FINAL REPORT

Title: A Long-Term Evaluation of the Interacting Effects of Fire and White-Nose Syndrome on Endangered Bats

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List of Abbreviations / Acronyms

- CADE = *Castanea dentata* – American chestnut
- CORA = *Corynorhinus rafinesquii* – Rafinesque's big-eared bat
- dbRDA = Distance-based Redundancy Analysis
- EKU = Eastern Kentucky University
- LYDI = *Lymantria dispar dispar* – European gypsy moth
- MACA = Mammoth Cave National Park
- MYO = *Myotis* spp.
- MYSE = *Myotis septentrionalis* – Northern long-eared bat
- MYSO = *Myotis sodalis* – Indiana bat
- NPS = United States National Park Service
- UK = University of Kentucky
- WNS = White-nosed Syndrome

List of Keywords

acoustic surveys, American chestnut, bat conservation, bat-moth interactions, *Castanea dentata*, *Corynorhinus rafinesquii*, endangered species, Indiana bat, insect diversity, *Myotis septentrionalis*, *Myotis sodalis*, fire return interval, fire seasonality, food habits, foraging ecology, Lepidoptera, moths, northern long-eared bat, prescribed burning, prescribed fire, Rafinesque's big-eared bat, seedling regeneration, White-nose Syndrome

Acknowledgements

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Abstract

Habitat use of bats may shift following population-level impacts of WNS. Specifically, the effect of WNS across forest landscapes is unclear in relation to prescribed fire. MACA has employed a prescribed fire regime since 2002, and WNS was detected on MACA in 2013. Thus, project #14-1-05-22 carried on past efforts of project #10-1-06-1, wherein bat activity was monitored across burned and unburned sites at MACA before (2010-2012) and after the detection of WNS (2013-2016) using acoustic detectors concurrent with insect survey techniques. Acoustic recordings of bats were classified to phonic groups (low, mid, MYO). There was a significant interaction between WNS and prescribed fire for the MYO phonic group, and activity levels of all phonic groups shifted after WNS appeared at MACA. Insects in blacklight traps were greater after WNS, with a trend towards unburned areas for Lepidoptera and burned areas for Coleoptera. Our data indicate substantial changes in both bat and insect composition at MACA concurrent with the arrival and impact of WNS.

From there we expanded our efforts to understand fire, predator, and prey in a post-WNS context. Lepidoptera are a core resource for many bats. These predators consume Lepidoptera of varying sizes. Considering this, we explored the relationships between caloric yield, body size, and wing presence using lab-reared and field-collected insects. Bomb calorimetry studies indicated that lab- and field-collected insects of varied species and sizes were of similar energetic quality on a per mass basis, thus we then assessed habitat quality for bats at MACA on the basis of insect capture rates and broader nutrient parameters reported for insects in the literature. We modeled the effects of WNS, fire, and insect availability on bat assemblage diversity and composition. To facilitate this, Lepidoptera were clustered into six classes defined by wingspan and characterized by dry mass and caloric value. Mean wingspan of prey differed across all size classes, suggesting our prey classification was effective. The best-fitting model for diversity of bat phonic groups included the relative abundance of dominant insect orders as well as WNS. A dbRDA was used to further define relationships between bats, insects and fire. The indirect effects of WNS on Lepidoptera are still not fully resolved, but our research suggests shifts in the composition of this assemblage following the arrival of WNS at MACA (in addition to our observations of shifting abundance). Expanding on our modeling efforts, we sought to establish a nutritional geometry framework for understanding habitat selection by bats at MACA. We estimated mean C:N ratios and elemental compositions of Coleoptera, Diptera, Hymenoptera, and Lepidoptera, and developed cumulative nutritional profiles for burn management units at MACA. We found that insect abundance and C:N ratios were not spatially autocorrelated. The distribution of nutrients in insects is not uniform across MACA, and does not align with simple prey abundance.

Finally, we sought to evaluate the impacts of varying fire exposure, burn history, on the regeneration and herbivory of hardwood species. Because of its historic loss from eastern deciduous forests, little is known about the effects of fire on CADE. In our study, forest soil was collected from a recent wildfire and from an adjacent unburned area to grow blight-resistant backcrossed CADE seeds in a 2×2 design in the greenhouse. Seedlings grown in burned soil and full sun had greater height growth and leaf availability than those grown in unburned soil and shade. Feeding assays with LYDI indicate that caterpillars may not alter their consumption of chestnut seedlings grown in soil burned by fire, but they may not grow as large under the

increased light typical of burned forests. Understanding the effects of fire on hardwood species, and discerning how fire may influence its native and non-native insect associates, is essential for the long-term success of hardwood regeneration.

We show that although WNS is obviously the primary factor impacting the abundance and distribution of bats at MACA, prescribed fire and insect communities contribute to observed patterns in bat assemblage diversity and composition. Further, we document post-WNS shifts in insect communities. Although the extent to which prey and land management may shape persistent bat assemblages remains unclear given the overwhelming influence of WNS, we have provided evidence that a relationship between bat foraging ecology, insects, and fire persists despite devastating declines. The implications of this work 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.

Objectives

Objective 1. The first suite of goals for #14-1-05-22 were directed towards **understanding direct relationships between WNS, bats, and prescribed fire**. These objectives (from the proposal) were met. Specifically, we tracked spatiotemporal patterns of bat activity across burned and unburned areas of MCNP to develop a post-WNS understanding of bat activity patterns at MCNP, and compare this with patterns in pre-WNS data to disentangle the relationships among WNS infection, declining bat populations, and prescribed fire. Additionally, we continued to assess changing populations, as well as health and body condition of cave-hibernating bats to measure the accumulating impacts of WNS within and across years at MCNP.

Objective 2. The second suite of goals for #14-1-05-22 were directed towards **understanding the expanded impacts of fire and WNS on the prey base of bats**. These objectives (from the proposal) were met. To do this we measured effects of prescribed burning on forest herbivores and other insects at MCNP. We evaluated potential changes in insect herbivore communities in response to effects of WNS on cave-dwelling populations of bats, including MYO. Additionally, in order to provide an understanding of how prescribed fire may directly impact the productivity of foraging habitats for bats, we evaluated consumption patterns and energetic profitability of various forest insects in calorimetric yield to MYO. We developed models that integrate energetic yield of primary prey groups (Coleoptera, Diptera, Lepidoptera) with their occurrence across landscapes of MCNP. These data provide an understanding of how prescribed fire may directly impact the productivity of foraging habitats for all insectivorous bats.

Objective 3. Finally, we sought to **evaluate the impacts of varying fire exposure, burn history, on the regeneration and herbivory of hardwood species**. We originally proposed evaluation of the changes in the growth of white oak (*Quercus alba*), shade-tolerant competitors (*Acer rubrum* and *Fagus grandifolia*), and associated herbivory loads, in areas that vary in fire exposure and burn history. However, we were not able to accomplish this. In absence of additional prescribed fires at MACA during the duration of #14-1-05-22, we instead pursued greenhouse investigations of the impacts of prescribed fire on the CADE, as understanding the effects of fire on this species, and discerning how fire may influence its native and non-native insect associates, is essential for the long-term success of the reintroduction of this masting species.

Background and Purpose

There is no greater threat to the persistence of bats in North America than WNS, a wildlife disease associated with a cold-loving fungus (*Pseudogymnoascus destructans*) that is responsible for catastrophic declines in populations of cave-hibernating bats throughout eastern North America (Blehert 2012). With mortality accounting for millions of bats (over 5 million bats through 2012), WNS poses an unprecedented threat to multiple endangered bat species (USFWS 2012). Further, previously common species now face declines attributable to this disease which may lead to shifts in distribution and possible extinction (Frick et al. 2010). Our proposal builds on project #10-1-06-1 at MACA. This national park supports the largest cave system known globally, possesses hibernacula for populations of several species of bats, and has a strong history of prescribed fire on the landscape (Figure 1). Funding for project #14-1-05-22 allowed for additional data collection commensurate with developing impacts of WNS on bats and at fire-managed forest ecosystems of MACA.

