $\pm$ standard error) wingspan of 7,842 Lepidoptera, collected at Mammoth Cave National Park, Kentucky, in each of six size classes defined in this work. ....	45
3.4. Biplot visualizing the results of distance-based redundancy analysis. ....	46
D.1. Percent of Lepidoptera species occurring at Mammoth Cave National Park in each of six size classes. ....	65
E.1. Percent composition of Lepidoptera size classes by family; the families Erebidae, Geometridae, and Noctuidae are highlighted due to their abundance and importance as prey resources for insectivorous bats.....	67

## CHAPTER 1

### Evaluating the energetic value of Lepidoptera using bomb calorimetry

#### *Introduction*

Lepidoptera are a core resource for many of North America's insectivorous bats, and have been detected in the diets of all Kentucky bat species tested (Lacki et al. 2007). The gleaning species *Myotis septentrionalis* and *Corynorhinus rafinesquii* are Lepidoptera specialists, with this insect order representing nearly 50% of the diet of *M. septentrionalis* (Dodd et al. 2012a) and more than 80% of the diet of *C. rafinesquii* (Lacki and Dodd 2011). Lepidoptera are also common in the diets of more generalist predators, including *Myotis lucifugus*, *Myotis sodalis*, and *Perimyotis subflavus*. Although *M. lucifugus* and *M. sodalis* may consume diverse diets, these species often rely on Lepidoptera (Brack and LaVal 1985, Whitaker 2004, Feldhamer et al. 2009, Clare et al. 2014). The generalist predator *P. subflavus* opportunistically consumes soft-bodied arthropods, including Lepidoptera (Whitaker 2004, Lacki et al. 2007, Dodd et al. 2014).

The ubiquity of Lepidoptera as a prey resource for insectivorous bats is thought to be a consequence of high digestive efficiency. The carbohydrate chitin, which forms arthropods' hard exoskeletons, is difficult for most mammals to digest (Strobel et al. 2013). However, some bat species have the ability to optimize digestion of arthropod prey due to specialized gastrointestinal microflora (Strobel et al. 2013, Whitaker et al. 2004). These bats, including *M. septentrionalis*, *M. lucifugus*, *M. sodalis*, and *P. subflavus*, host chitinase-producing bacteria in the digestive tract (Whitaker et al. 2004). The enzyme chitinase promotes the breakdown of chitin, but does not allow it to be completely digested. As a result, insects with high chitin levels have low digestive efficiency (Barclay et al. 1991).

Some bats (e.g., *Corynorhinus* species) reject body parts of Lepidoptera, such as the legs and wings (Lacki and Dodd 2011). This behavior may be a result of low palatability, but is thought to be due to low digestibility of these chitin-rich structures (Barclay et al. 1991). Smaller moths

have lower digestive efficiency, likely due to the increased difficulty of removing indigestible or unpalatable structures from small prey (Barclay et al. 1991). Although larger moths are more digestible, it is not yet clear whether selection of larger moths affords a caloric benefit.

The relationships between caloric yield, body size, and wing presence are poorly understood. Thus, my objectives were: (1) explore the relationships between caloric yield, body size, and wing presence by determining the mean gross heat (cal/g) generated across large, small, winged, and wingless representatives of a model species of Lepidoptera (*Trichoplusia ni*), (2) investigate potential differences in energetic value among species by using bomb calorimetry to combust *Malacosoma americanum*, *Halysidota tessellaris*, and *Iridopsis* sp. moths, and (3) evaluate the viability of bomb calorimetry as a method of conducting prey quality studies.

### *Methods*

*Malacosoma americanum* tents and larvae were field-collected in April 2012 at Mammoth Cave National Park. Tents were placed in plastic housing (32 cm × 26 cm × 9 cm) lined with paper towels to absorb moisture and provide substrate. The developing insects were supplied *ad libitum* with fresh, field-collected *Prunus* sp. foliage. Throughout the three-week rearing process, some tents were discarded to maintain hygienic conditions. Pupae were subsequently removed from plastic housing and placed individually in plastic diet cups (30 mL) until emergence. Adult moths were flash-frozen within 24 hours of emergence; adult moths (in diet cups) were submerged in liquid nitrogen for 5 – 10 seconds, and immediately stored in a -80°C freezer.

Larvae of *T. ni* were reared communally from 25 eggs on 110 g of a pinto bean-based diet in a 240-mL Styrofoam cup kept at ambient conditions (Evenden and Haynes 2001). Other details of the rearing methods are described by Shorey and Hale (1965). Pupae were separated, sexed, placed individually in diet cups (30 mL), and flash-frozen in liquid nitrogen within 24 hours of adult emergence. Specimens were then stored in a -20°C freezer. Adult *T. ni* were divided into large and small size classes (individual masses of  $118 \pm 0.80$  and  $87 \pm 0.69$  mg, respectively), and wings were removed from half of the moths in each size class.

Wild-caught moths were collected from June – July 2015 at the Mammoth Cave International Center for Science and Learning. A cotton sheet was hung vertically and stretched taut at ground level; the sheet was illuminated between approximately 2000 and 2300 hours with a 10-W black light and electrical harness <sup>1</sup>(Universal Light Trap, Bioquip Products, Rancho Dominguez, CA; Figure 1.1). Lepidoptera attracted to the sheet were collected in plastic diet cups and immediately placed on ice. Specimens were temporarily stored at -18°C and transferred to -80°C within 7 days. Although numerous taxa were collected, *H. tessellaris* and *Iridopsis* sp. were selected for combustion due to their abundance and conspicuous appearances (Covell 2005).

To prepare for combustion, all frozen Lepidoptera were transferred to open, heat-resistant vials and dried in a 55°C oven for approximately 24 hours. Specimens were consolidated by treatment (Table 1.1) and ground with a mortar and pestle for 30-60 seconds until a coarse powder was attained. A Parr 1281 Oxygen Bomb Calorimeter (Parr Instrument Company, Moline, IL) was calibrated daily using a 1.0 g benzoic acid pellet (Parr Instrument Company, Moline, IL). To determine whether sample weight affects gross heat generated by bomb calorimetry, *Ma. americanum* samples weighing 200 – 250 mg, 400 – 450 mg, 600 – 650 mg, and 800 – 850 mg were combusted. Following this assessment of methods, a standard sample weight of 250 mg was used for *T. ni*, *H. tessellaris*, and *Iridopsis* sp. treatments. The number of bomb calorimetry samples combusted was dependent upon the volume of processed Lepidoptera material available for each treatment. All treatments were combusted according to instructions provided by the bomb calorimeter manufacturer.

Mean gross heat (cal/g) generated by combustion was determined for each treatment. A one-way analysis of variance (ANOVA) was used to test for differences between *Ma. americanum* sample weight classes, and a 2×2 ANOVA was used to test for differences between *T. ni* treatments. To test for potential differences in energetic value among species, Wilcoxon Rank-Sum tests were used to make pairwise comparisons given the non-normal distribution of the response variable as indicated by a Kolmogorov-Smirnov test ( $P < 0.05$ ).

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<sup>1</sup> All figures and tables are presented in appendices at the end of this document.

## Results

The mean caloric yields of *Ma. americanum* ( $5126.6 \pm 31.8$  cal/g) and *Iridopsis* sp. ( $5039.5 \pm 19.8$  cal/g) differed significantly ( $W_{5,4} = 19$ ,  $P = 0.03$ ; Figure 1.2), although no additional differences in mean caloric yield were detected between pairwise comparisons including *T. ni* ( $5052.3 \pm 79.0$  cal/g) or *H. tessellaris* ( $5127.5 \pm 25.6$  cal/g). The mean caloric yields of *Ma. americanum* samples weighing 200 – 250 mg ( $5126.6 \pm 31.8$  cal/g), 400 – 450 mg ( $5160.8 \pm 30.9$  cal/g), 600 – 650 mg ( $5289.4 \pm 109.1$  cal/g), and 800 – 850 mg ( $5286.8 \pm 28.0$  cal/g) did not differ significantly ( $F_{3,14} = 1.6$ ,  $P > 0.05$ ; Figure 1.3). The mean caloric yields of small *T. ni* with wings removed ( $5138.3 \pm 26.8$  cal/g), small *T. ni* with wings present ( $4996.3 \pm 32.7$  cal/g), large *T. ni* with wings removed ( $4869.1 \pm 314.7$  cal/g), and large *T. ni* with wings present ( $5205.78 \pm 20.6$  cal/g) were not significantly different ( $F_{3,23} = 0.86$ ,  $P > 0.05$ ; Figure 1.4).

## Discussion

The lack of differences detected between *Ma. americanum* sample weight classes suggests gross heat generated by combustion is not likely affected by sample weight. These data indicate that any sample weight (adhering to manufacturer's specifications for safe calorimeter usage) could be combusted effectively. Based on these findings, I recommend that future studies reduce sample weights to conserve raw material and maximize the number of combustion reactions possible.

No differences in energetic value were detected between any *T. ni* treatment, suggesting that the removal of Lepidoptera wings by bats may be unrelated to caloric yield. These results support the commonly accepted hypothesis that bats reject the wings of Lepidoptera due to indigestibility (Barclay et al. 1991, Lacki and Dodd 2011). The lack of any significant differences between large and small *T. ni* indicates that caloric yield is independent of body size. However, *Ma. americanum* appears to have a significantly greater caloric yield than *Iridopsis* sp., likely due to the larger body size of *Ma. americanum*. This explanation is supported by previously published literature regarding the energy density of fish; Glover et al. (2010) found that the



caloric yield of Largemouth Bass is directly related to body mass, with larger individuals generally possessing greater energetic density.

Given that Lepidoptera are relatively soft-bodied (Freeman 1981), I suspect these prey may have comparatively less chitin than many insect orders, thus allowing predators to maximize digestive efficiency. Although it is likely that consuming Lepidoptera affords a digestive advantage, the similarity in energetic value among study species may suggest that Lepidoptera of various species and sizes are of similar prey quality. However, based on the inconsistency of my results regarding caloric yield and body size, I believe the lack of differences detected in this study indicates that my technique is likely too coarse of a method to capture subtle energetic differences among Lepidoptera. Future studies including additional insect orders will clarify the potential limitations of conducting prey quality studies by bomb calorimetry.

## CHAPTER 2

### Laboratory methods for maximizing DNA yield from bat fecal pellets

#### *Introduction*

Bat diets have historically been analyzed using morphological fecal analysis, however, this technique offers low resolution data and investigators using this method typically identify prey only at the ordinal or familial levels (Brigham 1990, Hamilton and Barclay 1998, Lacki et al. 1995, Whitaker 1988). Recent advances in gene-sequencing technology have provided the opportunity for dietary studies with much higher resolution; molecular techniques are increasingly being used to provide species-level identification using the DNA of prey extracted from bat fecal material (Clare et al. 2009, 2014, Dodd et al. 2012a, Razgour et al. 2011, Zeale et al. 2011). Although many molecular dietary studies have relied on classical sequencing methods (Clare et al. 2009, Dodd et al. 2012a, Zeale et al. 2011), high-throughput sequencing can increase sequencing efficiency (Bohmann et al. 2011, Pompanon et al. 2012, Shokralla et al. 2012) and provide a more thorough assessment of dietary composition (Bohmann et al. 2011, Razgour et al. 2011).

The methodology associated with modern molecular methods of bat dietary analysis necessarily involves amplification of insect DNA by polymerase chain reaction (Clare et al. 2014, Dodd et al. 2015, Salinas-Ramos et al. 2015). The polymerase chain reaction (PCR) technique involves first denaturing DNA and annealing primers to sequences of interest. Primer extension is catalyzed by DNA polymerase, leading to replication of the original double-stranded DNA (Schochetman et al. 1988). Zeale et al. (2011) developed novel primers targeting a gene sequence specific to the phylum Arthropoda; these primers have been widely used in bat dietary studies, and allow species-level identifications to be made for insect prey sequences extracted from fecal samples (Clare et al. 2014, Dodd et al. 2015, Razgour et al. 2011). Despite the recent success of such studies, molecular dietary analysis could be further improved by refining PCR parameters to

maximize DNA yield. The objectives of this study were to verify the success of current methods of preserving field-collected fecal samples for future analysis, as well as to optimize PCR conditions for use with the arthropod-specific primers designed by Zeale et al. (2011).

### *Methods*

A maternity colony of *Corynorhinus rafinesquii* at Mammoth Cave National Park was selected for my study due to accessibility, colony stability, and lack of non-target bat species. Being the same colony of bats considered by Dodd et al. (2015), and following a protocol similar to this earlier study, fecal pellets were collected from a plastic, 2.7-m x 3.7-m tarpaulin placed on the barn loft floor post-sunset and recovered after approximately 24 hours. Upon collection, pellets found on the tarpaulin were transferred to 1.5-mL microcentrifuge tubes filled with 95% ethanol and were stored at -80°C within one week to preserve prey DNA for analysis. Samples were collected in May and August of 2011 and 2016. Mean amplicon yield (nM) per year was evaluated using a Wilcoxon Rank-Sum Test with  $\alpha = 0.05$ .

The QIAamp DNA Stool Mini Kit (Qiagen Inc., Chatsworth, CA) was used to extract prey DNA from fecal samples on a per pellet basis according to the manufacturer's instructions (Clare et al. 2014, Dodd et al. 2012a, Zeale et al. 2011) with halved reagent quantities, resulting in a final elution volume of 100  $\mu$ L. A 157-bp region of the cytochrome c oxidase subunit I gene (COI) was amplified using the arthropod-specific primers designed by Zeale et al. (2011), ZBJ-ArtF1c (5' to 3' sequence: AGATATTGGAACWTTATATTTTATTTTGG) and ZBJ-ArtR2c (5' to 3' sequence: WACTAATCAATTWCCAAATCCTCC), and modified to include Illumina-specific adaptors and unique barcode sequences. To ensure that samples could be identified post-sequencing, each was amplified using a unique combination of barcoded forward and reverse primers. Polymerase chain reactions were conducted using Phusion Green Hot Start II High-Fidelity DNA Polymerase (ThermoFisher Scientific, Inc., Waltham, MA) and amplicon concentrations were measured using a Qubit 2.0 Fluorometer and Qubit dsDNA HS Assay Kit (ThermoFisher Scientific, Inc., Waltham, MA).

### Test 1

To minimize primer-dimer formation without compromising amplicon yield, primer concentration was optimized. A total of ten samples were amplified with 2.0  $\mu\text{L}$  (0.4  $\mu\text{M}$  concentration in reaction) each of forward and reverse primer; additionally, the same ten samples were also amplified with 2.5  $\mu\text{L}$  (0.5  $\mu\text{M}$  concentration in reaction) each of forward and reverse primer. Volume of polymerase (25  $\mu\text{L}$ ) and DNA (2  $\mu\text{L}$ ) were held constant, and the volume of molecular-grade water per reaction was adjusted to ensure that total reaction volume equaled 50  $\mu\text{L}$ . Protocol for amplification was as follows: 30 s at 98°C, 35 cycles of 10 s at 98°C, 30 s at 52°C, 30 s at 72°C, and 10 min at 72°C. Resultant amplicon yields (nM) were statistically analyzed using R (R Core Team 2016). A Kolmogorov-Smirnov Test indicated that the response variable differed significantly from the normal distribution ( $P < 0.05$ ) and a Wilcoxon Rank-Sum Test with  $\alpha = 0.05$  was used to test for differences in mean amplicon yield (nM) between samples amplified with either 2.0 or 2.5  $\mu\text{L}$  primer.

### Test 2

To optimize annealing temperature, a gradient PCR was performed; a single suite of six samples was used, so that each of the six was amplified at each temperature. Reagent quantities for the gradient PCR were 18  $\mu\text{L}$  molecular-grade water, 25  $\mu\text{L}$  polymerase, 2.5  $\mu\text{L}$  forward primer, 2.5  $\mu\text{L}$  reverse primer, and 2  $\mu\text{L}$  DNA. Protocol for amplification during the gradient PCR was as follows: 30 s at 98°C, 35 cycles of 10 s at 98°C, 30 s at gradient temperature from 50°C to 60°C, 30 s at 72°C, and 10 min at 72°C. Annealing temperature gradations were 60°C, 58°C, 56.1°C, 53.8°C, 51.9°C, and 50°C. Results were statistically analyzed using R (R Core Team 2016). Given the non-normal distribution of the response variable and repeated measures, a Friedman Rank-Sum Test with  $\alpha = 0.05$  was used to test for differences in mean amplicon yield (nM) across annealing temperatures used in the gradient PCR and a Nemenyi Test was used to make post-hoc comparisons.