Studies have demonstrated multiple benefits to bats that inhabit or use forests managed with prescribed fire, including creation of preferred roosting (Dickinson et al. 2010) and foraging (Lacki et al. 2009, Buchalski et al. 2013, Womack et al. 2013) habitats. These benefits may also extent into periods of swarming and staging for bats hibernating in caves within proximity of forested habitats managed with prescribed fire. Access to optimal roosting and foraging habitats, created by management with prescribed fire could confer an energetic advantage to hibernating bats, as they would likely enter hibernation in better body condition and potentially benefit from higher overwinter survival rates. These benefits could be especially important to populations of hibernating bats that become infected by WNS, as not all bats die immediately from WNS, and post-infection survival is believed to be contingent, in part, upon bat condition before and after hibernation (Bat Conservation International 2009).Thus, additional studies at MACA were doubly important for understanding the potential long-term impacts of fire management on cave-dwelling bats across North America.

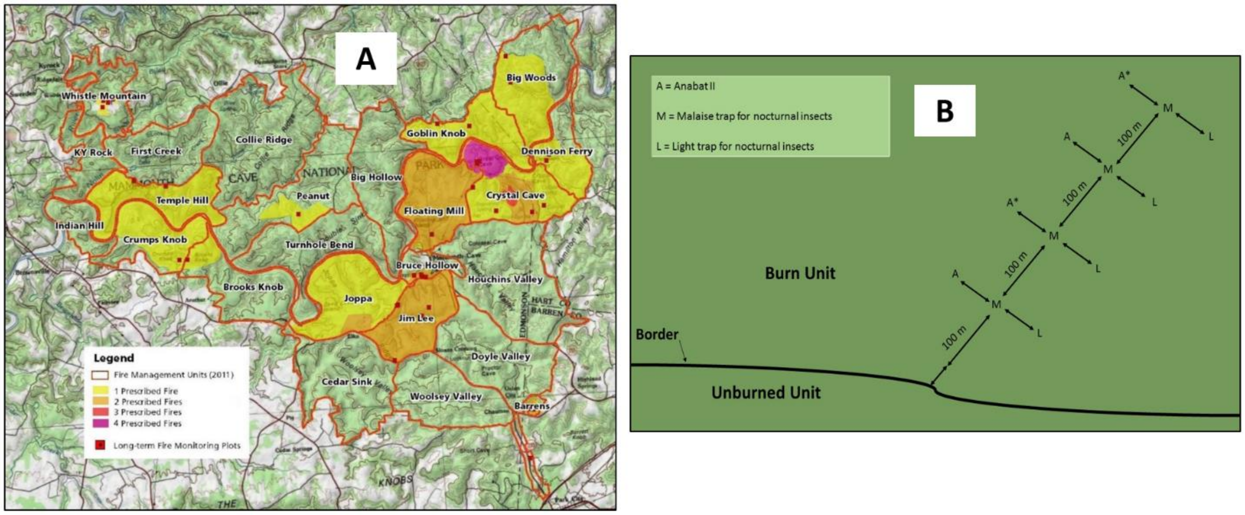

Figure 1. Overview of the core field surveys at MACA. The left panel (A) notes location and number of prescribed burns at MACA (image courtesy of NPS). The right panel (B) provides a

generalized figure of transects used to assess bat activity and insect community composition at MACA. A single burn unit is depicted but note this layout was mirrored in an unburned unit during each multi-night survey period. Asterisks indicate transect position at which an Anabat II was replaced with a Songmeter SM3 unit in 2015 in an effort to ensure data collection was robust and that acoustic recordings were maximized on a post-WNS landscape.

Materials and Methods

Objective 1. Direct relationships between WNS, bats, and prescribed fire.

Field sampling occurred at MACA from 2010 to 2016. MACA has employed a prescribed fire regime since 2002, and WNS was detected on MACA in 2013. Bat activity was monitored across burned and unburned sites at MACA before (2010-2012) and after the detection of WNS (2013-2016) using transects of acoustic detectors (Anabat II and Songmeter SM3) alongside insect sampling techniques (Figure 1; figures and descriptions of field deployments in Griffitts 2016). In addition to this landscape-level assessment of bat presence at MACA, we continued to assess changing capture rates, as well as health and body condition of MYO and other cave-hibernating bats to measure the accumulating impacts of WNS within and across years at MCNP. These monitoring efforts were carried out following Lacki et al. (2015).

Acoustic recordings were classified to phonic groups (low, mid, MYO) and species using automated classifiers (Bat Call Id v.2.7c and Kaleidoscope Pro v.3.1.4B). Subsequent analyses were conducted using bat passes with ≥ 5 pulses, with a 95% or 70% confidence interval for species and phonic group classification, respectively. Multiple automated identification procedures were used to ensure the accuracy of species-level identifications from acoustic surveys conducted at MACA (Britzke et al. 2011). Kaleidoscope v.1.2 (Wildlife Acoustics, Maynard, MA) was used to download acoustic data (zero-crossing format). Echolocation sequences containing ≥ 5 pulses were quantified as “passes” (i.e., a sequence of continuous pulses) and identified to species using the reference libraries and automated classifiers of Kaleidoscope Pro v.3.1.4B and Bat Call ID v. 2.7c (BCID; Kansas City, MO). When possible, the reference library specific to Kentucky was used for species identification. Additionally, echolocation calls were identified to low, mid, or MYO frequencies using BCID. For brevity’s sake, acoustics results in this report will rely upon phonic groups (see Griffitts 2016 for full details of results at species levels across identifiers). Only passes assigned a 70% confidence interval or greater for phonic group identification were used for analysis (Fulton et al. 2014). Subsequent response variables were the number of passes per detector / night across phonic groups. Response variables were considered in relation to two factors: WNS presence (pre-detection vs. post-detection), and prescribed fire (burned vs. unburned). We performed the two-factor ANOVA using the program ‘R’ v.3.1.2 (Peetor 2011; R Development Core Team 2016).

Objective 2. Understanding expanded impacts of fire and WNS on the prey base of bats.

Alongside acoustic methods outlined for Objective 1, blacklight traps were used as a means to assess the nocturnal phototactic insect community and malaise traps were used to sample the non-phototactic insect community (Southwood 1987) at MACA. Deployment of insect traps followed Dodd et al. (2012). Reference keys (Borror and White 1970; Triplehorn and Johnson

2005) were used to identify insects to a variety of taxonomic levels (i.e., order, family, and species; see Fulton 2017 for explicit accounting for identification levels).

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. Considering this, we explored 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 MACA in June – July 2015 (see Fulton et al. 2016 for full methods).

Recent advances in high-throughput gene-sequencing technology have provided the opportunity for bat dietary studies to be conducted with high resolution; thus we described methods for refining PCR parameters with the intent to maximize amplicon yield. Extending the efforts of Dodd et al. (2015), fecal pellets were collected in May and August of 2011 and 2016 from a maternity colony of CORA and stored in 95% ethanol at -80°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 (see Fulton 2017 for full methods).

Building from lab-based investigations, we sought to expand on relationships between bats, insects, and fire in a post-WNS context. Lepidoptera collected from 2010 – 2012 were 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 (Figure 2A). Selection of an optimal number of classes was informed by comparison of within-group sums of squares (Figure 2A; 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 2B), 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). From there, 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 Aikake'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. From there, dbRDA was also 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. 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.

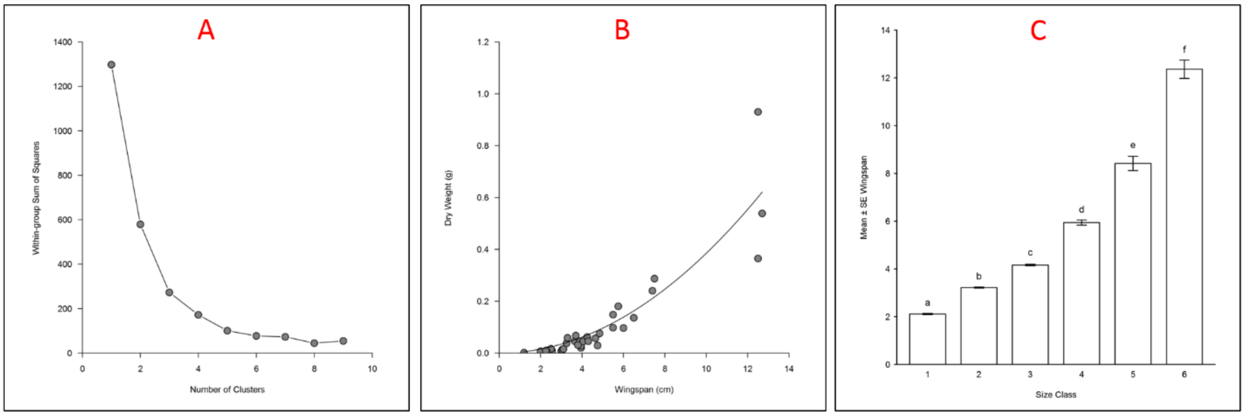

Figure 2. A graphical approach to selecting an ideal numbers of clusters for size-based classification of 541 species of Lepidoptera collected at MACA. Panel A shows decreasing within-group sum of squares with increasing number of clusters. Although little reduction in within-group sum of squares is observed beyond four clusters, we opted to use six clusters to better reflect naturally occurring trends in the data. Panel B shows the empirically-determined relationship of Lepidoptera dry weight to wingspan, based on 47 species. Multiple individuals (n = 2-3) per species were dried, weighed, and averaged. The curve is given by the equation $y = 0.0031 \times \text{wingspan}^2$. Panel C depicts mean (± standard error) wingspan of 7,842 Lepidoptera, collected at MACA, in each of six size classes defined in this work. Wingspan differed significantly across all size classes ($P < 0.05$). See Fulton (2017) for fuller context.

Finally, we sought to establish an expanded nutritional framework for understanding habitat selection by bats at MACA. Nutritional geometry studies have demonstrated nutrient-specific foraging by predators (Kohl et al. 2015, Mayntz et al. 2006), providing further evidence that insectivores, including bats, may selectively forage for nutrients. It has been suggested that selection based on taxonomy (i.e., prey shape) may be impossible due to acoustic or time constraints (Barclay and Brigham 1994), but the ability to differentiate among prey of various sizes is well-established (Barclay and Brigham 1994, Buchler 1976, Webster and Brazier 1965). This may provide adequate opportunity for nutrient-specific foraging. Thus, our objective was to characterize the nutrient composition of insect communities in Mammoth Cave National Park. We hypothesized that 1) nutrient availability would vary across the landscape and 2) the spatial distribution of nutrients would not reflect observed patterns in insect abundance. Relying upon insects collected in blacklight traps from 2010 to 2016, captured insects were identified to order and counted (Triplehorn and Johnson 2005). We calculated mean Carbon:Nitrogen (C:N) ratios for the insect orders Coleoptera, Diptera, Hymenoptera, and Lepidoptera from the terrestrial herbivore stoichiometry database compiled by Elser et al. (2000), available at http://www.nceas.ucsb.edu/ ecostoichiometry. These values were applied to our dataset and used to estimate the mean C:N ratio of insects (represented by the previously listed orders) collected in each trap throughout the sampling period. Replicate samples were averaged prior to statistical analysis to avoid pseudoreplication (Hurlbert 1984). We further characterized the orders Coleoptera, Diptera, Hymenoptera, and Lepidoptera by elemental composition. Mean values presented by Studier and Sevick (1992) for the iron (Fe), calcium (Ca), magnesium (Mg), sodium (Na), and potassium (K) content of each order were applied to our dataset and used to calculate the approximate, cumulative elemental composition of all insects from our focal orders in each trap. We described the location of each site by a single point along the associated transects. The shapefile containing the boundary of MACA was produced by the National Park Service (2009) and is available through the www.data.gov website. All geoprocessing and statistical analyses were conducted using R version 3.3.2 (R Core Team 2016). A complete list of packages used in the preparation, analysis, and presentation on the data is available in the metadata of the data workbook. Voronoi tessellation was used to convert point data to polygon data. We evaluated spatial autocorrelation with permutation tests for Moran's I statistic. We fit generalized linear mixed models using the gamma distribution to test for differences in insect abundance and C:N ratio across the landscape. For both models, site was included as a fixed effect and month within year as a nested random effect.

Objective 3. Evaluating the impacts of varying fire exposure, burn history, on the regeneration and herbivory of hardwood species.

Because of its loss from eastern deciduous forests due to the exotic chestnut blight fungus, little is known about the effects of fire on CADE and how changes in disturbance may alter vulnerability to insect herbivores, including LYDI. Forest fires may alter herbivory through changes in light and nutrient conditions. Forest soils were collected from a newly burned and adjacent unburned site on the Daniel Boone National Forest (April 2015) and used in pots to grow improved CADE from seed under full sun (no shade cloth) and shade (70% shade cloth) in a 2 × 2 greenhouse experiment (n = 20 trees / treatment, n = 80 tree total). This design included the main effects of soil (burned versus unburned) and light (full sun versus shade). Feeding assays were conducted after 30 days. Newly molted 4th instar LYDI larvae were starved for 48 hours before being placed on newly excised CADE leaves in assay chambers (N = 10 caterpillars per seedling treatment) and allowed to feed for 24 hours. Caterpillars, frass, and leaf material were weighed before and after the assay. See proceedings abstract by Dodd et al. (2015) for fuller context.

Results and Discussion

Objective 1. Direct relationships between WNS, bats, and prescribed fire.

Habitat use of bats shifted following population-level impacts of WNS. Notably, the number of passes classified as MYO decreased from 3,867 passes (consisting of 44,604 pulses) before the detection of WNS to 70 passes (consisting of 755 pulses) after the detection of WNS (Figure 3). The number of MYO passes / night decreased following arrival of WNS (3.4 ± 0.3 vs. 0.27 ± 0.11, $t_{1,344} = 9.6$, $P < 0.01$). Data from Lacki et al. (2015) and subsequent surveys demonstrated dramatic declines of MYSE and MYSO at previously-common hibernacula (Figure 3).

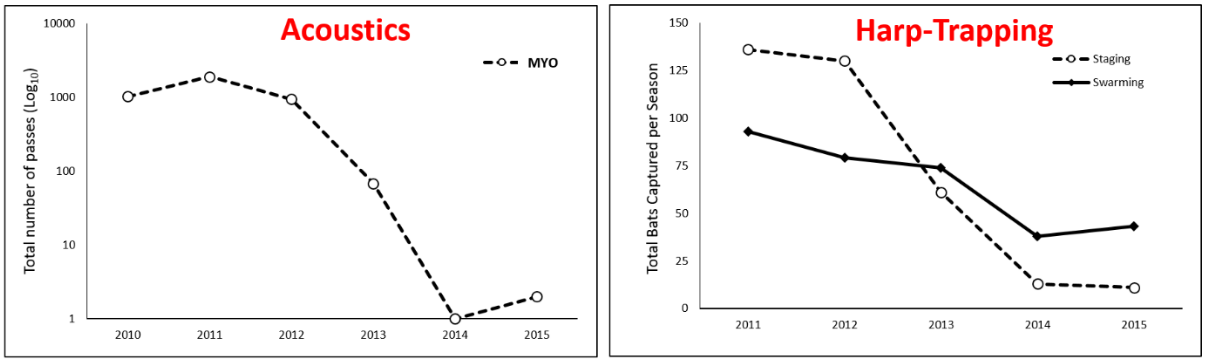

Figure 3. Trends in MYO populations at MACA from 2010 – 2015. Panel A shows MYO passes / year, as classified using BCID. Panel B shows summary capture data for harp-trapping at Colossal Cave. WNS was detected at MACA in January of 2013. See Lacki et al. (2015) and Griffitts et al. (2016) for fuller context.

Findings at MACA are consistent with acoustic surveys conducted before and after the detection of WNS in other localities (Dzal et al. 2011; Coleman et al. 2014). WNS can have an indirect impact on bat species which are not susceptible to WNS infection. The decline of MYO can potentially alter niche partitioning of bat species within a forest community (Jachowski et al. 2014), with bat species not affected by WNS, e.g. *Lasiurus borealis* (eastern red bat) and *Nycticeius humeralis* (evening bat), expanding their use of habitats previously occupied by WNS impacted species (see Thalkin et al. 2018 for further MACA-specific findings).

Beyond the dramatic impacts of WNS on bats at MACA, there were varied effects of prescribed fire on bats at MACA (Figure 4).