### Test 3

The ideal number of PCR cycles was determined by amplifying ten samples using a protocol with 30 cycles (30 s at 98°C, 30 cycles of 10 s at 98°C, 30 s at 52°C, 30 s at 72°C, and 10 min at 72°C)

and the same ten samples using a protocol with 35 cycles (30 s at 98°C, 35 cycles of 10 s at 98°C, 30 s at 52°C, 30 s at 72°C, and 10 min at 72°C). Reagent quantities were as follows: 18 µL molecular-grade water, 25 µL polymerase, 2.5 µL forward primer, 2.5 µL reverse primer, and 2 µL DNA. Results were statistically analyzed using R (R Core Team 2016). A Kolmogorov-Smirnov Test indicated non-normal distribution of the response variable ( $P < 0.05$ ) and a Wilcoxon Rank-Sum Test with  $\alpha = 0.05$  was used to test for differences in mean amplicon yield (nM) between samples amplified with either 30 or 35 PCR cycles.

### *Results*

Mean amplicon yield for samples collected in 2011 ( $78.6 \pm 6.08$  nM) was approximately equal that of samples collected in 2016 ( $84.4 \pm 6.41$  nM), and was not found to be significantly different across years ( $P > 0.05$ ; Fig 2.1). Primer concentration was significant ( $W = 19.5$ ,  $P = 0.02$ ; Fig. 2.2) and the mean amplicon yield of samples amplified with 0.5 µM primers ( $34.2 \pm 2.39$  nM) was greater than that of samples amplified with 0.4 µM primers ( $23.0 \pm 3.56$  nM). Mean amplicon yield differed significantly across annealing temperatures ( $\chi^2_5 = 15.6$ ,  $P = 0.008$ ), but post-hoc analysis indicated only one significant comparison (Fig. 2.3); amplicon yield was greater in samples amplified at 50°C ( $45.5 \pm 11.6$  nM) than in those amplified at 60°C ( $11.9 \pm 2.82$  nM). Number of PCR cycles was significant ( $W = 0$ ,  $P = 0.0002$ ; Fig. 2.4); samples amplified with 35 cycles had a greater mean amplicon yield ( $104.8 \pm 21.2$  nM) than those amplified with 30 cycles ( $19.5 \pm 2.02$  nM).

### *Discussion*

Results indicate that, when using the primers designed by Zeale (2011) in a 50-µL reaction, a primer concentration of 0.5 µM results in more successful amplification than does a 0.4 µM concentration. This conclusion is supported by bat dietary studies that have used the same ratio of primer volume to total reaction volume (Salinas-Ramos et al. 2015, Zeale et al. 2011), and I recommend that future studies use a 1:20 ratio of each primer to total reaction volume.

Additionally, numerous studies use an annealing temperature of 52°C (Bohmann et al. 2011, Clare et al. 2014, Razgour et al. 2011, Salinas-Ramos et al. 2015); I found this to be appropriate, as my results show that mean DNA yield generally decreases with increasing annealing temperature across a gradient of 50°C to 60°C. Finally, I found that amplification with 35 cycles resulted in significantly higher mean amplicon yield than amplification with 30 cycles. However, 50-cycle amplification is commonly reported in the literature (Bohmann et al. 2011, Clare et al. 2014, Razgour et al. 2011, Salinas-Ramos et al. 2015), suggesting that optimal number of PCR cycles may be reagent dependent.

Sample collection for many bat dietary studies has involved preservation of fecal pellets using either ethanol, freezing, or both (Clare 2014, Dodd et al. 2012a, 2015, Razgour et al. 2011); my results indicate that samples can be successfully stored in 95% ethanol at -80°C for at least five years. These findings are supported by the literature: Frantzen et al. (1998) reported freezing and storage in ethanol as effective preservation methods for mitochondrial DNA in field-collected fecal samples. Further, Nsubuga et al. (2004) demonstrated that storage of fecal samples in ethanol followed by silica desiccation resulted in significantly greater DNA yield than preservation by silica desiccation alone. Successful preservation methods indicate that DNA extracted and amplified from recently-collected fecal pellets may be directly compared to older collections, allowing analyses of diets over time. Such comparisons may be of great ecological interest, as dietary shifts may be indicative of previously undetected impacts of biological invasions, disease outbreaks, and environmental disturbances that occur on a temporal scale.

Understanding relationships between bats and their insect prey following the arrival of  
White-nose Syndrome to a fire-managed landscape

*Introduction*

The body size and wing morphology of insectivorous bats are associated with maneuverability in cluttered habitat (Norberg and Rayner 1987) and therefore impact both foraging strategy and habitat use (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Although some studies have reported little partitioning among insectivorous bats of similar morphology (Bell 1980), spatial and temporal segregation has been repeatedly documented for cryptic sympatric species (Arlettaz 1999, Ashrafi et al. 2011, Kunz 1973, Nicholls and Racey 2006, Razgour et al. 2011). Additionally, White-nose Syndrome (WNS), an infectious fungal disease impacting the cave-hibernating bats of eastern North America (Turner et al. 2011), has been associated with relaxed spatial and temporal partitioning (Jachowski et al. 2014). Although vertebrate insectivores are associated with strong trophic cascades (Mooney et al. 2010), potential post-WNS shifts in bat-insect relationships have not been investigated.

Further, forest structure is thought to be a primary determinant of bat habitat use (Ford et al. 2005, Loeb and O'Keefe 2006, Müller et al. 2012) and insect abundance (Müller et al. 2012, Ober and Hayes 2008). As a result, forest management techniques including silvicultural treatments and prescribed fire are associated with availability of arthropod prey resources and patterns of bat foraging behavior (Dodd et al. 2012b, Silvis et al. 2016). Griffiths (2016) observed an interactive effect of prescribed fire and WNS on habitat use, suggesting that the occurrence of WNS may influence bat responses to forest management. Additionally, a post-WNS increase in total insect abundance was reported (Griffitts 2016) and may indicate a trophic cascade initiated by the mass mortality of insectivorous bats due to WNS. However, potential shifts in insect

community composition and spatial predator-prey dynamics in managed landscapes have not been analyzed in the context of WNS.

The composition, distribution, and abundance of lepidopteran assemblages may be of particular interest, as Lepidoptera are ubiquitous in the diets of eastern North American bats (Feldhamer et al. 2009, Lacki et al. 2007, Whitaker 2004). The carbohydrate chitin, a significant structural component of insect endo- and exocuticle, is poorly digested by most mammals (Bell 1990). Although chitinase is known to occur in the gastrointestinal tracts of insectivorous bats (Strobel et al. 2013, Whitaker et al. 2004), undigested chitin particles persist in the intestines (Whitaker et al. 2004) and intact, identifiable insect fragments can be recovered from fecal pellets (Kunz and Whitaker 1983). Lepidoptera are relatively soft-bodied (Freeman and Lemen 2007) and have been described as 'tractable' insects due to a comparatively thin cuticle (Evans and Sanson 2005). Barclay et al. (1991) suggest that Lepidoptera may be more readily digested than heavily chitinized insects such as those in the order Coleoptera.

Although a diet rich in Lepidoptera may afford comparatively high digestive efficiency, nutritive quality may vary within the order. Griffiths (1977) suggests that caloric density (cal/g) of insects may increase with body size, although Redford and Dorea (1984) found little variation in the nutritional content of adult insects. This pattern is reflected within Lepidoptera, and Fulton et al. (2016) detected no significant differences in the caloric densities of four species of Lepidoptera. Robel et al. (1995) found caloric densities of 5271 and 5248 cal/g for samples of mixed Lepidoptera; these values approximate the grand mean of 5289 cal/g presented by Cummins and Wuycheck (1971) for terrestrial insects. Due to low variation in the caloric densities of Lepidoptera, both within and across orders, total caloric content may be assumed to be a function of size. As a result, body size metrics such as wingspan and dry mass may serve as an energetically informative basis for classifying Lepidoptera and contextualizing their role as a prey resource for insectivorous bats. Given that body mass index (Lacki et al. 2015) and nutrition (Frank et al. 2012) have been linked to WNS vulnerability in eastern North American bats, I sought to: (1) explore the relationship between bat assemblages and insect communities, emphasizing Lepidoptera, in the context of WNS and prescribed fire, (2) develop a size-based classification for Lepidoptera as prey for insectivorous bats.



## Methods

Field sampling occurred at Mammoth Cave National Park (MACA) from 2010 to 2016. As the first detection of WNS at MACA occurred in early 2013 (NPS 2013) with initial bat declines observed in 2014 (Lacki et al. 2015), data from 2013 and 2014 were omitted to avoid drawing conclusions from data collected in periods of unclear disease impact. I consider samples collected from 2010 through 2012 to represent a pre-WNS period and those collected in 2015 and 2016 to represent a post-WNS period. Randomly generated points were used to establish transects in unburned, historically burned (prior to when the study began in 2010), and recently burned (after 2010) forest stands across the landscape, resulting in six paired sites (adjacent burned and unburned land parcels). Acoustic detection was used to approximate bat abundance (Ford et al. 2011). Following Dodd et al. (2013), Anabat II acoustic detectors (Titley Electronics, Columbia, MO) were used to record echolocation calls from sunset to sunrise; either two or four detectors were deployed along each transect and were located at least 100 m apart. Detectors were operational for up to eight nights per deployment and repeated measures were averaged across nights. Calls containing a minimum of five pulses were analyzed with BCID Eastern USA v.2.7c (Bat Call Identification, Kansas City, MO) and assigned a phonic group (low-, mid-, or *Myotis*-frequency) at a 70% confidence level (Fulton et al. 2014).

Insects were collected concurrently along transects using 10-W blacklight traps (Bioquip Products, Rancho Dominguez, CA) containing dichlorvos-based insecticide (Dodd et al. 2013). Traps were deployed 100 m from acoustic detectors and were operational from sunrise to sunset on a single night. Captured insects were identified to order, and Lepidoptera collected from 2010 – 2012 were further identified to species. Species were assigned mean wingspan values derived from wingspan ranges presented by Covell (2005), and the `classInt` package (Bivand 2015) written for R (R Core Team 2016) was used to cluster species into size classes with endpoints defined by Fisher's natural breaks (Table 3.1). Selection of an optimal number of classes was informed by comparison of within-group sums of squares (Figure 3.1; Hartigan and Wong 1979) as well as practical consideration of the data. This classification was extended to Lepidoptera collected in 2015 and 2016, given wingspan measurements rather than specific identification. Classification efficacy was assessed by testing for differences in the mean

wingspans of each size class using a linear model constructed in the R programming language (R Core Team 2016). A subset of Lepidoptera with species-level identifications were dried at approximately 55°C for at least 24 hours and weighed, providing an empirical basis for the prediction of dry weights via least-squares estimation for each species collected at MACA (Figure 3.2), and by extension, each size class. Size classes were further characterized by total caloric estimates per individual given a grand mean caloric density of 5289 cal/g for terrestrial insects (Cummins and Wuycheck 1971).

A set of 12 *a priori* candidate models were constructed to relate phonic group diversity, calculated as the reciprocal of Simpson's Diversity ( $1/D$ ), to insect community composition. Statistical analyses were conducted using the R programming language (R Core Team 2016). Linear mixed models were fit using the lme4 package (Bates et al. 2015). Fixed effects included burn treatment, presence of WNS, numerical abundances of dominant insect orders, and relative abundances of dominant insect orders. Site was included as a random effect in all candidate models. Bias-corrected Akaike's Information Criterion values (AICc; Hurvich and Tsai 1989) were used to select a best-fitting model using the AICcmodavg package (Mazerolle 2016). Likelihood ratio tests were used to determine the significance of terms included in the best-fitting model. Distance-based redundancy analysis (dbRDA) was used to evaluate the effects of insect community composition, burn history, and WNS on the composition of bat assemblages and was conducted using the vegan package (Oksanen et al. 2017). Significance was determined under 999 permutations of the bat assemblage matrix. Eight candidate models were also constructed to relate the diversity of Lepidoptera size classes, calculated as the reciprocal of Simpson's Diversity ( $1/D$ ), to bat assemblage composition following the statistical methods outlined above. Fixed effects included burn treatment, presence of WNS, and the relative abundance of low-, mid-, and *Myotis*-frequency phonic groups. Site and month were included as random effects in all candidate models.

## Results

Acoustic surveys and insect sampling spanned 202 concurrent nights across 5 years of surveys. In total, my acoustic data includes 902 detector nights ( $n = 697$  pre-WNS;  $n = 205$  post-WNS) and my insect data includes 413 trap nights ( $n = 318$  pre-WNS;  $n = 95$  post-WNS). I recorded 4,760 echolocation passes and collected 125,445 insects across all years. The compositions of bat assemblages, insect communities, and Lepidoptera assemblages before and after detection of WNS at MACA are summarized in Table 3.2. A total of 7,842 Lepidoptera collected pre-WNS were identified to species and assigned size classes, resulting in a taxa list consisting of 541 species in 28 families; the distribution of size classes in the subset selected for drying ( $n = 43$  species, 15 families) was representative (within 5% of the relative abundance of each class in the assemblage). Post-WNS, 3,839 Lepidoptera were assigned size classes on the basis of wingspan. Mean wingspan differed significantly across all size classes ( $F_{1,539} = 3440$ ,  $P < 0.05$ ; Figure 3.3) as a consequence of classification.

Model selection resulted in two competing models for bat phonic group diversity (Table 3.3). The best model included WNS and the relative abundances of Coleoptera, Diptera, and Lepidoptera. This model indicates that phonic diversity has a positive relationship with Coleoptera and Lepidoptera, and a negative relationship with Diptera and WNS, but only WNS was significant at  $\alpha = 0.05$  (Table 3.4). The competing model ( $\Delta \text{AICc} = 1.22$ ) included only WNS, which was a significant predictor of phonic diversity ( $P < 0.05$ , Table 3.4). Results of the dbRDA indicate constraining variables are significantly associated with bat assemblage composition (pseudo- $F_{12,6} = 3.37$ ,  $P < 0.05$ ; Figure 3.4) and explain 62.0% of the total inertia. Cumulatively, the first two constrained axes account for 54.2% of the total inertia and 87.2% of the explainable inertia. The best-fitting model for Lepidoptera size class diversity included only WNS (Table 3.5) and indicated a significant positive relationship between WNS and Lepidoptera diversity ( $0.60 \pm 0.14$ ,  $P < 0.05$ ).

## Discussion

The results of both model selection and ordination implicate WNS as the primary driver of bat assemblage diversity and composition. The effect of WNS is well documented; this epizootic is conservatively estimated to have killed over six million bats within five years of its first detection in the eastern United States (Froschauer and Coleman 2012). Nearly all *Myotis* species in eastern North America have experienced some degree of population decline, and several formerly common species (e.g. *Myotis septentrionalis* and *Myotis lucifugus*) have declined dramatically (Coleman et al. 2014, Powers et al. 2015, Turner et al. 2011). Populations of *M. lucifugus* and *Myotis sodalis* at MACA are estimated to have declined by approximately 80% (Toomey 2015), fundamentally altering assemblage diversity and composition. Additionally, my ordination suggests that the abundance of the mid-frequency phonic group may behave similarly to the *Myotis* group with respect to WNS. Most species in the mid-frequency phonic group are mildly affected or unaffected by WNS, but *Perimyotis subflavus* has suffered substantial population declines (Coleman et al. 2014, Reynolds et al. 2016, Turner et al. 2011). Although I was unable to directly evaluate potential declines in *P. subflavus* activity at MACA due to phonic group classification, monitoring by the National Park Service suggests declines approaching 70% (Toomey 2015). Thus, the contribution of the mid-frequency phonic group to observed trends in assemblage composition are likely due to reduced populations of *P. subflavus*. My results indicate that post-WNS bat assemblages at MACA are dominated by low-frequency echolocating bats (e.g. *Eptesicus fuscus*, *Nycticeius humeralis*); this conclusion is supported by recent findings of increased capture rates of *E. fuscus* (Pettit and O'Keefe 2017) and *N. humeralis* (Pettit and O'Keefe 2017, Thalken et al. in review).

Given the impact of WNS, burn history does not appear informative with respect to phonic diversity, but does relate to bat assemblage composition. Ordination results demonstrate that although the second component is defined by burn history, historical occurrence of prescribed fire has a weaker relationship to assemblage composition than recent application of fire. The low-frequency phonic group is positively associated with fire, which may be due to the preference for open habitat exhibited by this group (Norberg and Rayner 1987). In contrast, the abundance of mid-frequency echolocation calls appears unrelated to burn history and the

*Myotis* group demonstrates a slight negative association with fire. However, several studies have found a positive relationship between *Myotis* bats and prescribed fire due to the creation of roosting habitat (Johnson et al. 2009, 2010). The impact of prescribed fire on bats may be dependent upon variables not measured here, such as burn intensity and duration. In keeping with previous work demonstrating that composition of Lepidoptera assemblages is influenced by regional rather than local floristic variation (Summerville and Crist 2003), burn history was not included in my best-fitting model.

Although not statistically significant, the relationships of Coleoptera and Diptera to bat phonic diversity show clear directionality; diversity appears positively associated with Coleoptera and negatively associated with Diptera. Qualitatively, Coleoptera appear to constitute a greater proportion of bat diets than Diptera (Feldhamer et al. 2009, Whitaker 2004) and as a result, insect communities rich in Coleoptera may support comparatively high bat diversity. The relative abundance of Lepidoptera appears to be of less significance to bats at MACA relative to other common groups of prey, but may be obscured by the effects of WNS. Lepidoptera are a documented prey source for all bat species in eastern North America (Lacki et al. 2007) but many consume diverse diets (Feldhamer et al. 2009, Whitaker 2004). Persisting bat species may increasingly consume Lepidoptera in response to presumably reduced competition arising from declines in *Myotis* populations, resulting in little net change in the relative abundance of Lepidoptera post-WNS. Alternatively, the weak influence of Lepidoptera may be an artifact of acoustic sampling. Acoustic bat detectors are typically unable to record bats with low-intensity echolocation calls (O'Farrell and Gannon 1999), such as *Corynorhinus rafinesquii*. Therefore, this species is not likely represented in my data despite the existence of numerous roosts at MACA (Johnson and Lacki 2013). As Lepidoptera represent more than 80% of the diet of *C. rafinesquii* (Lacki and Dodd 2011), this study likely underappreciates the importance of Lepidoptera to the full bat assemblage at MACA.

My classification of Lepidoptera by size on the basis of wingspan was successful, and provides a promising method for integration into future bat foraging research. I suggest that size-based classification may be useful for future study of Lepidoptera, as classification by size (given pre-determined classes) does not require taxonomic identification and may facilitate efficient,

informative data collection by biologists lacking an entomological background. Although model selection indicated that Lepidoptera size class diversity differs significantly following WNS, the best fitting model did not include factors relating directly to bat assemblage composition. Therefore, I concede that differences in size class diversity may be attributable to natural yearly variation rather than WNS. It was not possible to account for this variation in my models due to the collinearity of WNS and year (i.e. the presence of WNS at MACA does not vary within years). Future efforts to relate bat and Lepidoptera assemblages may wish to analyze pre- and post-WNS data separately to allow year to be included as a random effect. Alternatively, observed pre- and post-WNS differences in Lepidoptera diversity may be due to an overall decline in bat activity rather than declines of any given phonic group. Although overall bat abundance has measurably declined at MACA following WNS, I did not include total bat activity in candidate models due to uneven pre- and post-WNS sampling effort and therefore cannot address the degree to which assemblage-level bat declines may influence Lepidoptera. Due to the substantial difficulty of detecting mid-frequency and *Myotis* bats post-WNS, and the mathematical limitations imposed by data dominated by zero values, increased sampling effort may not meaningfully contribute to the strength and predictive power of analyses.

Ultimately, my results contribute to the breadth of existing literature documenting the profound effects of WNS on the bats of eastern North America and document preliminary trends in the post-WNS composition of insect communities and Lepidoptera assemblages. The effects of WNS and corresponding bat declines on Lepidoptera remain unclear, necessitating further study and long-term monitoring efforts. I found supporting evidence that burn history and insect community composition impacts the phonic diversity and composition of bat assemblages. I also observed general trends in bat diversity and assemblage composition in relation to insect community composition, as well as a significant post-WNS increase in the size class diversity of Lepidoptera. My study includes only two years of post-WNS data; bat populations may still be actively declining at MACA, masking more subtle ecological relationships. Given the results of this study, I suggest that conservation efforts emphasizing prey resources or land management are unlikely to have quantifiable impacts until bat populations have stabilized following initial detection of WNS, but may still have ecologically meaningful impacts on the long-term viability of local populations of imperiled bat species.

## IMPLICATIONS

My thesis work indicates that meaningful conclusions can be drawn from post-WNS bat data, despite the methodological and analytical limitations imposed by dramatically reduced populations. I have provided evidence that an empirical approach to optimizing laboratory procedures and defining study parameters can be used to mitigate the effects of uneven or low sample sizes, common to post-WNS studies of bats. Additionally, I selected flexible statistical analyses including nonparametric tests, generalized linear modelling, and ordination to ensure that these aspects of the data were accounted for. I recommend that future studies of post-WNS bat ecology include customized methods and carefully selected analyses, as strict reliance on previously established protocols may result in suboptimal processing of samples or the unnecessary exclusion of data. Given the difficulty of generating robust datasets in light of widespread bat mortality, every effort should be taken to avoid artificially reducing post-WNS sample sizes based on pre-WNS preconceptions.

I have shown that although WNS is unquestionably the primary factor impacting the abundance and distribution of bats in affected regions, prescribed fire and the composition of insect communities contribute to observed patterns in bat assemblage diversity and composition. Further, I documented a post-WNS increase in the size diversity of Lepidoptera. Although the extent to which prey and land management shape bat assemblages remains unclear given the overwhelming influence of WNS, I have provided evidence that a relationship between bat foraging ecology, insects, and fire (well documented pre-WNS) persists despite devastating declines. The implications are optimistic: fundamental habitat associations and predator-prey dynamics appear largely unchanged, indicating that conservation efforts emphasizing prey availability and habitat manipulation may provide some degree of support to imperiled bats, although the short-term success of such strategies may be difficult to quantify.

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## APPENDICES

APPENDIX A  
Tables

Table 1.1. Summary of *Trichoplusia ni*, *Malacosoma americanum*, *Halysidota tessellaris*, and *Iridopsis* sp. treatments. The treatment marked with an asterisk was not included in the initial comparison of small vs. large-bodied and winged vs. wingless *T. ni*, but was included in the comparison of species. *n* = number of samples combusted per treatment.

Species	Size Class	Wings	Sample Weight (mg)	<i>n</i>
<i>T. ni</i>	Large	Yes	250	6
<i>T. ni</i>	Large	No	250	6
<i>T. ni</i>	Small	Yes	250	6
<i>T. ni</i>	Small	No	250	6
<i>T. ni</i> *	-	Yes	250	2
<i>Ma. americanum</i>	-	Yes	200 – 250	5
<i>Ma. americanum</i>	-	Yes	400 – 450	5
<i>Ma. americanum</i>	-	Yes	600 – 650	5
<i>Ma. americanum</i>	-	Yes	800 – 850	3
<i>H. tessellaris</i>	-	Yes	250	7
<i>Iridopsis</i> sp.	-	Yes	250	4



Table 3.1. Size-based classification for Lepidoptera based on 541 species in 28 families collected at Mammoth Cave National Park, Kentucky. Discrete classes were defined by wingspan and characterized by the approximate dry weight and caloric yield of a given individual in each class. Mean wingspan differs significantly across all classes ( $P < 0.05$ ).

Size Class	Wingspan (cm)	Dry Weight (g) Mean $\pm$ SE	Calories Mean $\pm$ SE
1	0.00 - 2.70	0.0138 $\pm$ 0.0003	73.079 $\pm$ 1.7185
2	2.71 - 3.70	0.0322 $\pm$ 0.0006	170.24 $\pm$ 3.0476
3	3.71 - 4.90	0.0528 $\pm$ 0.0009	279.11 $\pm$ 5.0244
4	4.91 - 7.10	0.1144 $\pm$ 0.0048	605.21 $\pm$ 25.163
5	7.11 - 10.2	0.2384 $\pm$ 0.0149	1260.8 $\pm$ 78.739
6	10.3 - 13.0	0.4540 $\pm$ 0.0445	2401.3 $\pm$ 235.33

Table 3.2. Pre- and post-WNS compositions of bat assemblages (organized by phonic group), insect communities, and Lepidoptera assemblages at Mammoth Cave National Park, Kentucky based on 4,760 echolocation passes and collection of 125,445 insects. Lepidoptera size classes refer to the wingspan-based classification developed in this study.

	Pre-WNS (%)	Post-WNS (%)
Bat Assemblage		
Low-frequency	2.99	100.0
Mid-frequency	32.3	0.00
<i>Myotis</i>	64.7	0.00
Insect Community		
Lepidoptera	22.1	43.2
Coleoptera	13.9	27.7
Diptera	23.6	16.0
Other	40.4	13.2
Lepidoptera Assemblage		
Size Class 1	50.5	42.3
Size Class 2	35.5	38.6
Size Class 3	12.0	15.8
Size Class 4	1.06	2.08
Size Class 5	0.82	0.47
Size Class 6	0.15	0.81

Table 3.3. Summary of support for candidate models for the diversity of bat phonic groups (low-, mid-, or *Myotis*-frequency) acoustically detected at Mammoth Cave National Park, Kentucky, calculated as the reciprocal of Simpson's Diversity ( $1/D$ ). All models were constructed as linear mixed models including site as a random effect.

Model	K	AICc	$\Delta$ AICc	$W_i$
Null	3	158.5	10.4	0.00
WNS	4	149.3	1.22	0.29
Burn	5	162.2	14.1	0.00
WNS*Burn	8	157.6	9.54	0.00
Numerical Abundance				
Lepidoptera + Coleoptera + Diptera	6	163.3	15.2	0.00
Lepidoptera + Coleoptera + Diptera + WNS	7	151.3	3.27	0.10
Lepidoptera + Coleoptera + Diptera + Burn	8	167.4	19.4	0.00
Lepidoptera + Coleoptera + Diptera + WNS + Burn	9	155.5	7.40	0.01
Relative Abundance				
Lepidoptera + Coleoptera + Diptera	6	162.2	14.2	0.00
Lepidoptera + Coleoptera + Diptera + WNS	7	148.1	0.00	0.53
Lepidoptera + Coleoptera + Diptera + Burn	8	166.2	18.2	0.00
Lepidoptera + Coleoptera + Diptera + WNS + Burn	9	152.3	4.28	0.06

Table 3.4. Summary of the coefficients and significance of fixed effects in the best-fitting linear mixed models for bat phonic diversity at Mammoth Cave National Park, Kentucky, selected using an information theoretic approach. Site was included as a random effect. Terms in the insect community model refer to the relative abundance of each order. Likelihood-ratio tests were used to determine significance at  $\alpha = 0.05$ .

Model Terms	Coefficient ( $\pm$ SE)	<i>P</i>
Insect Community Model		
Lepidoptera	0.08 $\pm$ 0.20	0.43
Coleoptera	0.35 $\pm$ 0.30	0.44
Diptera	-0.34 $\pm$ 0.21	0.10
WNS	-0.58 $\pm$ 0.14	< 0.05
White-nose Syndrome Model		
WNS	-0.47 $\pm$ 0.14	< 0.05

Table 3.5. Summary of support for candidate models for the diversity of Lepidoptera size classes (classification presented in this work) observed at Mammoth Cave National Park, Kentucky, calculated as the reciprocal of Simpson's Diversity ( $1/D$ ). All models were constructed as linear mixed models including month and site as random effects.

Model	K	AICc	$\Delta$ AICc	$W_i$
Null	4	258.6	13.1	0.00
WNS	5	245.6	0.00	0.83
Burn	6	259.4	13.8	0.00
Burn*WNS	9	250.0	4.46	0.09
Low Phonic + Mid Phonic + <i>Myotis</i> Phonic	7	260.1	14.5	0.00
Low Phonic + Mid Phonic + <i>Myotis</i> Phonic + WNS	8	250.5	4.91	0.07
Low Phonic + Mid Phonic + <i>Myotis</i> Phonic + Burn	9	261.4	15.8	0.00
Low Phonic + Mid Phonic + <i>Myotis</i> Phonic + Burn*WNS	12	256.0	10.4	0.00

APPENDIX B  
Figures



Figure 1.1. Cotton sheet deployed at Mammoth Cave National Park to sample Lepidoptera, illuminated by 10-W black lights with electrical harnesses.

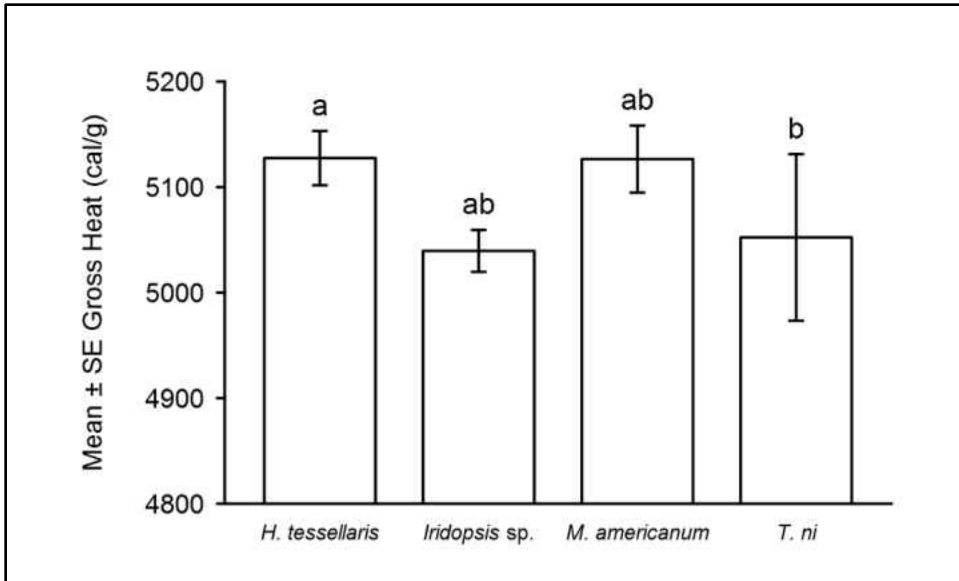


Figure 1.2. Mean ( $\pm$  standard error) gross heat (cal/g) generated by combustion of coarsely ground samples of *Malacosoma americanum*, *Trichoplusia ni*, *Halysidota tessellaris*, and *Iridopsis sp.* using bomb calorimetry. Five samples of *Ma. americanum*, twenty-six of *T. ni*, seven of *H. tessellaris*, and four of *Iridopsis sp.* were combusted.



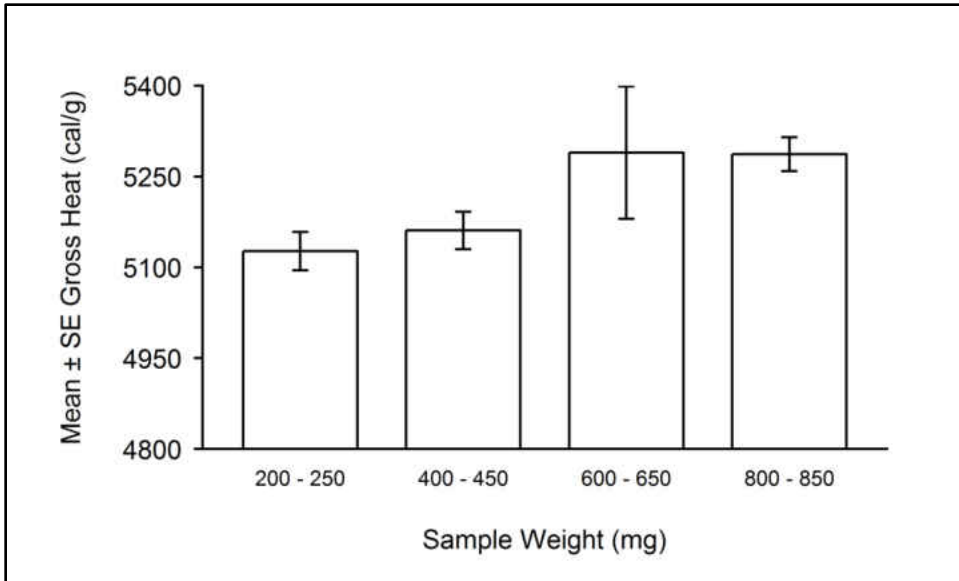


Figure 1.3. Mean ( $\pm$  standard error) gross heat (cal/g) generated by combustion of coarsely ground *Malacosoma americanum* samples using bomb calorimetry. Five samples weighing 200-250 mg, 400-450 mg, and 600-650 mg, and three samples weighing 800-850 mg were combusted.