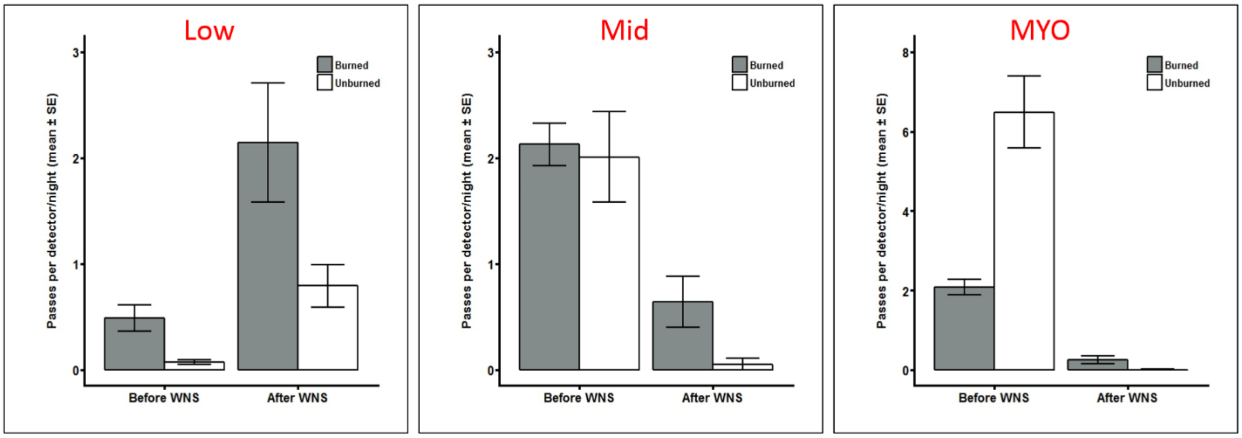

Figure 4. Interacting effects of WNS and fire on various phonic groups of bats at MACA. Activity is expressed as passes per/detector night (mean ± SE). Years 2010 – 2012 were before the detection of WNS and 2013 – 2016 were after the detection of WNS. See Griffitts (2016) for fuller context.

Our global model for bat activity in the low phonic group was significant ($F_{3, 1534} = 11.06$, $P < 0.01$). Low phonic activity was greater in burned habitats, and low phonic activity increased following the detection of WNS at MACA ($P \leq 0.05$). The interaction was not significant ($P > 0.05$). Our global model for bat activity in the mid phonic group was significant ($F_{3, 1534} = 8.43$, $P < 0.01$). While mid phonic activity did not differ in regard to prescribed fire ($P > 0.05$), or the interaction of WNS with prescribed fire ($P > 0.05$), mid phonic activity decreased following the detection of WNS at MACA ($P \leq 0.05$). Finally, the global model was significant for MYO phonic activity ($F_{3, 1534} = 33.4$, $P < 0.01$) at MACA. The effects of prescribed fire and WNS were significant for MYO phonic, as well as the interaction ($P \leq 0.05$). Before the detection of WNS, MYO activity was less in burned habitats than unburned habitats, but after the detection of WNS MYO activity was greater in burned habitats than unburned habitats. See Griffitts et al. (2016) for full reports of summary statistics.

Our study provides community-level data regarding the responses of various phonic groups to prescribed fire and WNS. These results provide evidence that prescribed fire impacts bat activity across the landscape of MACA, and that WNS has had an interacting effect on the shift in habitat use for some phonic groups of bats. This study demonstrates that WNS has immediate impacts on bat species that do not suffer from the disease, e.g., members of the low phonic group. We postulate that WNS altered the bat community as a whole at MACA, not just through mortality of bats in the genus MYO, but also through competitive release of other bat species. Open-space foragers at MACA used burned habitats more than unburned habitats. This is in agreement with the morphological characteristics of open-space foragers. Prescribed fire decreases the amount of clutter in the mid- and under-story of eastern deciduous forests (Arthur et al. 2012; Perry 2011; Cox et al. 2016). Open-space foragers would likely use habitats with open canopies and reduced amounts of clutter, as these bats can maintain higher flight speeds and encounter less echolocation interference (Adams et al. 2009; Müller et al. 2012). Activity of open-space foragers increased in this study after the detection of WNS, likely due to decreased competition from other phonic groups. In contrast, mid phonic group bats at MACA did not display the degree of use of burned habitats as did open-space foragers. Members of this phonic group is tolerant of increasing amounts of clutter (Brooks 2009). Assuming mid phonic group bats can forage efficiently in open and closed canopies, these species likely transition between burned and unburned habitats to locate abundant prey. While we observed no change in habitat use, there was a decline in overall activity of mid-phonic bats after the detection of WNS. The decline of the mid phonic group as a whole is likely attributed to the mortality of *Perimyotis subflavus*, a cave hibernating, WNS-impacted species (Foley et al. 2011; Alves et al. 2014). Since the detection of WNS, populations of impacted MYO and *P. subflavus* have declined on MACA (Lacki et al. 2015). Even so, the temporal drop in activity for the mid phonic bat group was not as dramatic as for MYO.

Before the arrival of WNS, MYO used unburned habitats more than burned habitats, presumably because many MYO species are tolerant of clutter (Norberg and Rayner 1987; Bergeson et al. 2013; Silvis et al. 2016). Their wing morphology allows for a high degree of maneuverability and their echolocation call characteristics are suited to detecting a greater amount of obstacles over a shorter distance (Thomson 1982; Caceres and Barclay 2000). We postulate that WNS infected bats emerging from hibernation with lowered body mass and impaired wing function will likely use areas for foraging that are least energetically expensive and that require less flight maneuverability (Cryan et al. 2010; Lacki et al. 2015). Fuller et al. (2011) found that *Myotis lucifugus* with high levels of wing damage from WNS had impaired body conditions and likely suffered repeated damage from exposure to the fungus across multiple hibernation periods. We suggest that MYO foraging in burned habitats would have less energetic costs associated with foraging in more open canopy structures. Results from MACA are consistent with previous findings concerning the responses of bats to prescribed fire; burned habitats had greater bat activity, and open-space foragers had a more dramatic response than MYO species (Loeb et al. 2008; Cox et al. 2016). Most research is in agreement that foraging bats respond positively to prescribe fire because of a decrease in canopy clutter (Boyles and Aubrey 2006; Lacki et al. 2009; Perry 2011; Silvis et al. 2016). Given that WNS has caused a drastic decline in some cave-hibernating species (Frick et al. 2010; Foley et al. 2011; Thogmartin et al. 2012; USFWS 2015a), these results are consistent with other acoustic surveys that demonstrate declines in activity of WNS-impacted species, with either no change or an increase in activity levels of bat species not susceptible to WNS (Brooks 2011; Dzal et al. 2011; Coleman and Reichard 2014).

Objective 2. Understanding expanded impacts of fire and WNS on the prey base of bats.

Concurrent with the impacts of WNS on bats at MACA, we also observed varied effects of prescribed fire and WNS on insects at MACA (Figure 5).

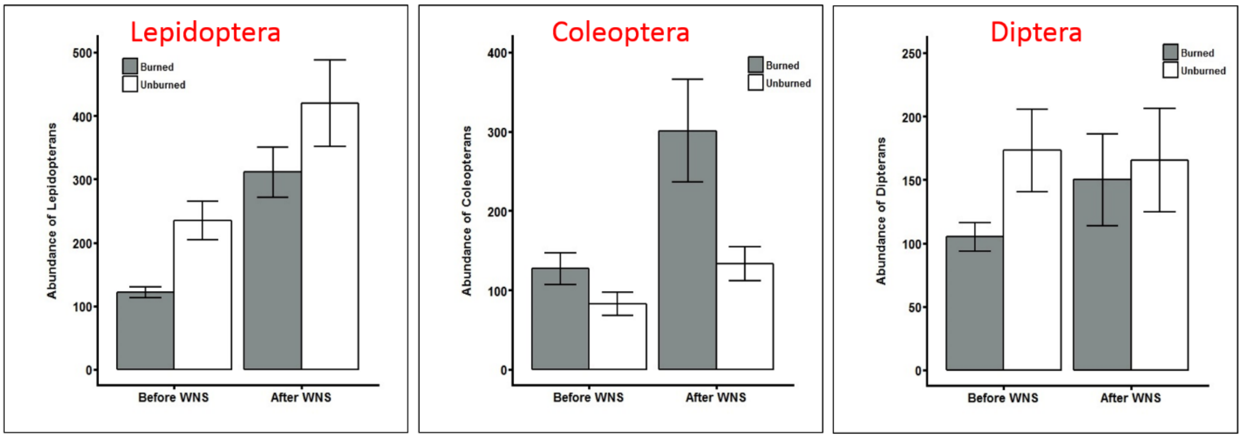

Figure 5. Interacting effects of WNS and fire on various nocturnal insects at MACA. Abundance is expressed as individual insects per trap/night. Years 2010 – 2012 were before the detection of WNS and 2013 – 2016 were after the detection of WNS. See Griffitts (2016) for fuller context, as well as description of malaise trap results.