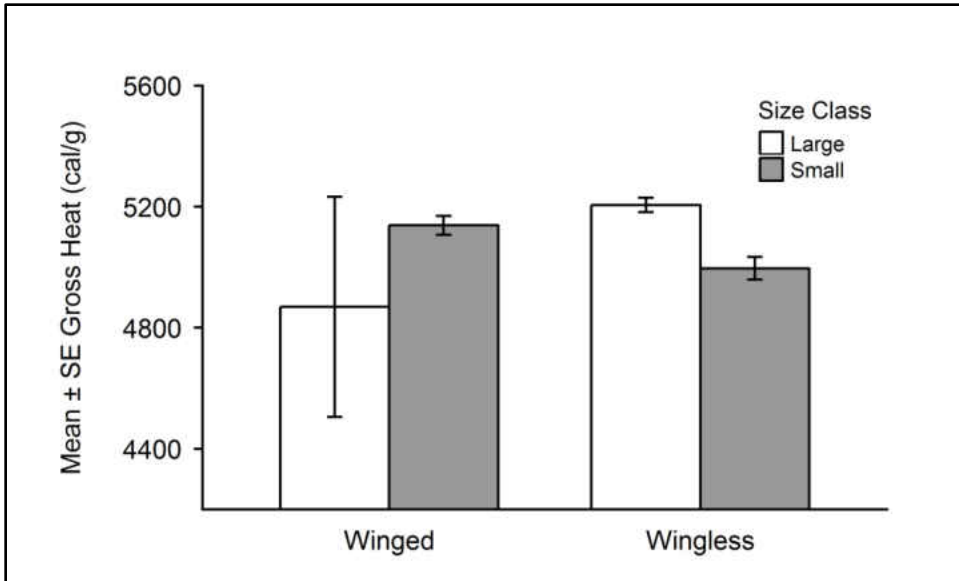


Figure 1.4. Mean ( $\pm$  standard error) gross heat (cal/g) generated by combustion of coarsely ground *Trichoplusia ni* samples using bomb calorimetry. Six samples were combusted per treatment (small with wings present, small with wings removed, large with wings present, large with wings removed).

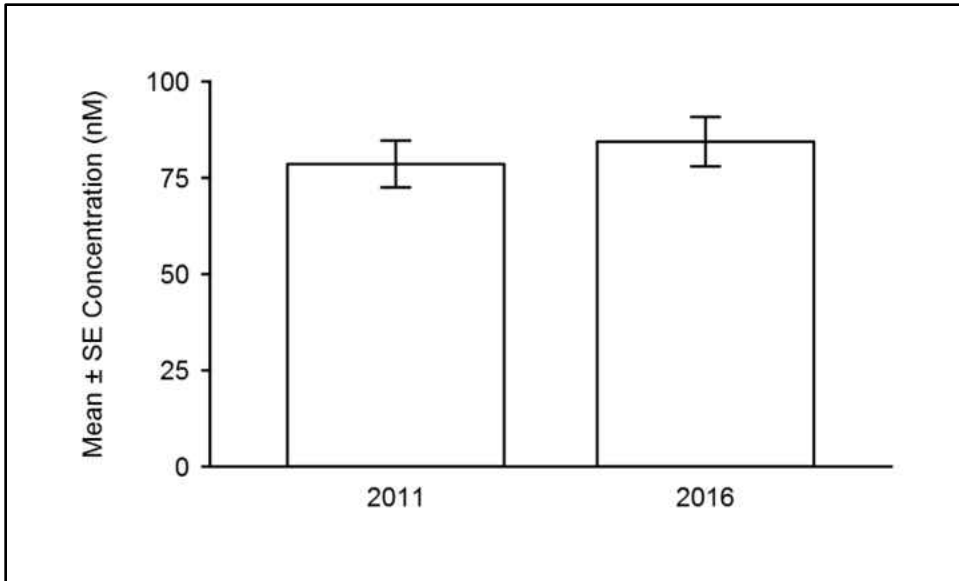


Figure 2.1. Mean ( $\pm$  standard error) amplicon concentration (nM) of insect DNA extracted and amplified from bat fecal pellets collected in 2011 ( $n = 55$ ) and 2016 ( $n = 55$ ) at Mammoth Cave National Park, Kentucky. Samples were stored in 95% ethanol at  $-80^{\circ}\text{C}$  after collection. Differences across years were not significant ( $P > 0.05$ ).

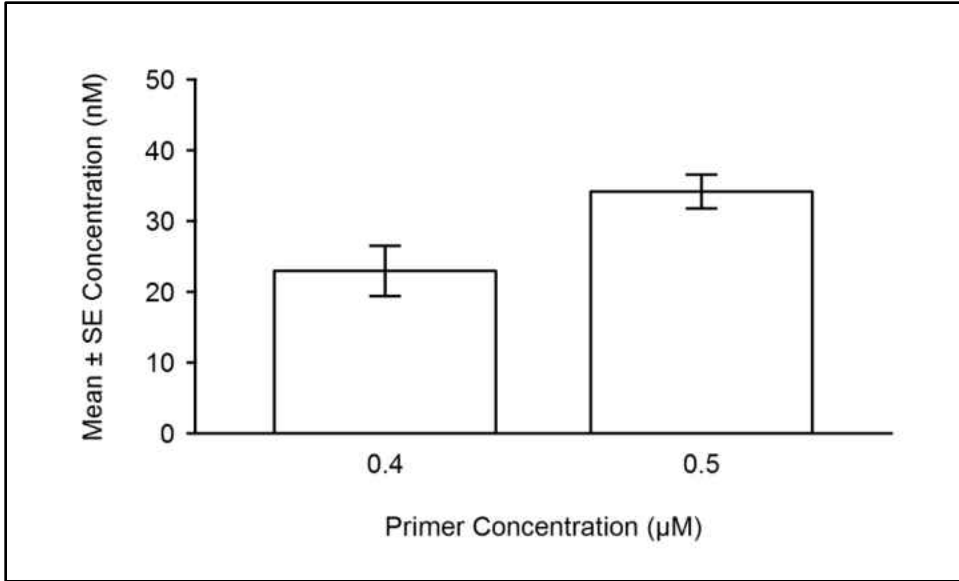


Figure 2.2. Mean ( $\pm$  standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at Mammoth Cave National Park, Kentucky and amplified with either 0.4 or 0.5  $\mu$ M forward and reverse primer.  $n = 10$  samples per treatment; the same suite of ten samples was used to test each primer concentration. Samples amplified with 0.5  $\mu$ M primers had a significantly higher yield than those amplified with 0.4  $\mu$ M primers ( $W = 19.5$ ,  $P = 0.02$ ).

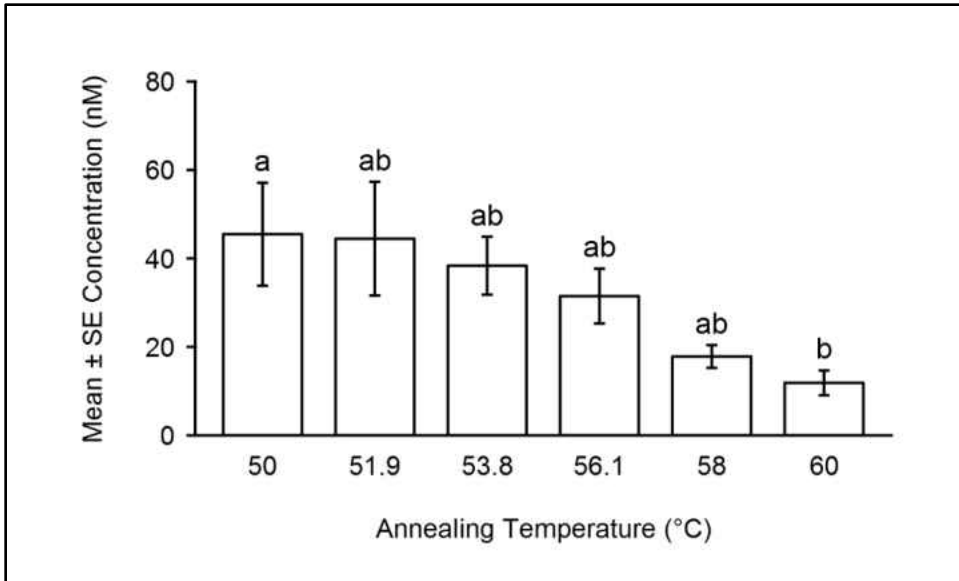


Figure 2.3. Mean ( $\pm$  standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at Mammoth Cave National Park, Kentucky and amplified with a gradient PCR procedure.  $n = 6$  samples per treatment; a single suite of six samples was used so that each of the six was amplified at each temperature. Mean yield differed significantly across annealing temperatures ( $\chi^2_{25} = 15.6$ ,  $P = 0.008$ ), and letters indicate comparison-wise significance.

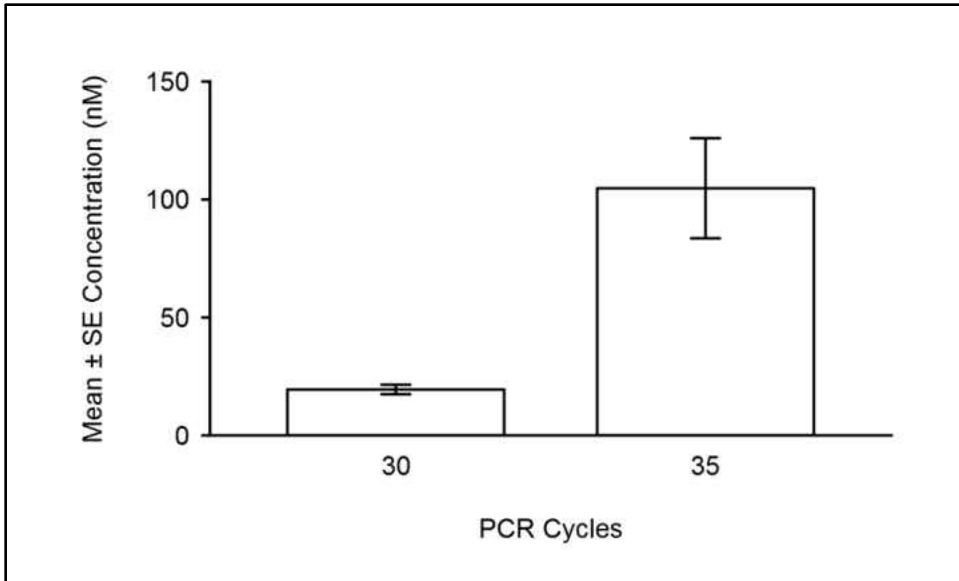


Figure 2.4. Mean ( $\pm$  standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at Mammoth Cave National Park, Kentucky and amplified with either 30 or 35 PCR cycles.  $n = 10$  samples per treatment; the same suite of ten samples was used in each treatment. Samples amplified with 35 cycles had significantly greater yield than those amplified with 30 cycles ( $W = 0$ ,  $P = 0.0002$ ).

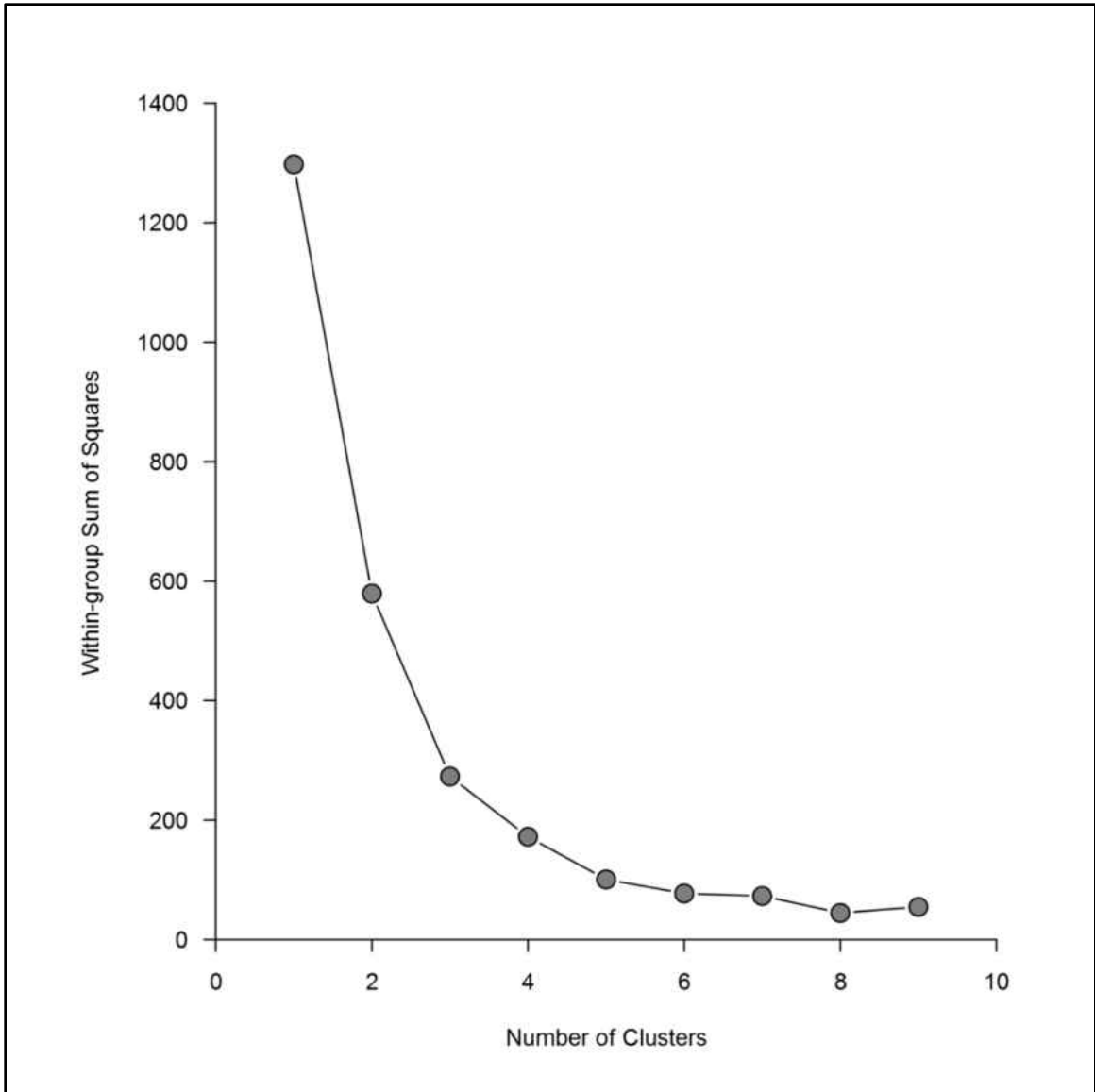


Figure 3.1. Graphical approach to selecting an ideal numbers of clusters for a size-based classification of 541 species of Lepidoptera collected at Mammoth Cave National Park, Kentucky. The plot shows decreasing within-group sum of squares with increasing number of clusters. Although little reduction in within-group sum of squares is observed beyond four clusters, I opted to use six clusters to better reflect naturally occurring trends in the data.