Nocturnal insects were sampled at MACA for 414 trap/nights across all years. A total of 285,804 insects were collected, with Coleoptera, Diptera, and Lepidoptera accounting for ca. 60% of all captures. The global model for total insect abundance in malaise traps was not significant ($P > 0.05$; see Griffitts 2016 for full description of these results). The global model for Lepidoptera captured in blacklight traps was significant ($F_{3, 414} = 19.7$, $P < 0.01$). Lepidoptera were more abundant after WNS and in unburned areas ($P < 0.01$); there was no interaction effect ($P > 0.5$). The global model for Coleoptera captured in blacklight traps was significant ($F_{3, 414} = 7.7$, $P < 0.01$). Coleoptera were more abundant after WNS and in burned areas ($P < 0.05$); there was no interaction effect ($P > 0.5$). The global model for Diptera captured in blacklight traps was not significant ($P > 0.05$). From this point, we expanded our efforts to further elucidate the relationships between bats and insects in a post-WNS context.

Bats 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. Considering this, we explored the relationships between caloric yield, body size, and wing presence of Lepidoptera (Figure 6). While caloric yields of *Malacasoma americanum* and *Iridopsis* sp. differed significantly ($W_{5,4} = 19$, $P = 0.03$), no additional differences in mean caloric yield were detected between pairwise comparisons. The mean caloric yields of *Ma. americanum* across varying sample weights did not differ significantly ($F_{3,14} = 1.6$, $P > 0.05$). The mean caloric yields of small *T. ni* with wings removed, small *T. ni* with wings present, large *T. ni* with wings removed, and large *T. ni* with wings present were not significantly different ($F_{3,23} = 0.86$, $P > 0.05$).

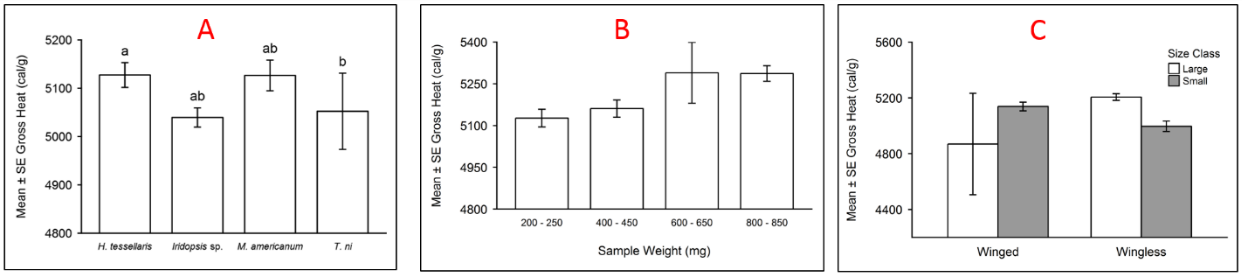

Figure 6. Relationships between caloric yield, body size, and wing presence of Lepidoptera. Panel A shows the mean (± standard error) gross heat (cal/g) generated by combustion of coarsely ground samples of *Malacosoma americanum*, *Trichoplusia ni*, *Halysidota tessellaris*, and *Iridopsis* sp. using bomb calorimetry. Five samples of *Ma. americanum*, twenty-six of *T. ni*, seven of *H. tessellaris*, and four of *Iridopsis* sp. were combusted. Panel B shows the mean (± 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. Panel C shows the mean (± 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). See Fulton et al. (2016) for fuller narrative for the three experiments.

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, we recommend that any future calorimetric studies should reduce sample weights to conserve raw material and maximize the number of combustion reactions possible, as this is a clear hurdle towards reaching a robust sample size.

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 (*Micropterus salmoides*) is directly related to body mass, with larger individuals generally possessing greater energetic density.

Given that Lepidoptera are relatively soft-bodied (Freeman 1981), we 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 results regarding caloric yield and body size, we believed the lack of differences detected in this study indicated that the technique was likely too coarse of a method to capture subtle energetic differences among Lepidoptera. Thus, further modeling efforts for #14-1-05-22 assessed habitat quality for bats at MACA on the basis of insect capture rates and broader nutrient parameters reported for insects in the literature.

Recent advances in high-throughput gene-sequencing technology have provided the opportunity for bat dietary studies to be conducted with high resolution; thus we describe methods for refining PCR parameters with the intent to maximize amplicon yield (Figure 7).

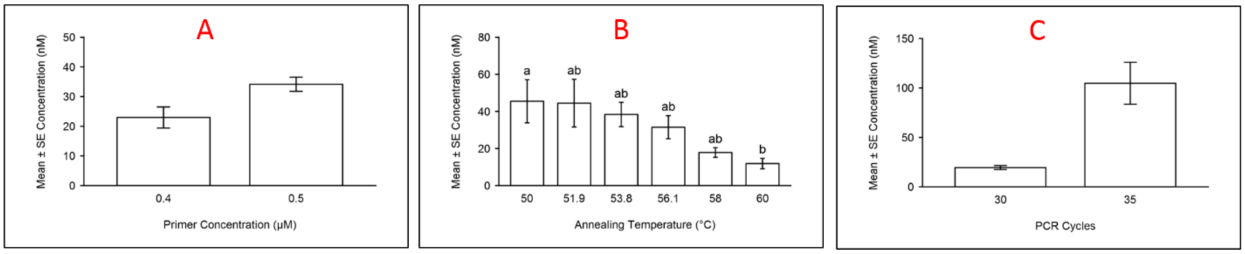

Figure 7. Optimization experiments for PCR of bat fecal samples. Panel A shows the mean (± standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected at MACA and amplified with either 0.4 or 0.5 µM forward and reverse primer. n = 10 samples per treatment; the same suite of ten samples was used to test each primer concentration. Samples amplified with 0.5 µM primers had a significantly higher yield than those amplified with 0.4 µM primers (W = 19.5, P = 0.02). Panel B shows the mean (± 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 ($X_{25} = 15.6$, $P < 0.01$), and letters indicate comparison-wise significance. Panel C shows the mean (± standard error) amplicon concentration (nM) of insect DNA extracted from bat fecal pellets collected MACA 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 ($W \sim \infty$, $P < 0.01$).

Expanding from lab-based investigations, we modeled the effects of WNS, as well as prescribed fire and insect availability, on bat assemblage diversity and composition. Acoustic surveys and insect sampling useful for modeling spanned 202 concurrent nights across 5 years of surveys. In total, acoustic data included 902 detector nights (n = 697 pre-WNS; n = 205 post-WNS) and insect data included 413 trap nights (n = 318 pre-WNS; n = 95 post-WNS). For this analysis, we recorded 4,760 echolocation passes and collected 125,445 insects across all years. Composition of bat assemblages, insect communities, and Lepidoptera assemblages varied dramatically before and after detection of WNS at MACA(Table 1).

Table 1. Pre- and post-WNS compositions of bat assemblages (organized by phonic group), insect communities, and Lepidoptera assemblages at MACA 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. See Fulton (2017) for fuller context.

Faunal Response	Pre-WNS (%)	Post-WNS (%)
Bat Assemblage		
Low-frequency	2.99	100.0
Mid-frequency	32.3	0.00
MYO	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

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 2) as a consequence of classification.

Model selection resulted in two competing models for bat phonic group diversity (Table 2). 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). The competing model (Δ AICc = 1.22) included only WNS, which was a significant predictor of phonic diversity ($P < 0.05$, Table 3).

Table 2. Summary of support for candidate models for the diversity of bat phonic groups (low-, mid-, or MYO) acoustically detected at MACA, calculated as the reciprocal of Simpson's Diversity (1/*D*). All models were constructed as linear mixed models including site as a random effect. See Fulton (2017) for fuller context.

Model	K	AICc	Δ 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. Summary of the coefficients and significance of fixed effects in the best-fitting linear mixed models for bat phonic diversity at MACA, 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 α = 0.05. See Fulton (2017) for fuller context.

Model Terms	Coefficient (± SE)	*P*
Insect Community Model		
Lepidoptera	0.08 ± 0.20	0.43
Coleoptera	0.35 ± 0.30	0.44
Diptera	-0.34 ± 0.21	0.10
WNS	-0.58 ± 0.14	< 0.05
White-nose Syndrome Model		
WNS	-0.47 ± 0.14	< 0.05

Results of the dbRDA indicate constraining variables are significantly associated with bat assemblage composition (pseudo-$F_{12,6}$ = 3.37, $P < 0.05$; Figure 8) 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 4) and indicated a significant positive relationship between WNS and Lepidoptera diversity (0.60 ± 0.14, $P < 0.05$).