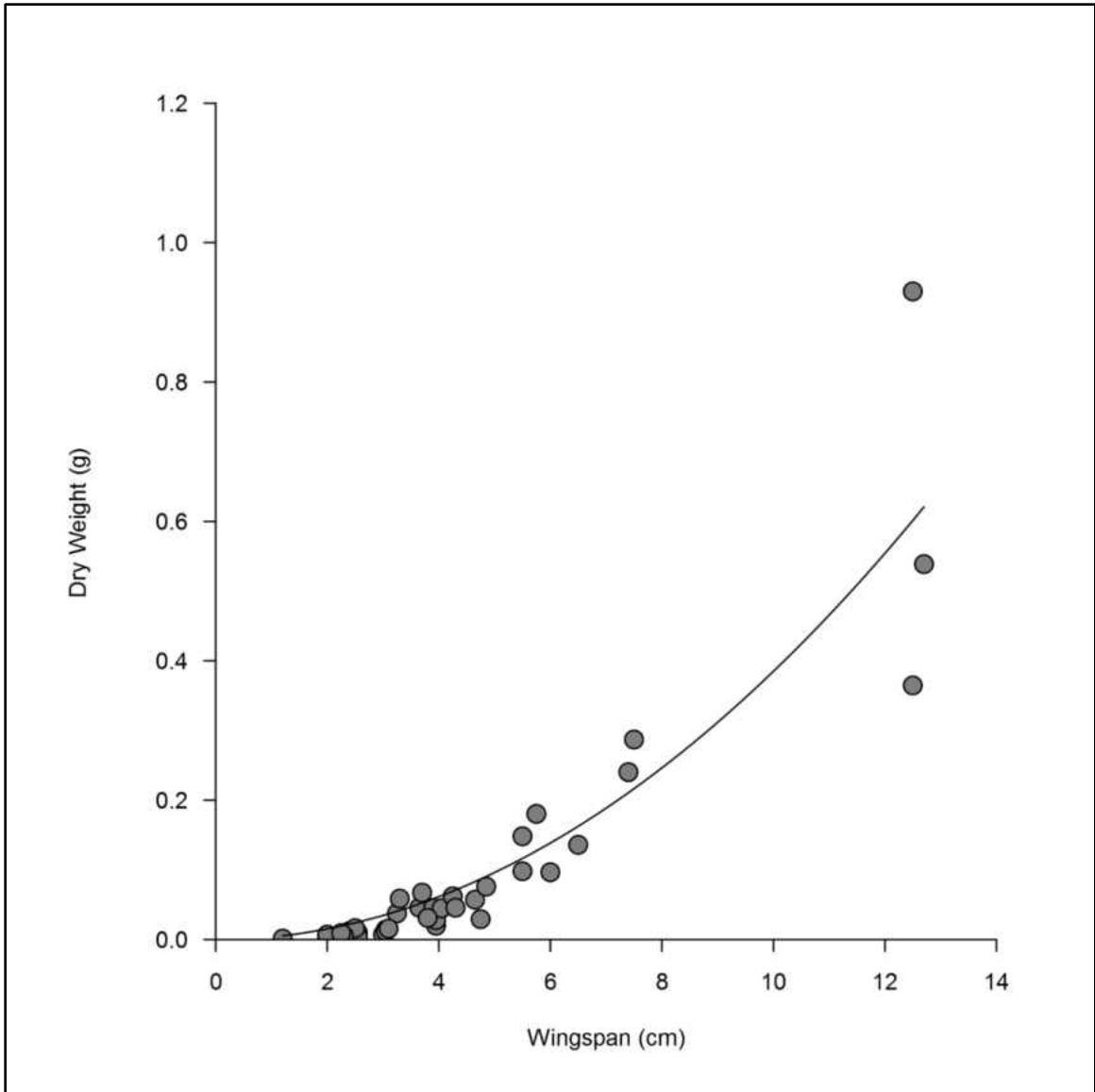


Figure 3.2. Empirically-determined relationship of Lepidoptera dry weight to wingspan, based on 47 species collected at Mammoth Cave National Park, Kentucky. Multiple individuals ( $n = 2 - 3$ ) per species were dried, weighed, and averaged. The curve is given by the equation  $y = 0.0031 \times \text{wingspan}^2$ .



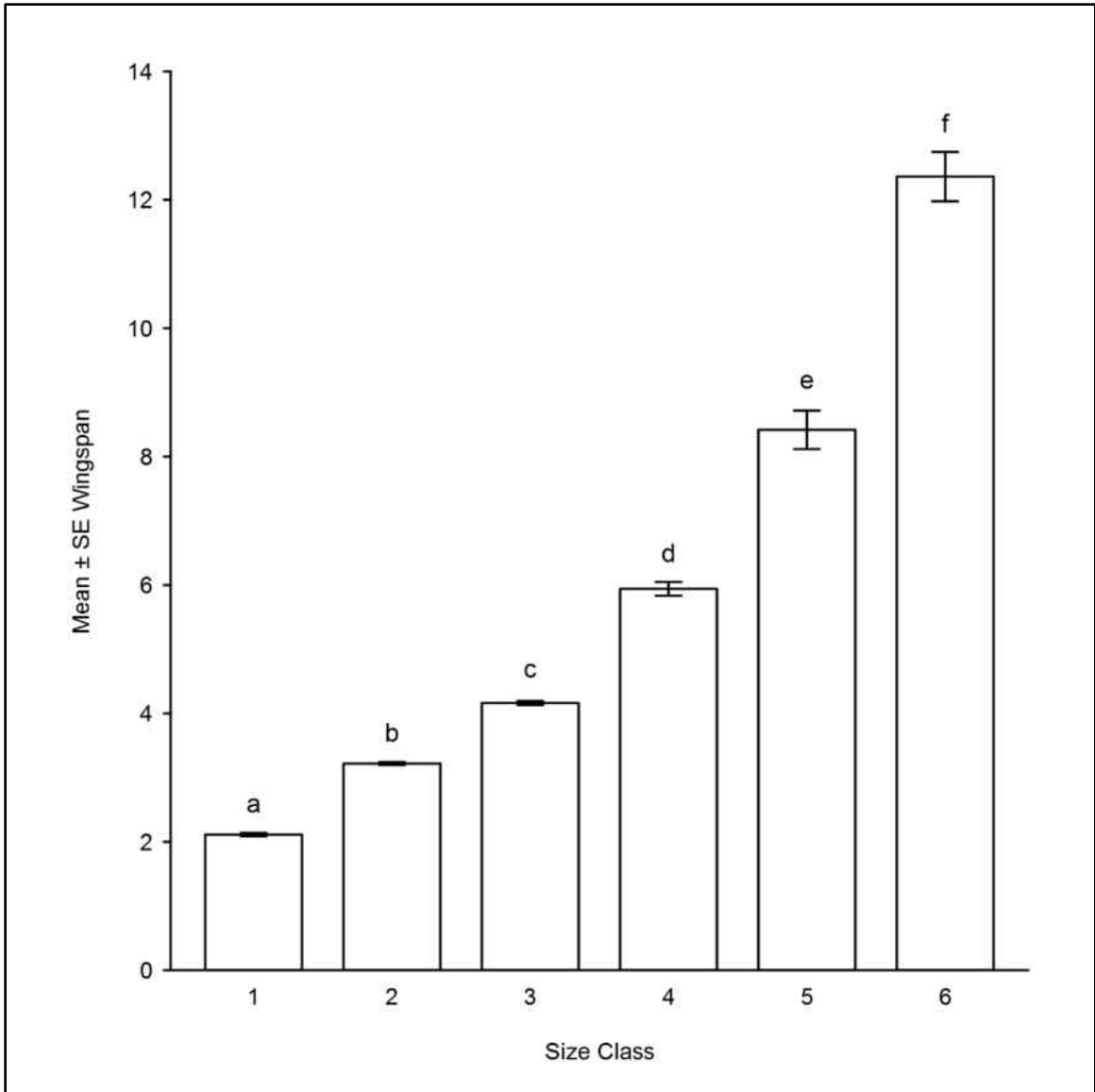


Figure 3.3. Mean ( $\pm$  standard error) wingspan of 7,842 Lepidoptera, collected at Mammoth Cave National Park, Kentucky, in each of six size classes defined in this work. Wingspan differed significantly across all size classes ( $P < 0.05$ ).

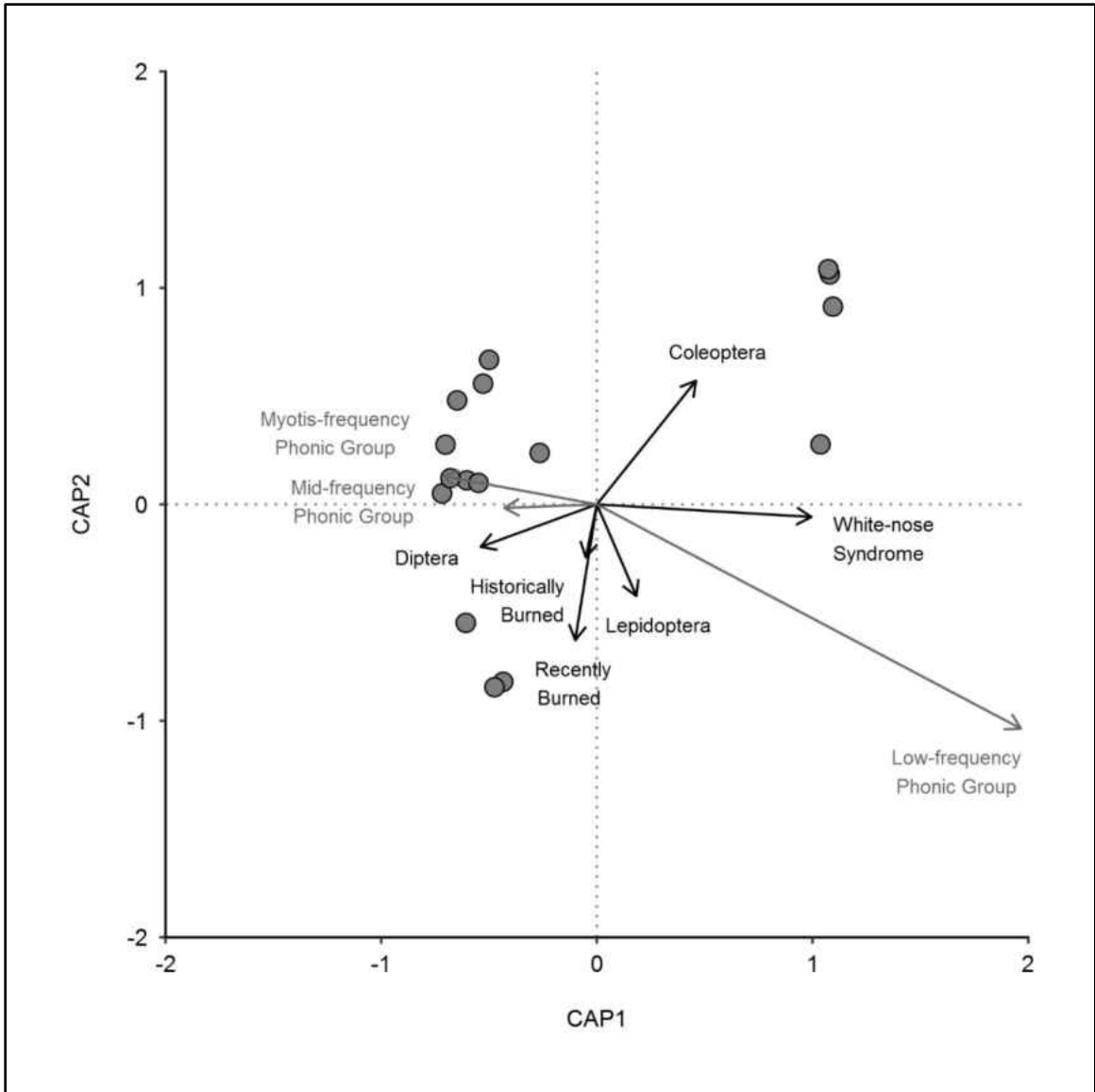


Figure 3.4. Biplot visualizing the results of distance-based redundancy analysis. Gray arrows represent the numerical abundances of bat phonic groups as estimated by acoustic detection. Black arrows represent the constraining variables; all insect variables refer to relative abundance. Solid points represent sites. Ordination was significant ( $P < 0.05$ ) under 999 permutations. Cumulatively, CAP1 and CAP2 account for 87.2% of the explainable inertia in bat assemblage composition.

APPENDIX C

List of Lepidoptera known to occur at Mammoth Cave National Park  
and corresponding size and energetic metrics.

Table C.1. List of Lepidoptera known to occur at Mammoth Cave National Park and corresponding size and energetic metrics. Size classes were assigned following the classification developed in this work. Body length, wingspan, and dry weight are presented as means; mean body length and wingspan were derived from published values. Calories are presented on a per-individual basis and were calculated using a mean caloric density of 5,289 calories per gram<sup>1</sup>.

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
Acrolophidae					
<i>Acrolophus plumifrontella</i>	2	1.72	3.10	0.030	156.9
Apatelodidae					
<i>Apatelodes torrefacta</i>	2	2.00	3.70	0.067	356.5
<i>Olceclostera angelica</i>	2	2.00	3.70	0.042	223.6
Coleophoridae					
<i>Glyphidocera lactiflosella</i>	1	0.75	1.25	0.005	25.5
Cossidae					
<i>Prionoxystus macmurtei</i>	4	3.15	6.35	0.125	658.5
<i>Prionoxystus robiniae</i>	4	3.60	6.40	0.126	668.9
Crambidae					
<i>Achyra rantalis</i>	1	1.05	2.00	0.012	65.3
<i>Agriphila vulgivagellus</i>	2	1.80	2.95	0.027	142.1
<i>Blepharomastix ranalis</i>	1	1.00	1.80	0.010	52.9
<i>Crambus agitatellus</i>	1	1.35	1.95	0.012	62.1
<i>Crambus laqueatellus</i>	1	1.50	2.65	0.022	114.7
<i>Crocidophora tubercularis</i>	1	0.90	2.10	0.014	72.0
<i>Desmia funeralis</i>	1	1.60	2.45	0.019	98.0
<i>Desmia maculalis</i>	1	1.20	2.10	0.014	72.0
<i>Diacme elealis</i>	1	2.00	2.00	0.012	65.3
<i>Dicymolomia julianalis</i>	1	0.95	1.60	0.008	41.8
<i>Herpetogramma thestealis</i>	2	1.69	3.05	0.029	151.9
<i>Hymenia perspectalis</i>	1	1.10	1.90	0.011	59.0
<i>Microcrambus elegans</i>	1	0.90	1.35	0.006	29.8
<i>Nomophila nearctica</i>	2	1.50	2.95	0.027	142.1
<i>Ostrinia nubilalis</i>	2	1.50	2.80	0.024	128.0
<i>Palpita magniferalis</i>	1	1.50	2.50	0.019	102.1
<i>Pantographa limata</i>	2	1.85	3.35	0.035	183.3
<i>Pediasia trisecta</i>	1	1.60	2.65	0.022	114.7
<i>Perispasta caecularis</i>	1	0.85	1.60	0.008	41.8

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Phlyctaenia coronata tertialis</i>	1	1.30	2.00	0.012	65.3
<i>Polygrammodes flavidalis</i>	2	1.45	2.95	0.027	142.1
<i>Pyrausta acronalis</i>	1	0.85	1.60	0.008	41.8
<i>Pyrausta bicoloralis</i>	1	1.00	1.65	0.008	44.5
<i>Pyrausta niveiciliaris</i>	1	1.27	2.25	0.016	82.7
<i>Pyrausta orphisalis</i>	1	0.85	1.60	0.008	41.8
<i>Pyrausta signatalis</i>	1	0.95	1.85	0.011	55.9
<i>Pyrausta tyralis</i>	1	0.83	1.40	0.006	32.0
<i>Udea rubigalis</i>	1	1.00	1.80	0.010	52.9
<i>Urola nivalis</i>	1	1.20	1.90	0.011	59.0
<i>Vaxi auratella</i>	1	0.90	1.65	0.008	44.5
<i>Vaxi critica</i>	1	1.00	1.65	0.008	44.5
Drepanidae					
<i>Drepana arcuata</i>	2	1.77	3.20	0.032	167.2
<i>Euthyatira pudens</i>	3	2.40	4.30	0.057	302.0
<i>Oreta rosea</i>	2	1.64	2.95	0.027	142.1
<i>Pseudothyatira cymatophoroides</i>	3	2.40	4.20	0.054	288.1
Elachistidae					
<i>Agonopterix robiniella</i>	1	1.00	2.00	0.012	65.3
<i>Antaeotricha schlaegeri</i>	1	1.30	2.55	0.020	106.2
<i>Antaeotricha leucillana</i>	1	1.09	1.90	0.011	59.0
<i>Ethmia trifurcella</i>	1	1.01	1.75	0.009	50.0
<i>Ethmia zelleriella</i>	1	1.25	2.45	0.019	98.0
<i>Machimia tentoriferella</i>	1	1.30	2.30	0.016	86.4
<i>Psilocorsis reflexella</i>	1	0.95	2.05	0.013	68.6
Epipyropidae					
<i>Fulgoraecia exigua</i>	1	0.60	0.95	0.003	14.7
Erebidae					
<i>Allotria elonympha</i>	3	2.15	3.90	0.045	240.4
<i>Apantesis phalerata</i>	2	1.90	3.60	0.040	211.7
<i>Apantesis vittata</i>	2	2.03	3.70	0.042	223.6
<i>Bleptina caradrinalis</i>	1	1.45	2.70	0.023	119.1
<i>Caenurgia chloropha</i>	2	1.75	3.15	0.031	162.0
<i>Caenurgina crassiuscula</i>	2	1.95	3.50	0.038	200.1
<i>Caenurgina erechtea</i>	2	2.00	3.60	0.040	211.7