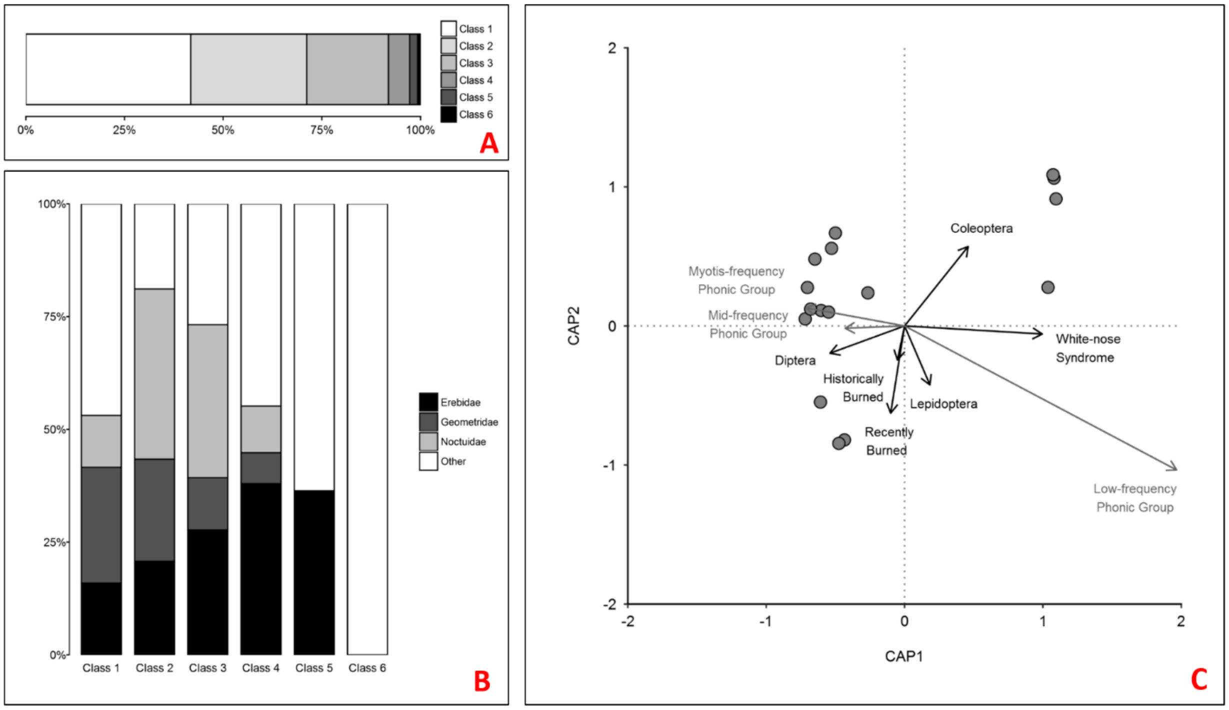

Figure 8. Size distribution of Lepidoptera and dbRDA results for the project. Panel A shows the percentage Lepidoptera species occurring at MACA in each of six size classes. Panel B shows the percent composition of Lepidoptera size classes by family; the families Erebidae, Geometridae, and Noctuidae are highlighted due to their abundance and importance as prey resources for insectivorous bats. Panel C is a biplot visualizing the results of the dbRDA. 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. See Fulton (2017) for fuller context.

Table 4. Summary of support for candidate models for the diversity of Lepidoptera size classes (classification presented in this work) observed at MACA, 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	Δ 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 + MYO Phonic	7	260.1	14.5	0.00
Low Phonic + Mid Phonic + MYO Phonic + WNS	8	250.5	4.91	0.07
Low Phonic + Mid Phonic + MYO Phonic + Burn	9	261.4	15.8	0.00
Low Phonic + Mid Phonic + MYO Phonic + Burn*WNS	12	256.0	10.4	0.00

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 five million bats within five years of its first detection in the eastern United States (USFWS 2012). Nearly all MYO in eastern North America have experienced some degree of population decline, and several formerly common species have declined dramatically (Coleman et al. 2014, Powers et al. 2015, Turner et al. 2011). Populations of *M. lucifugus* and *M. sodalis* at MACA are estimated to have declined by approximately 80% (Toomey 2015), fundamentally altering assemblage diversity and composition. Additionally, the ordination suggests that the abundance of the mid-frequency phonic group may behave similarly to the MYO group with respect to WNS. Most species in the mid-frequency phonic group are mildly affected or unaffected by WNS (see Figure 4), but *P. subflavus* has suffered substantial population declines (Coleman et al. 2014, Reynolds et al. 2016, Turner et al. 2011). These results underscore that post-WNS bat assemblages at MACA are dominated by low-frequency echolocating bats; 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. 2018).

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 MYO group demonstrates a slight negative association with fire. However, several studies have found a positive relationship between MYO 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 the 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 MYO 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 CORA. Therefore, this species is not likely represented in our data despite the existence of numerous roosts at MACA (Johnson and Lacki 2013). As Lepidoptera represent more than 80% of the diet of CORA (Lacki and Dodd 2011), this study likely underappreciates the importance of Lepidoptera to the full bat assemblage at MACA.

The classification of Lepidoptera by size on the basis of wingspan was successful, and provides a promising method for integration into future bat foraging research. We 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, we 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, we 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, these results contribute to the breadth of existing literature documenting the profound effects of WNS on the bats of eastern North America and document preliminary changes in the post-WNS composition of insect communities and Lepidoptera assemblages. In a final effort to expand on our modeling efforts, we sought to establish a nutritional geometry framework for understanding habitat selection by bats at MACA. In total, this data set represented 412 trap nights and 285,786 insects. This includes 220,656 insects from our focal orders (85,297 Lepidoptera; 68,434 Coleoptera; 56,192 Diptera; 20,733 Hymenoptera). We generated maps visualizing mean insect abundance and C:N ratios across site-associated polygons (Figure 9). Moran's I statistic for the insect abundance dataset was not significant under 999 permutations ($P = 0.07$) and we assume spatial independence. Site was a significant predictor of insect abundance for the polygons associated with two sites, Buffalo Trail A ($P = 0.01$) and Buffalo Trail B ($P = 0.01$). For all other sites, $P > 0.05$. Moran's I statistic for the C:N ratio dataset was not significant under 999 permutations ($P = 0.403$) and we assume spatial independence. Site was a significant predictor of C:N ratio for only two polygons, those associated with the Crystal Cave ($P = 0.04$) and Dennison Ferry ($P = 0.036$) sites. See Figure 1 for labeled site locations. For all remaining sites, $P > 0.05$. We observed little variation in the elemental composition of insect communities across the dataset (Table 5).

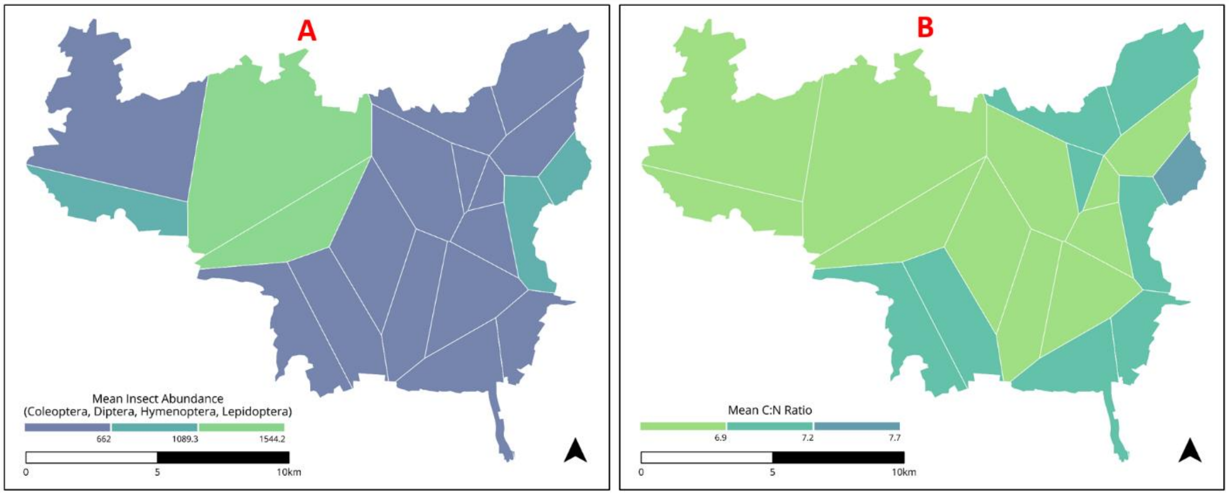

Figure 9. Maps visualizing mean insect abundance (Panel A) and C:N ratios (Panel B) across site-associated polygons at MACA.