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Calyptra canadensis</i>	2	2.05	3.65	0.041	217.6
<i>Catocala agrippina</i>	5	4.01	7.50	0.174	918.6
<i>Catocala andromedae</i>	3	2.45	4.50	0.063	330.7
<i>Catocala dejecta</i>	4	3.46	6.45	0.128	679.4
<i>Catocala flebilis</i>	4	3.20	5.95	0.109	578.2
<i>Catocala ilia</i>	5	3.95	7.35	0.167	882.3
<i>Catocala lacrymosa</i>	4	3.75	7.10	0.156	823.3
<i>Catocala obscura</i>	4	3.50	6.60	0.135	711.4
<i>Catocala palaeogama</i>	4	3.45	6.50	0.130	690.0
<i>Catocala residua</i>	4	3.50	6.65	0.137	722.2
<i>Catocala resecta</i>	4	3.55	6.75	0.141	744.1
<i>Catocala vidua</i>	5	4.05	7.70	0.183	968.3
<i>Celiptera frustulum</i>	3	2.00	3.75	0.043	229.7
<i>Chytolita morbidalis</i>	2	1.75	3.20	0.032	167.2
<i>Cisseps fulvicollis</i>	2	1.80	3.30	0.034	177.9
<i>Cissusa spadix</i>	2	1.95	3.55	0.039	205.8
<i>Cisthene packardii</i>	1	0.90	1.65	0.008	44.5
<i>Cisthene plumbea</i>	1	1.09	1.90	0.011	59.0
<i>Clemensia albata</i>	1	1.10	2.00	0.012	65.3
<i>Crambidia lithosoides</i>	1	0.88	1.50	0.007	36.7
<i>Crambidia pallida</i>	1	1.10	2.20	0.003	18.3
<i>Cycnia tenera</i>	2	1.90	3.50	0.038	200.1
<i>Dasychira basiflava</i>	3	2.20	4.20	0.054	288.1
<i>Dasychira dorsipennata</i>	3	2.32	4.25	0.056	295.0
<i>Dasychira manto</i>	3	2.16	3.95	0.048	254.8
<i>Dasychira obliquata</i>	3	2.25	4.55	0.064	338.1
<i>Estigmene acrea</i>	4	3.05	5.65	0.099	521.3
<i>Euchaetes egle</i>	3	1.95	3.75	0.043	229.7
<i>Euclidia cuspidata</i>	2	2.30	3.50	0.038	200.1
<i>Euparthenos nubilis</i>	4	3.35	6.30	0.123	648.2
<i>Grammia anna</i>	3	2.55	4.65	0.067	353.1
<i>Grammia arge</i>	3	2.30	4.40	0.060	316.2
<i>Grammia figurata</i>	2	1.90	3.65	0.041	217.6
<i>Grammia oithona</i>	3	2.11	3.85	0.046	242.1
<i>Grammia parthenice intermedia</i>	3	2.30	4.50	0.063	330.7
<i>Grammia virgo</i>	4	3.05	5.75	0.102	540.0
<i>Halysidota tessellaris</i>	3	2.35	4.25	0.062	328.4
<i>Haploa clymene</i>	3	2.50	4.75	0.029	155.1
<i>Haploa contigua</i>	3	2.25	4.25	0.056	295.0

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Haploa lecontei</i>	3	2.25	4.30	0.057	302.0
<i>Haploa reversa</i>	3	2.50	4.75	0.070	368.5
<i>Hypena baltimoralis</i>	2	1.70	2.90	0.026	137.3
<i>Hypena manalis</i>	1	1.45	2.55	0.020	106.2
<i>Hypena palparia</i>	2	1.70	3.00	0.028	147.0
<i>Hypena scabra</i>	2	1.80	3.00	0.028	147.0
<i>Hypena sordidula</i>	1	1.55	2.70	0.023	119.1
<i>Hypercompe scribonia</i>	5	3.40	7.40	0.240	1270.9
<i>Hyperstrotia pervertens</i>	1	0.90	1.80	0.010	52.9
<i>Hyperstrotia secta</i>	1	0.85	1.70	0.009	47.2
<i>Hyphantria cunea</i>	2	1.65	3.20	0.032	167.2
<i>Hypoprepia fucosa</i>	2	1.60	3.00	0.007	38.3
<i>Hypsoropha hormos</i>	2	1.60	2.95	0.027	142.1
<i>Hypsoropha monilis</i>	2	2.03	3.70	0.042	223.6
<i>Idia aemula</i>	1	1.35	2.50	0.019	102.1
<i>Idia americalis</i>	1	1.35	2.50	0.019	102.1
<i>Idia diminuendis</i>	1	1.00	1.75	0.009	50.0
<i>Idia lubricalis</i>	2	1.95	3.00	0.028	147.0
<i>Idia scobialis</i>	1	1.20	2.10	0.014	72.0
<i>Lascoria ambigualis</i>	1	1.30	2.30	0.016	86.4
<i>Ledaea perditalis</i>	1	1.45	2.45	0.019	98.0
<i>Lesmone detrahens</i>	2	1.61	2.90	0.026	137.3
<i>Leucanopsis longa</i>	3	2.34	4.30	0.057	302.0
<i>Metalectra discalis</i>	1	1.38	2.45	0.019	98.0
<i>Metalectra quadrisignata</i>	2	1.66	3.00	0.028	147.0
<i>Metalectra richardsi</i>	1	0.93	1.60	0.008	41.8
<i>Nigetia formosalis</i>	1	1.20	1.80	0.010	52.9
<i>Orgyia definita</i>	1	1.60	2.65	0.022	114.7
<i>Orgyia leucostigma</i>	2	1.85	3.00	0.028	147.0
<i>Oruza albocostaliata</i>	1	1.12	1.95	0.012	62.1
<i>Palthis angulalis</i>	1	1.80	2.30	0.016	86.4
<i>Palthis asopialis</i>	1	1.60	2.10	0.014	72.0
<i>Pangrapta decoralis</i>	1	1.30	2.40	0.018	94.1
<i>Panopoda carneicosta</i>	3	2.30	4.20	0.054	288.1
<i>Panopoda repanda</i>	3	2.19	4.00	0.049	261.3
<i>Panopoda rufimargo</i>	3	2.35	4.30	0.046	242.2
<i>Parallelia bistriaris</i>	3	2.30	3.80	0.031	164.8
<i>Phalaenophana pyramusalis</i>	1	1.30	2.30	0.016	86.4
<i>Phalaenostola larentioides</i>	1	1.15	2.05	0.013	68.6

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Phoberia atomaris</i>	3	2.05	3.95	0.048	254.8
<i>Phyprosopus callitrichoides</i>	2	1.70	3.15	0.031	162.0
<i>Phytometra rhodarialis</i>	1	1.05	1.95	0.012	62.1
<i>Plusiodonta compressipalpis</i>	2	1.60	2.90	0.026	137.3
<i>Pyrrharctia isabella</i>	4	2.85	5.50	0.098	518.9
<i>Renia flavipunctalis</i>	1	1.65	2.55	0.020	106.2
<i>Renia fraternalis</i>	1	1.35	2.40	0.018	94.1
<i>Renia nemoralis</i>	2	1.53	2.75	0.023	123.5
<i>Renia sobrialis</i>	1	1.40	2.55	0.020	106.2
<i>Rivula propinqualis</i>	1	1.05	1.70	0.009	47.2
<i>Scolecocampa liburna</i>	3	2.15	3.90	0.047	248.4
<i>Spiloloma lunilinea</i>	3	2.45	4.90	0.074	392.1
<i>Spilosoma congrua</i>	2	1.95	3.70	0.042	223.6
<i>Spilosoma latipennis</i>	3	2.10	3.95	0.048	254.8
<i>Spilosoma virginica</i>	2	2.15	3.50	0.038	200.1
<i>Tetanolita mynesalis</i>	1	1.20	2.25	0.016	82.7
<i>Virbia aurantiaca</i>	1	1.20	2.25	0.016	82.7
<i>Virbia opella</i>	2	1.40	2.80	0.024	128.0
<i>Zale aeruginosa</i>	3	2.11	3.85	0.046	242.1
<i>Zale bethunei</i>	2	1.95	3.55	0.039	205.8
<i>Zale galbanata</i>	2	1.93	3.50	0.038	200.1
<i>Zale horrida</i>	3	2.06	3.75	0.043	229.7
<i>Zale lunata</i>	3	2.58	4.75	0.070	368.5
<i>Zale lunifera</i>	3	2.24	4.10	0.052	274.5
<i>Zale unilineata</i>	3	2.45	4.50	0.063	330.7
<i>Zanclognatha cruralis</i>	2	1.60	2.90	0.026	137.3
<i>Zanclognatha laevigata</i>	2	1.95	3.00	0.028	147.0
<i>Zanclognatha lituralis</i>	1	1.35	2.45	0.019	98.0
<i>Zanclognatha obscuripennis</i>	1	1.51	2.70	0.023	119.1
<i>Zanclognatha pedipilalis</i>	1	1.55	2.70	0.023	119.1
Eutiliidae					
<i>Marathyssa basalis</i>	2	1.65	2.85	0.025	132.7
<i>Marathyssa inficita</i>	1	1.55	2.65	0.022	114.7
<i>Paectes abrostoloides</i>	2	1.60	2.95	0.027	142.1
<i>Paectes oculatrix</i>	1	1.50	2.40	0.018	94.1
<i>Paectes pygmaea</i>	1	1.15	2.10	0.014	72.0

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

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<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.



Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
Gelechiidae					
<i>Dichomeris ligulella</i>	1	0.95	1.65	0.008	44.5
<i>Trichotaphe flavocostella</i>	1	0.96	1.65	0.008	44.5
Geometridae					
<i>Anavitrinella pampinaria</i>	2	1.59	2.85	0.025	132.7
<i>Besma endropiaria</i>	2	1.82	3.30	0.034	177.9
<i>Besma quercivoraria</i>	2	1.87	3.40	0.036	188.8
<i>Biston betularia cognataria</i>	3	2.32	4.25	0.056	295.0
<i>Cabera erythemaria</i>	1	1.38	2.45	0.019	98.0
<i>Campaea perlata</i>	3	2.16	3.95	0.020	105.6
<i>Chlorochlamys chloroleucaria</i>	1	1.07	1.85	0.011	55.9
<i>Chlorochlamys phyllinaria</i>	1	1.07	1.85	0.011	55.9
<i>Cladara atroliturlata</i>	2	1.53	2.75	0.023	123.5
<i>Costaconvexa centrostrigaria</i>	1	1.14	2.00	0.012	65.3
<i>Cyclophora packardi</i>	1	1.14	2.00	0.012	65.3
<i>Cyclophora pendulinaria</i>	1	1.20	2.10	0.014	72.0
<i>Dichorda iridaria</i>	1	1.40	2.50	0.019	102.1
<i>Digrammia continuata</i>	1	1.33	2.35	0.017	90.2
<i>Digrammia ocellinata</i>	1	1.35	2.40	0.018	94.1
<i>Disclisioprocta stellata</i>	2	1.61	2.90	0.026	137.3
<i>Ectropis crepuscularia</i>	2	1.74	3.15	0.031	162.0
<i>Ennomos magnaria</i>	4	2.79	5.15	0.082	433.2
<i>Ennomos subsignaria</i>	2	1.98	3.60	0.040	211.7
<i>Epimecis hortaria</i>	3	2.65	4.90	0.074	392.1
<i>Epirrhoe alternata</i>	1	1.25	2.20	0.015	79.0
<i>Eubaphe mendica</i>	1	1.43	2.55	0.003	17.6
<i>Euchlaena amoenaria</i>	3	2.16	3.95	0.028	147.7
<i>Euchlaena irraria</i>	3	2.32	4.25	0.056	295.0
<i>Euchlaena johnsonaria</i>	2	1.74	3.15	0.031	162.0
<i>Euchlaena obtusaria</i>	3	2.06	3.75	0.043	229.7
<i>Euchlaena pectinaria</i>	3	2.08	3.80	0.045	235.8
<i>Eugonobapta nivosaria</i>	1	1.51	2.70	0.023	119.1
<i>Eulithis diversilineata</i>	2	1.69	3.05	0.014	75.4
<i>Euphyia intermediata</i>	1	1.40	2.50	0.019	102.1
<i>Eupithecia herefordaria</i>	1	1.01	1.75	0.009	50.0
<i>Eupithecia miserulata</i>	1	0.93	1.60	0.008	41.8
<i>Eusarca confusaria</i>	2	1.93	3.50	0.038	200.1
<i>Eutrapela clemataria</i>	3	2.55	4.70	0.068	360.8

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Exelis pyrolaria</i>	1	1.33	2.35	0.017	90.2
<i>Glena cribrataria</i>	1	1.51	2.70	0.023	119.1
<i>Glenoides texanaria</i>	1	1.07	1.85	0.011	55.9
<i>Heliomata cycladata</i>	1	1.12	1.95	0.012	62.1
<i>Heterophleps refusaria</i>	1	1.48	2.65	0.022	114.7
<i>Heterophleps triguttaria</i>	1	1.20	2.10	0.014	72.0
<i>Hydrelia albifera</i>	1	0.96	1.65	0.008	44.5
<i>Hydrelia inornata</i>	1	1.12	1.95	0.012	62.1
<i>Hydriomena divisaria</i>	1	1.51	2.70	0.023	119.1
<i>Hypagyrtis brendae</i>	2	1.79	3.25	0.033	172.5
<i>Hypagyrtis esther</i>	2	1.93	3.50	0.038	200.1
<i>Hypagyrtis unipunctata</i>	2	1.85	3.35	0.035	183.3
<i>Hypomecis umbrosaria</i>	2	1.82	3.30	0.034	177.9
<i>Idaea demissaria</i>	1	0.96	1.65	0.008	44.5
<i>Idaea furciferata</i>	1	0.93	1.60	0.008	41.8
<i>Idaea obfusaria</i>	1	1.14	2.00	0.012	65.3
<i>Iridopsis defectaria</i>	2	1.66	3.00	0.028	147.0
<i>Iridopsis ephyraria</i>	1	1.43	2.55	0.020	106.2
<i>Iridopsis humaria</i>	1	1.46	2.60	0.021	110.4
<i>Iridopsis larvaria</i>	2	1.72	3.10	0.030	156.9
<i>Lambdina fervidaria</i>	2	1.72	3.10	0.030	156.9
<i>Lambdina fervidaria athasaria</i>	2	1.72	3.10	0.030	156.9
<i>Lambdina pellucidaria</i>	2	1.90	3.45	0.037	194.4
<i>Leptostales rubromarginaria</i>	1	0.99	1.70	0.009	47.2
<i>Lomographa glomeraria</i>	1	1.35	2.40	0.018	94.1
<i>Lomographa vestaliata</i>	1	1.17	2.05	0.013	68.6
<i>Lophosis labeculata</i>	1	0.73	1.20	0.001	7.4
<i>Lycia rachelae</i>	2	1.93	3.50	0.038	200.1
<i>Lytrosis unitaria</i>	4	2.79	5.15	0.082	433.2
<i>Macaria aemulataria</i>	1	1.20	2.10	0.014	72.0
<i>Macaria bicolorata</i>	2	1.64	2.95	0.027	142.1
<i>Macaria bisignata</i>	1	1.35	2.40	0.018	94.1
<i>Macaria fissinotata</i>	1	1.33	2.35	0.017	90.2
<i>Macaria granitata</i>	1	1.40	2.50	0.019	102.1
<i>Macaria minorata</i>	1	1.20	2.10	0.014	72.0
<i>Macaria multilineata</i>	1	1.38	2.45	0.019	98.0
<i>Macaria promiscuata</i>	1	1.46	2.60	0.021	110.4
<i>Melanolophia canadaria crama</i>	2	1.77	3.20	0.032	167.2
<i>Melanolophia signataria</i>	2	1.79	3.25	0.033	172.5

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Mellilla xanthometata</i>	1	1.07	1.85	0.011	55.9
<i>Metanema inatomaria</i>	2	1.69	3.05	0.029	151.9
<i>Metarranthis angularia</i>	3	2.06	3.75	0.043	229.7
<i>Metarranthis duaria</i>	3	2.06	3.75	0.043	229.7
<i>Metarranthis homuraria</i>	2	1.61	2.90	0.026	137.3
<i>Nematocampa resistaria</i>	1	1.25	2.20	0.015	79.0
<i>Nemoria lixaria</i>	1	1.40	2.50	0.019	102.1
<i>Orthonama obstipata</i>	1	1.07	1.85	0.011	55.9
<i>Patalene olyzonaria puber</i>	1	0.99	1.70	0.009	47.2
<i>Pero honestaria</i>	2	1.93	3.50	0.038	200.1
<i>Pero hubneraria</i>	2	1.87	3.40	0.036	188.8
<i>Phaeoura quernaria</i>	3	2.52	4.65	0.067	353.1
<i>Plagodis alcoolaria</i>	2	1.69	3.05	0.012	62.1
<i>Plagodis fervidaria</i>	1	1.51	2.70	0.023	119.1
<i>Plagodis phlogosaria</i>	2	1.53	2.75	0.023	123.5
<i>Plagodis pulveraria</i>	2	1.61	2.90	0.026	137.3
<i>Pleuroprucha insularia</i>	1	1.01	1.75	0.009	50.0
<i>Probole amicarica</i>	2	1.59	2.85	0.025	132.7
<i>Probole nyssaria</i>	2	1.69	3.05	0.029	151.9
<i>Prochoerodes lineola</i>	3	2.32	4.25	0.056	295.0
<i>Protitame virginalis</i>	1	1.25	2.20	0.015	79.0
<i>Protoarmia porcelaria</i>	2	1.66	3.00	0.028	147.0
<i>Rheumaptera prunivorata</i>	2	1.72	3.10	0.030	156.9
<i>Scopula caecumanaria</i>	1	1.17	2.05	0.013	68.6
<i>Scopula inductata</i>	1	1.17	2.05	0.013	68.6
<i>Scopula limboundata</i>	1	1.40	2.50	0.019	102.1
<i>Semiothisa quadrinotaria</i>	1	1.38	2.45	0.019	98.0
<i>Speranza coortaria</i>	1	1.35	2.40	0.018	94.1
<i>Speranza pustularia</i>	1	1.27	2.25	0.009	49.4
<i>Synchlora aerata</i>	1	1.07	1.85	0.011	55.9
<i>Tetracis cachexiata</i>	3	2.39	4.40	0.060	316.2
<i>Tetracis crocallata</i>	2	1.93	3.50	0.038	200.1
<i>Venusia comptaria</i>	1	1.09	1.90	0.011	59.0
<i>Xanthorhoe labradorensis</i>	1	1.27	2.25	0.016	82.7
<i>Xanthorhoe lacustrata</i>	1	1.30	2.30	0.016	86.4
<i>Xanthotype urticaria</i>	2	1.93	3.50	0.038	200.1
Lasiocampidae					
<i>Artace cribrarius</i>	3	2.25	4.35	0.058	309.0

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Malacosoma americanum</i>	2	1.95	3.30	0.059	311.0
<i>Malacosoma disstria</i>	2	1.90	3.00	0.028	147.0
<i>Phyllodesma americana</i>	3	2.00	3.90	0.047	248.4
Limacodidae					
<i>Acharia stimulea</i>	2	1.80	3.45	0.037	194.4
<i>Apoda biguttata</i>	1	1.25	2.45	0.019	98.0
<i>Apoda y-inversum</i>	1	1.30	2.55	0.020	106.2
<i>Euclea delphinii</i>	1	1.25	2.50	0.016	86.7
<i>Lithacodes fasciola</i>	1	1.15	2.15	0.014	75.5
<i>Natada nasoni</i>	1	1.27	2.25	0.016	82.7
<i>Packardia geminata</i>	1	1.00	2.10	0.014	72.0
<i>Parasa chloris</i>	1	1.20	2.25	0.016	82.7
<i>Parasa indetermina</i>	1	1.35	2.65	0.022	114.7
<i>Phobetron pithecium</i>	1	1.25	2.40	0.018	94.1
<i>Prolimacodes badia</i>	1	1.45	2.45	0.019	98.0
<i>Tortricidia flexuosa</i>	1	1.00	2.00	0.012	65.3
<i>Tortricidia testacea</i>	1	1.00	2.05	0.013	68.6
Megalopygidae					
<i>Lagoa crispata</i>	2	1.79	3.25	0.038	199.4
<i>Megalopyge opercularis</i>	2	1.66	3.00	0.028	147.0
<i>Norape ovina</i>	2	1.66	3.00	0.028	147.0
Mimallonidae					
<i>Cicinnus melsheimeri</i>	3	2.35	4.25	0.056	295.0
<i>Lacosoma chiridota</i>	1	2.60	2.60	0.021	110.4
Noctuidae					
<i>Abagrotis alternata</i>	3	2.21	4.05	0.051	267.9
<i>Achatia distincta</i>	2	2.00	3.35	0.035	183.3
<i>Acronicta afflicta</i>	3	2.00	4.00	0.049	261.3
<i>Acronicta americana</i>	4	3.25	5.75	0.180	954.1
<i>Acronicta betulae</i>	3	2.00	3.75	0.043	229.7
<i>Acronicta fragilis</i>	2	1.60	3.05	0.029	151.9
<i>Acronicta funeralis</i>	2	1.90	3.60	0.040	211.7
<i>Acronicta haesitata</i>	2	2.40	3.65	0.041	217.6
<i>Acronicta impleta</i>	3	2.40	4.40	0.060	316.2
<i>Acronicta inclara</i>	2	1.77	3.20	0.032	167.2

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Acronicta interrupta</i>	3	2.10	3.85	0.046	242.1
<i>Acronicta lithospila</i>	3	2.05	3.80	0.045	235.8
<i>Acronicta lobeliae</i>	4	2.65	5.10	0.080	424.8
<i>Acronicta noctivaga</i>	2	2.00	3.50	0.038	200.1
<i>Acronicta ovata</i>	2	1.70	3.15	0.031	162.0
<i>Acronicta pruni</i>	3	2.13	3.90	0.047	248.4
<i>Acronicta radcliffei</i>	2	1.90	3.65	0.046	242.4
<i>Acronicta vinnula</i>	2	1.60	3.00	0.028	147.0
<i>Agriopodes fallax</i>	2	1.85	3.35	0.035	183.3
<i>Agrotis gladaria</i>	2	1.90	3.35	0.035	183.3
<i>Agrotis ipsilon</i>	3	2.20	4.15	0.053	281.3
<i>Allagrapha aerea</i>	2	1.90	3.50	0.038	200.1
<i>Amphipoea americana</i>	2	1.70	3.20	0.032	167.2
<i>Amphipyra pyramidoides</i>	3	2.55	4.50	0.063	330.7
<i>Anagrapha falcifera</i>	2	2.00	3.60	0.040	211.7
<i>Anathix ralla</i>	2	1.90	3.05	0.029	151.9
<i>Anicla infecta</i>	2	1.85	3.50	0.038	200.1
<i>Anterastria teratophora</i>	1	1.20	2.20	0.015	79.0
<i>Apamea sordens</i>	2	2.10	3.60	0.040	211.7
<i>Athetis tarda</i>	2	1.45	2.90	0.026	137.3
<i>Autographa bimaculata</i>	3	2.10	3.90	0.047	248.4
<i>Autographa precationis</i>	2	1.90	3.40	0.036	188.8
<i>Baileya australis</i>	1	1.40	2.45	0.019	98.0
<i>Baileya levitans</i>	2	1.60	2.95	0.027	142.1
<i>Baileya ophthalmica</i>	2	1.55	2.75	0.023	123.5
<i>Balsa labecula</i>	1	1.45	2.70	0.023	119.1
<i>Basilodes pepita</i>	3	2.10	4.00	0.049	261.3
<i>Callopietria cordata</i>	1	1.55	2.65	0.022	114.7
<i>Callopietria mollissima</i>	1	1.50	2.40	0.018	94.1
<i>Cerastis tenebrifera</i>	2	1.85	3.50	0.038	200.1
<i>Cerma cerintha</i>	2	1.60	3.05	0.029	151.9
<i>Cheophora fungorum</i>	3	2.40	4.00	0.049	261.3
<i>Chytonix palliatricula</i>	2	1.70	3.05	0.029	151.9
<i>Cirrhophanus triangulifer</i>	2	2.05	3.70	0.042	223.6
<i>Colocasia flavicornis</i>	2	2.00	3.65	0.041	217.6
<i>Comachara cadburyi</i>	1	1.25	2.20	0.015	79.0
<i>Condica vecors</i>	2	1.70	3.35	0.035	183.3
<i>Condica videns</i>	2	1.55	2.90	0.026	137.3
<i>Cosmia calami</i>	2	1.60	2.95	0.027	142.1

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Crocigrapta normani</i>	3	1.85	3.75	0.043	229.7
<i>Ctenoplusia oxygramma</i>	3	2.05	3.75	0.043	229.7
<i>Egira alternans</i>	2	1.95	3.05	0.029	151.9
<i>Elaphria chalconia</i>	1	1.40	2.60	0.021	110.4
<i>Elaphria festivoidea</i>	1	1.38	2.45	0.019	98.0
<i>Elaphria grata</i>	1	1.30	2.30	0.016	86.4
<i>Elaphria versicolor</i>	1	1.40	2.35	0.017	90.2
<i>Eosphoropteryx thyatyroides</i>	2	1.85	3.45	0.037	194.4
<i>Eudryas grata</i>	3	2.40	4.05	0.045	237.8
<i>Euxoa divergens</i>	2	1.90	3.30	0.034	177.9
<i>Feltia herilis</i>	3	2.30	3.90	0.047	248.4
<i>Feltia jaculifera</i>	2	2.10	3.50	0.038	200.1
<i>Feltia subgothica</i>	3	1.95	3.75	0.043	229.7
<i>Galgula partita</i>	1	1.20	2.30	0.016	86.4
<i>Helicoverpa zea</i>	3	2.00	3.85	0.046	242.1
<i>Hyppa xylinoides</i>	3	2.25	3.75	0.043	229.7
<i>Lacanobia grandis</i>	3	2.25	3.80	0.045	235.8
<i>Lacinipolia anguina</i>	2	1.55	2.95	0.027	142.1
<i>Lacinipolia implicata</i>	2	1.60	2.85	0.025	132.7
<i>Lacinipolia meditata</i>	2	1.60	3.00	0.028	147.0
<i>Lacinipolia renigera</i>	1	1.45	2.55	0.020	106.2
<i>Leucania inermis</i>	2	1.70	3.30	0.034	177.9
<i>Leucania multilinea</i>	3	1.95	4.15	0.053	281.3
<i>Leucania scirpicola</i>	2	1.95	3.65	0.041	217.6
<i>Leuconycta diptheroides</i>	2	1.55	2.95	0.027	142.1
<i>Magasa divaricata</i>	3	2.00	3.85	0.046	242.1
<i>Maliattha synochitis</i>	1	0.95	1.90	0.011	59.0
<i>Marimatha nigrofimbria</i>	1	1.10	2.00	0.007	37.4
<i>Megalographa biloba</i>	2	1.95	3.70	0.042	223.6
<i>Melanchra adjuncta</i>	2	2.00	3.45	0.037	194.4
<i>Morrisonia confusa</i>	3	2.00	3.85	0.046	242.1
<i>Morrisonia latex</i>	3	2.40	4.50	0.063	330.7
<i>Mythimna unipuncta</i>	3	2.25	4.10	0.052	274.5
<i>Nedra ramosula</i>	3	2.00	3.80	0.045	235.8
<i>Nephelodes minians</i>	3	2.45	4.25	0.056	295.0
<i>Noctua pronuba</i>	4	3.25	5.50	0.093	494.0
<i>Ochropleura implecta</i>	2	1.50	2.85	0.025	132.7
<i>Ogdoconta cinereola</i>	1	1.25	2.15	0.014	75.5
<i>Orthodes cynica</i>	2	1.60	3.05	0.029	151.9

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Orthodes majuscula</i>	2	1.90	3.15	0.031	162.0
<i>Orthosia rubescens</i>	2	2.00	3.50	0.038	200.1
<i>Panthea furcilla</i>	3	2.25	4.15	0.053	281.3
<i>Papaipema arctivorens</i>	2	1.75	3.30	0.034	177.9
<i>Papaipema cerussata</i>	3	2.10	4.75	0.070	368.5
<i>Papaipema nebris</i>	2	1.80	3.60	0.040	211.7
<i>Papaipema rigida</i>	2	1.66	3.00	0.028	147.0
<i>Perigea xanthioides</i>	2	1.64	2.95	0.027	142.1
<i>Phlogophora periculosa</i>	3	2.70	4.60	0.065	345.6
<i>Phosphila miselioides</i>	2	1.80	3.40	0.036	188.8
<i>Polygrammate hebraeicum</i>	2	1.40	3.10	0.016	83.0
<i>Ponometia candefacta</i>	1	1.20	2.00	0.012	65.3
<i>Ponometia erastrioides</i>	1	0.95	1.80	0.010	52.9
<i>Protodeltote muscosula</i>	1	1.10	2.10	0.014	72.0
<i>Protolampra brunneicollis</i>	3	2.10	3.80	0.045	235.8
<i>Proxenus miranda</i>	1	1.40	2.50	0.019	102.1
<i>Psaphida electilis</i>	2	2.15	3.45	0.037	194.4
<i>Pseudeustrotia carneola</i>	1	1.20	2.20	0.015	79.0
<i>Pseudohermonassa bicarnea</i>	3	2.10	3.75	0.043	229.7
<i>Pseudorthodes vecors</i>	2	1.50	2.85	0.025	132.7
<i>Raphia frater</i>	2	1.85	3.55	0.039	205.8
<i>Schinia arcigera</i>	1	1.25	2.35	0.017	90.2
<i>Schinia lynx</i>	1	1.10	2.00	0.012	65.3
<i>Schinia rivulosa</i>	2	1.50	2.80	0.024	128.0
<i>Schinia trifascia</i>	1	1.45	2.55	0.020	106.2
<i>Spodoptera dolichos</i>	3	2.29	4.20	0.054	288.1
<i>Spodoptera exigua</i>	1	1.55	2.70	0.023	119.1
<i>Spodoptera frugiperda</i>	2	1.75	3.25	0.033	172.5
<i>Spodoptera ornithogalli</i>	3	2.10	3.80	0.045	235.8
<i>Spragueia leo</i>	1	0.85	1.50	0.007	36.7
<i>Sunira bicolorago</i>	2	1.90	3.30	0.034	177.9
<i>Sympistis badistriga</i>	2	1.75	3.10	0.030	156.9
<i>Sympistis infixia</i>	2	1.85	3.35	0.035	183.3
<i>Tarache aprica</i>	1	1.20	2.20	0.015	79.0
<i>Ulolonche culea</i>	2	1.80	3.25	0.033	172.5
<i>Xanthopastis timais</i>	3	2.25	4.20	0.054	288.1
<i>Xestia badicollis</i>	3	1.95	4.00	0.049	261.3
<i>Xestia dolosa</i>	3	2.05	4.15	0.053	281.3
<i>Xestia smithii</i>	3	2.15	3.75	0.043	229.7