Table 5. Mean ± standard error values (ppt) for the cumulative iron (Fe), calcium (Ca), magnesium (Mg), sodium (Na), and potassium (K) content of Coleoptera, Diptera, Hymenoptera, and Lepidoptera collected at MACA.

Element	Mean ± SE (ppt)
Fe	0.28 ± 0.005
Ca	1.23 ± 0.005
Mg	1.79 ± 0.014
Na	1.22 ± 0.021
K	9.12 ± 0.008

Our results suggest that insect abundance and C:N ratio are not spatially autocorrelated; similarly, Summerville et al. (2008) found that forest communities of Lepidoptera were not spatially autocorrelated. The significance of C:N ratio for two sites indicates that the distribution of insect-derived nutrients is not uniform across the landscape. Although abundance was also significant for two sites, these sites were not the same two highlighted by our C:N ratio model. Therefore, it is apparent that patterns of C:N ratio do not mirror patterns of abundance. As a result, the quality of an insect-based diet at MACA would vary across the landscape, necessitating selective foraging to maintain optimal nutrition.

Objective 3. Evaluating the impacts of varying fire exposure, burn history, on the regeneration and herbivory of hardwood species.

Finally, we sought to evaluate the impacts of varying fire exposure on the growth and herbivory of CADE. Chestnut seedlings grown in burned soil and full sun had greater height growth and leaf availability than those grown in unburned soil and shade ($F_{3,18} = 12.0$, $P \leq 0.05$, and $F_{3,18} = 4.8$, $P \leq 0.05$, respectively; Figure 10). To test the effects of soil and light on caterpillar performance, changes in caterpillar and leaf weights (%) were fitted to a generalized linear model. No differences were detected in consumption of leaf material ($P > 0.05$), but caterpillars fed leaves grown in shade had greater mass than those fed leaves grown in full sun at the end of the 24 hr feeding trial ($F_{3,38} = 4.9$, $P \leq 0.05$; Figure 11). These data indicate that LYDI caterpillars may not alter their consumption of chestnut seedlings grown in soil burned by fire, but they may not grow as large under the increased light typical of burned forests. Understanding the effects of fire on chestnut, and discerning how fire may influence its native and non-native insect associates, is essential for the long-term success of chestnut reintroduction.

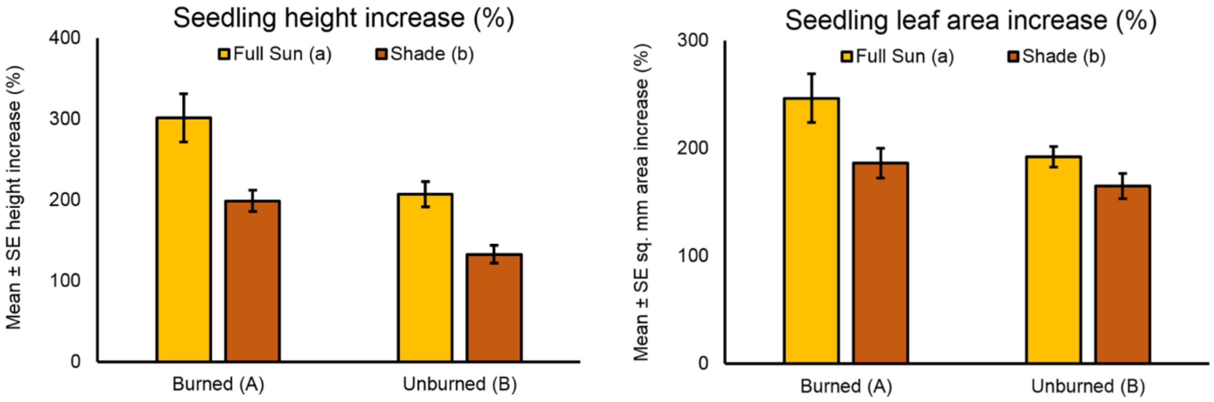

Figure 10. Performance of CADE in relation to conditions afforded by prescribed fire. Different parenthetical letters denote differences at P < 0.05.

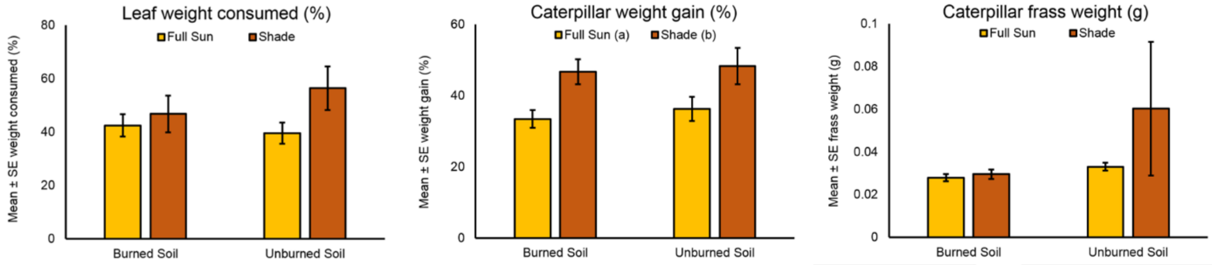

Figure 11. Performance of LYDI that were fed improved CADE grown in conditions afforded by prescribed fire. Different parenthetical letters denote differences at P < 0.05.

Science delivery activities.

The investigators have not only disseminated the results of project #14-1-05-22, but have also facilitated science delivery of other JFSP-funded projects and sought to integrate their activities with the larger fire science community. Most notably, the PI of #14-1-05-22 worked alongside the Consortium of Appalachian Fire Managers and Scientists and the Kentucky Prescribed Fire Council to organize a two-day event that brought together JFSP researchers with KY stewards and managers. Beyond this capstone event and the robust technical writing to date, project #14-1-05-22 has in total organized two multi-day field demonstrations / workshops (the aforementioned, and also another alongside a Kentucky State Nature Preserve), contributed to two webinars (NPS and also North Atlantic Fire Exchange), and contributed to the 5th Fire in Eastern Oak Forests Conference. See Appendix B for full accounting of science delivery activities.

Conclusions and Implications for Management/ Policy and Future Research

All phonic groups of bats on MACA used prescribed burns more after arrival of WNS, suggesting these habitats are of importance for sustaining populations of foraging bats vulnerable to WNS. Conservation efforts for WNS-impacted species are especially important now due to the drastic decline in population numbers of susceptible bat species. While our data demonstrate community-wide changes in bat activity since the detection of WNS, further research and monitoring is needed to determine if open-space foragers fill the ecological niches that MYO once served at MACA.

Although the extent to which prey and land management shape bat assemblages remains unclear given the overwhelming influence of WNS, we provide 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.

Managers implementing prescribed fire regimes for silvicultural practices can take into consideration the positive effects of prescribed fire for foraging bats, particularly species suffering from WNS. Prescribed burns that take place at regular intervals maintain lower levels of clutter in the canopy. Prescribed fire is a versatile silvicultural tool which can additionally be used to manage a forest for foraging bat species in the wake of WNS.