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
Nolidae					
<i>Meganola minuscula</i>	1	1.00	1.90	0.011	59.0
<i>Nola cilicoides</i>	1	0.95	1.75	0.009	50.0
<i>Nola triquetrana</i>	1	0.95	1.75	0.009	50.0
Notodontidae					
<i>Clostera inclusa</i>	2	1.80	2.95	0.027	142.1
<i>Dasylophia anguina</i>	2	1.95	3.55	0.039	205.8
<i>Dasylophia thyatiroides</i>	3	2.40	4.15	0.053	281.3
<i>Datana angusii</i>	3	2.25	4.30	0.057	302.0
<i>Datana contracta</i>	3	2.40	4.65	0.057	302.9
<i>Datana drexelii</i>	3	2.45	4.80	0.071	376.3
<i>Datana integerrima</i>	3	2.45	4.50	0.063	330.7
<i>Datana ministra</i>	3	2.40	4.65	0.067	353.1
<i>Datana perspicua</i>	4	2.75	5.05	0.079	416.5
<i>Ellida caniplaga</i>	3	2.15	3.90	0.047	248.4
<i>Furcula borealis</i>	3	2.05	3.80	0.045	235.8
<i>Gluphisia septentrionis</i>	2	1.55	2.90	0.026	137.3
<i>Heterocampa biundata</i>	3	2.75	4.70	0.068	360.8
<i>Heterocampa guttivitta</i>	3	2.40	3.85	0.046	242.1
<i>Heterocampa obliqua</i>	3	2.40	4.50	0.063	330.7
<i>Heterocampa subrotata</i>	2	1.80	3.20	0.032	167.2
<i>Heterocampa umbrata</i>	4	2.80	5.20	0.083	441.6
<i>Hyperaeschra georgica</i>	3	2.15	4.05	0.051	267.9
<i>Lochmaeus bilineata</i>	2	2.05	3.60	0.040	211.7
<i>Lochmaeus manteo</i>	3	2.35	4.35	0.058	309.0
<i>Macrurocampa marthesia</i>	3	2.60	4.65	0.067	353.1
<i>Misogada unicolor</i>	3	2.50	4.50	0.063	330.7
<i>Nadata gibbosa</i>	3	2.50	4.85	0.076	402.5
<i>Nerice bidentata</i>	2	2.05	3.50	0.038	200.1
<i>Oligocentria lignicolor</i>	3	2.55	4.75	0.070	368.5
<i>Oligocentria semirufescens</i>	3	2.45	3.75	0.043	229.7
<i>Peridea angulosa</i>	3	2.25	4.50	0.063	330.7
<i>Peridea basitriens</i>	3	2.25	4.25	0.056	295.0
<i>Pheosia rimosa</i>	4	2.85	5.35	0.088	467.4
<i>Schizura apicalis</i>	2	1.61	2.90	0.026	137.3
<i>Schizura concinna</i>	2	1.90	3.35	0.035	183.3
<i>Schizura ipomeae</i>	3	2.25	4.15	0.053	281.3
<i>Schizura leptinoides</i>	3	2.40	3.95	0.048	254.8

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.



Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Schizura unicornis</i>	2	2.15	3.00	0.028	147.0
<i>Symmerista albifrons</i>	3	2.00	3.90	0.047	248.4
Pterophoridae					
<i>Platyptilia carduidactylus</i>	1	1.27	2.25	0.016	82.7
Pyralidae					
<i>Aglossa cuprina</i>	1	1.70	2.25	0.016	82.7
<i>Clydonopteron tecomae</i>	1	1.14	2.00	0.012	65.3
<i>Compacta capitalis</i>	2	1.85	3.35	0.035	183.3
<i>Conchylodes ovulalis</i>	1	1.43	2.55	0.010	51.8
<i>Condylolomia participalis</i>	1	0.75	1.35	0.006	29.8
<i>Epipagis huronalis</i>	1	1.27	2.25	0.016	82.7
<i>Epipaschia superatalis</i>	1	1.10	2.10	0.014	72.0
<i>Euzophera ostricolorella</i>	3	1.90	3.75	0.043	229.7
<i>Galasa nigrinodis</i>	1	1.10	1.65	0.008	44.5
<i>Helvibotys helvialis</i>	1	0.93	1.60	0.008	41.8
<i>Herculia infimbrialis</i>	1	1.27	2.25	0.016	82.7
<i>Herculia olinalis</i>	1	1.14	2.00	0.012	65.3
<i>Hypsopygia costalis</i>	1	1.00	1.60	0.008	41.8
<i>Munroessa gyralis</i>	1	1.30	2.30	0.016	86.4
<i>Peoria approximella</i>	1	0.80	1.70	0.009	47.2
<i>Plodia interpunctella</i>	1	0.83	1.35	0.006	29.8
<i>Pococera asperatella</i>	1	1.30	2.25	0.016	82.7
<i>Sciota basilaris</i>	1	1.25	2.20	0.015	79.0
<i>Tosale oviplagalis</i>	1	0.85	1.50	0.007	36.7
<i>Uresiphita reversalis</i>	2	1.69	3.05	0.029	151.9
Saturniidae					
<i>Actias luna</i>	5	4.79	9.00	0.250	1322.9
<i>Anisota stigma</i>	4	3.00	5.50	0.148	784.0
<i>Antheraea polyphemus</i>	6	6.62	12.50	0.365	1928.7
<i>Automeris io</i>	4	3.49	6.50	0.136	719.3
<i>Callosamia angulifera</i>	5	5.05	9.50	0.279	1473.9
<i>Callosamia promethea</i>	5	4.53	8.50	0.223	1180.0
<i>Dryocampa rubicunda</i>	3	2.60	4.30	0.057	302.0
<i>Eacles imperialis</i>	6	6.72	12.70	0.539	2849.4
<i>Hyalophora cecropia</i>	6	6.88	13.00	0.522	2760.0

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

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<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
Sesiidae					
<i>Synanthedon acerni</i>	1	1.25	2.15	0.014	75.5
<i>Synanthedon exitiosa</i>	1	1.75	2.35	0.017	90.2
Sphingidae					
<i>Amorpha juglandis</i>	4	3.50	6.00	0.097	511.4
<i>Ceratomia amyntor</i>	5	5.50	10.15	0.318	1682.5
<i>Ceratomia hageni</i>	5	4.58	8.60	0.228	1207.9
<i>Ceratomia undulosa</i>	5	5.25	9.40	0.273	1443.1
<i>Darapsa choerilus</i>	4	3.50	6.60	0.135	711.4
<i>Darapsa myron</i>	4	3.30	5.75	0.102	540.0
<i>Deidamia inscriptum</i>	4	3.15	5.75	0.102	540.0
<i>Manduca sexta</i>	6	6.00	11.25	0.391	2067.0
<i>Paonias astylus</i>	4	3.23	6.00	0.111	587.9
<i>Paonias excaecata</i>	5	4.25	7.50	0.287	1518.3
<i>Paonias myops</i>	4	3.35	6.00	0.111	587.9
Tortricidae					
<i>Acleris semipurpurana</i>	1	0.80	1.55	0.007	39.2
<i>Acleris subnivana</i>	1	0.70	1.35	0.006	29.8
<i>Amorbia humerosana</i>	1	1.30	2.55	0.020	106.2
<i>Archips argyrosbila</i>	1	1.00	1.90	0.011	59.0
<i>Archips fervedana</i>	1	1.00	2.15	0.014	75.5
<i>Argyrotaenia alisellana</i>	1	1.20	2.15	0.014	75.5
<i>Argyrotaenia juglandana</i>	1	1.04	1.80	0.010	52.9
<i>Argyrotaenia mariana</i>	1	1.10	2.00	0.012	65.3
<i>Argyrotaenia quercifoliata</i>	1	1.30	2.00	0.003	14.8
<i>Argyrotaenia velutinana</i>	1	0.90	1.45	0.006	34.3
<i>Cenopsis pettitana</i>	1	1.15	2.30	0.016	86.4
<i>Cenopsis reticulatana</i>	1	1.10	1.60	0.008	41.8
<i>Choristoneura fractivittana</i>	1	1.15	2.20	0.015	79.0
<i>Choristoneura parallela</i>	1	1.25	2.20	0.015	79.0
<i>Choristoneura pinus</i>	1	1.30	2.55	0.020	106.2
<i>Choristoneura rosaceana</i>	1	1.20	2.50	0.005	28.0
<i>Cydia latiferreana</i>	1	1.10	1.65	0.008	44.5
<i>Cydia pomonella</i>	1	1.20	1.85	0.011	55.9
<i>Ecdytolopha insiticiana</i>	1	1.20	2.35	0.017	90.2
<i>Gymnandrosoma punctidiscanum</i>	1	1.10	2.10	0.014	72.0
<i>Pandemis limitata</i>	1	1.10	2.10	0.014	72.0

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

Table C.1 (continued).

Family	Size Class	Body Length <sup>2</sup> (cm)	Wingspan <sup>3</sup> (cm)	Dry Weight (g)	Calories
<i>Platynota flavedana</i>	1	0.83	1.40	0.006	32.0
<i>Sparganothis sulphureana</i>	1	1.00	1.50	0.007	36.7
<i>Syndemis afflictana</i>	1	1.00	2.05	0.013	68.6
Uraniidae					
<i>Calledapteryx dryopterata</i>	1	1.14	2.00	0.012	65.3
<i>Callizzia amorata</i>	1	1.07	1.85	0.011	55.9
Yponomeutidae					
<i>Atteva aurea</i>	1	1.30	2.40	0.012	64.7
<i>Lactura pupula</i>	1	1.20	2.10	0.014	72.0
<i>Yponomeuta multipunctella</i>	1	1.20	1.85	0.011	55.9
Zygaenidae					
<i>Harrisina americana</i>	1	1.25	2.30	0.016	86.4
<i>Pyromorpha dimidiata</i>	1	1.00	2.30	0.016	86.4

<sup>1</sup>Source: Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Communications of the International Association of Theoretical and Applied Limnology 18:158 pp.

<sup>2</sup>Source: Beadle, D., and S. Leckie. 2012. Peterson field guide to moths of northeastern North America. First edition. Houghton Mifflin Harcourt Publishing Company, New York, NY. 611 pp.

<sup>3</sup>Source: Covell, C. V. 2005. A field guide to moths of eastern North America. Second edition. Virginia Museum of Natural History, Martinsville, VA. 496 pp.

APPENDIX D  
Percent of Lepidoptera species occurring at Mammoth Cave National Park  
in each of six size classes.

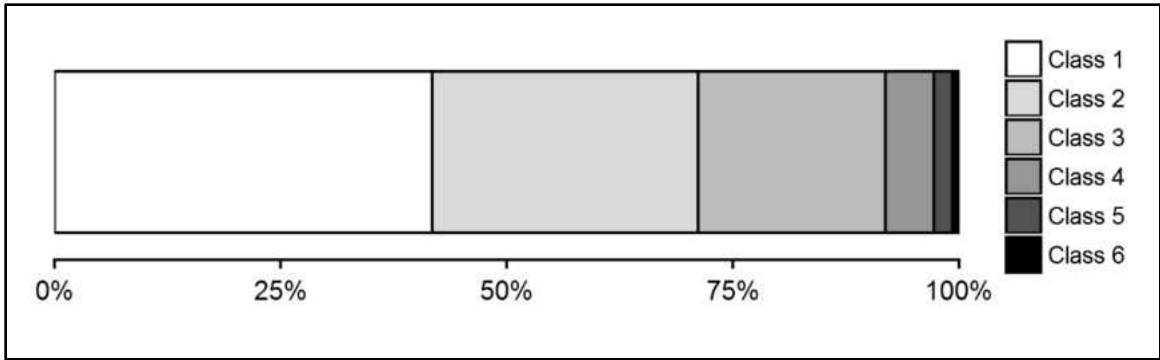


Figure D.1. Percent of Lepidoptera species occurring at Mammoth Cave National Park in each of six size classes.

#### APPENDIX E

Percent composition of Lepidoptera size classes by family; the families Erebidae, Geometridae, and Noctuidae are highlighted due to their abundance and importance as prey resources for insectivorous bats.

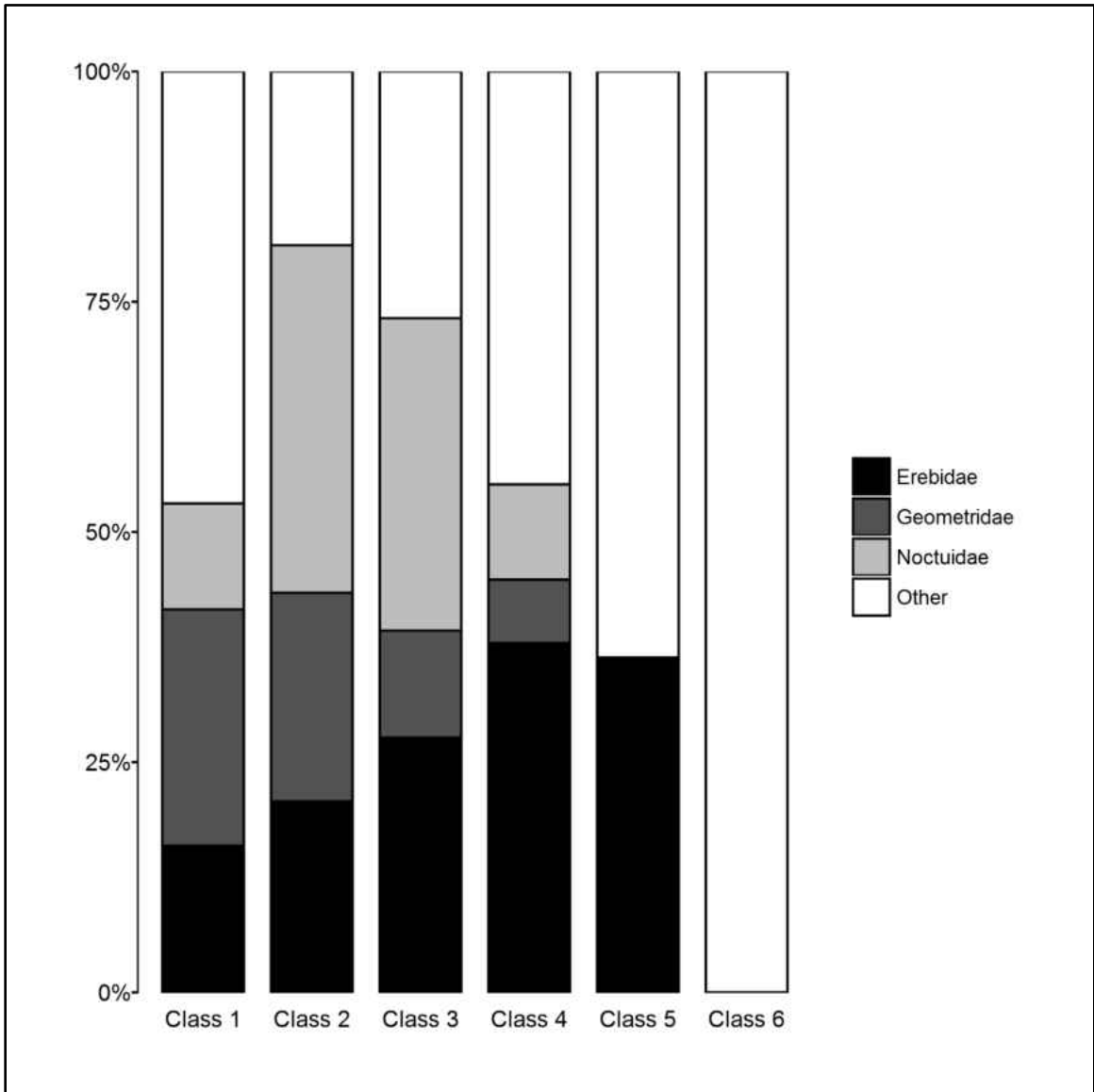


Figure E.1. Percent composition of Lepidoptera size classes by family; the families Erebidae, Geometridae, and Noctuidae are highlighted due to their abundance and importance as prey resources for insectivorous bats.