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Appendix B. List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

M.S. Theses:

1. Fulton, S.A., M.S. Biology, Eastern Kentucky University. Thesis title: Local impacts of White-nose Syndrome on the foraging ecology of insectivorous bats. Available at: https://encompass.eku.edu/etd/526/
2. Rachael Griffitts, M.S. Biology, Eastern Kentucky University. Thesis title: Assessing the effects of prescribed fire on foraging bats at Mammoth Cave National Park after the arrival of White-nose Syndrome. Available at: http://encompass.eku.edu/etd/370/

Refereed Materials:

1. Fulton, S.A., V.E. Peters, M.B. Dickinson, M.J. Lacki, L.K. Rieske, and L.E. Dodd. *In Prep*. Relationships between bats and their insect prey following the arrival of white nose syndrome to a fire-managed landscape. Previously rejected by Oecologia, Expect to submission to Mammalian Biology by June 2019.
2. Griffitts, R.E., M.J. Lacki, N.S. Skowronski, L.K. Rieske, M.B. Dickinson, and L.E. Dodd. *In Prep*. Interacting effects of prescribed fire and White-nose Syndrome on bat activity across the forest landscape of Mammoth Cave National Park. Expect to submission to the Journal of Wildlife Management by June 2019.
3. Fulton, S.A., and L.E. Dodd. 2018. Acoustic activity of bats in Kentucky during the total solar eclipse of 2017. Northeastern Naturalist, 25: 24-26.
4. Lacki, M.J., L.E. Dodd, N.S. Skowronski, M.B. Dickinson, and L.K. Rieske. 2017. Relationships among burn severity, forest canopy structure, and bat activity from spring burns in oak-hickory forests. Funded across JFSP #10-1-06-1 and #14-1-05-22. International Journal of Wildlife Fire, WF16159.
5. Dodd, L.E., M.J. Lacki, J.S. Johnson, and L.K. Rieske. 2015. Prey size and dietary niche of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). Funded across JFSP #10-1-06-1 and #14-1-05-22. Southeastern Naturalist, 14: 685-696.
6. Lacki, M.J., L.E. Dodd, R.S. Toomey, S.C. Thomas, Z.L. Couch, and B.S. Nichols. 2015. Body condition of cave-hibernating bats during staging and swarming in Mammoth Cave National Park. Journal of Fish and Wildlife Management, 6: xx–xx. e1944-687X. doi: 10.3996/042015-JFWM-033. Funded across JFSP #10-1-06-1 and #14-1-05-22. Available at: http://www.fwspubs.org/doi/10.3996/042015-JFWM-033

Non-Refereed Proceedings/Transactions:

1. Dodd, L.E., N.S. Skowronski, M.B. Dickinson, L.K. Rieske, and M.J. Lacki. 2016. Modeling activity of the Indiana bat (*Myotis sodalis*) at Mammoth Cave National Park using remotely-sensed descriptors of forest canopy structure, In: Proceedings of Mammoth Cave National Park's 11th Research Symposium, ed. S.R. Trimboli, L.E Dodd, and D. Young, Mammoth Cave National Park, Pp. 163-165 (of 172p). Funded across JFSP #10-1-06-1 and #14-1-05-22. Available at: http://digitalcommons.wku.edu/mc_reserch_symp/

2. Fulton, S.A., L.E. Dodd, and L.K. Rieske. 2016. Evaluating the energetic value of Lepidoptera using bomb calorimetry, In: Proceedings of Mammoth Cave National Park's 11th Research Symposium, ed. S.R. Trimboli, L.E Dodd, and D. Young, Mammoth Cave National Park, Pp. 85-90 (of 172p). Available at: http://digitalcommons.wku.edu/mc_reserch_symp/
3. Griffitts, R.E., L.E. Dodd, and M.J. Lacki. 2016. The activity of *Myotis sodalis* and *Myotis septentrionalis* changes on the landscape of Mammoth Cave National Park following the arrival of White-nose Syndrome, In: Proceedings of Mammoth Cave National Park's 11th Research Symposium, ed. S.R. Trimboli, L.E Dodd, and D. Young, Mammoth Cave National Park, Pp. 70-75 (of 172p). Available at: http://digitalcommons.wku.edu/mc_reserch_symp/

Field Demonstrations / Hosted Workshops:

1. Kentucky Prescribed Fire Annual Meeting and Bats and Fire Workshop, 24-25 September 2018, Workshop organizer in conjunction with the Consortium of Appalachian Fire Managers and Scientists and the Kentucky Prescribed Fire Council (76 registered attendees), Cave City, KY. See https://apfire.wixsite.com/kypfc for agenda.
2. Field Study Workshop, "Lepidoptera in Kentucky," 30-31 July 2016, Floracliff Nature Sanctuary, Richmond, KY.

Webinars:

1. L.E. Dodd. Long-term acoustic surveys of bat activity across Mammoth Cave National Park. *NPS Online Bat Acoustic Data Management Training*, 14 December 2017.
2. L.E. Dodd and M.J. Lacki. Fire and the northern long-eared bat: vulnerability and management considerations. *North Atlantic Fire Science Exchange*, 14 October 2015. Available at: http://www.firesciencenorthatlantic.org/events-webinars-source/2015/8/5/nafse-webinar-fire-and-the-northern-long-eared-bat-vulnerability-and-management-considerations

Oral Papers:

1. Dodd, L.E., R.E. Burch, and S.A. Fulton. Shifting occurrence of insect communities in the wake of White-nose Syndrome. *Joint Annual Meeting of the Entomological Society of America, ESC, and ESBC*, Vancouver, BC, 11-14 November 2018.
2. Fulton, S., and L.E. Dodd. Relationships between bats and their insect prey following the arrival of White-nose Syndrome to a fire-managed landscape. *Annual Meeting of the Kentucky Bat Working Group*, Barren River Lake State Resort Park, KY, 8-9 November 2018.
3. Burch, R.E., and L.E. Dodd. Patterns of bat and insect activity in relation to prescribed fire following the arrival of White-nose Syndrome at Mammoth Cave National Park. *Kentucky Prescribed Fire Annual Meeting and Bats and Fire Workshop*, Cave City, KY, 24-25 September 2018.
4. Fulton, S.A., and L.E. Dodd. Modeling the spatial distribution of insect abundance and insect-derived nutrients at Mammoth Cave National Park. *Kentucky Prescribed Fire*

Annual Meeting and Bats and Fire Workshop, Cave City, KY, 24-25 September 2018.

5. Fulton, S.A., and L.E. Dodd. Spatial distribution of insect-derived nutrients at Mammoth Cave National Park. *North American Joint Bat Working Group Meeting and Colloquium on the Conservation of Mammals in the Eastern United States*, Roanoke, VA, 26-29 March 2018.
6. Fulton, S.A., and L.E. Dodd. Documenting bat emergence patterns during a total solar eclipse. *Annual Meeting of the Kentucky Bat Working Group*, Natural Bridge State Park, KY, 5-6 October 2017.
7. Fulton, S.A., and L.E. Dodd. Modeling relationships between insects and imperiled bats in a fire-managed central hardwoods forest. *58th Annual Southern Forest Insect Work Conference*, Melbourne, FL, 25-28 July 2017.
8. Fulton, S.A., L.E. Dodd, and L.K. Rieske. Size metrics as predictors of the energetic value of lepidopteran prey. *Annual Meeting of Southeastern Bat Diversity Network and Colloquium on the Conservation of Mammals in the Eastern United States,* Asheville, NC, 16-17 February 2017.
9. Griffitts, R.E., L.E. Dodd, M.J. Lacki, N.S. Skowronski, L.K. Rieske, and M.B. Dickinson. Interacting effects of prescribed fire and White-Nose Syndrome on bat activity across the forest landscape of Mammoth Cave National Park, *Annual Meeting of Southeastern Bat Diversity Network and Colloquium on the Conservation of Mammals in the Eastern United States*, Asheville, NC, 16-17 February 2017.
10. Dodd, L.E., M.J. Lacki, N.S. Skowronski, M.B. Dickinson, and L.K. Rieske. Modeling the activity of imperiled bats at Mammoth Cave NP using remotely sensed descriptors of habitat conditions. *96th Annual Meeting of the National Academy of Science's Travel Research Board*, Washington D.C., 8 January 2017.
11. Griffitts, R.E., and L.E. Dodd. Effects of prescribed fire and white-nose syndrome on bat activity across the landscape of Mammoth Cave National Park. *Annual Meeting of the Kentucky Bat Working Group,* Rough, KY, 9 November 2016.
12. Fulton, S.A., and L.E. Dodd. Laboratory methods for maximizing DNA yield from bat fecal samples. *Annual Meeting of the Kentucky Bat Working Group*, Rough, KY, 9 November 2016.
13. Dodd, L.E., N.S. Skowronski, M.B. Dickinson, L.K. Rieske, and M.J. Lacki. Modeling activity of the Indiana bat (*Myotis sodalis*) at Mammoth Cave National Park using remotely-sensed descriptors of forest canopy structure. *Mammoth Cave National Park's 11th Research Symposium*, Mammoth Cave, KY, 18-20 April 2016.
14. Fulton, S.A., L.E. Dodd, and L.K. Rieske. Evaluating the energetic value of Lepidoptera using bomb calorimetry. *Mammoth Cave National Park's 11th Research Symposium*, Mammoth Cave, KY, 18-20 April 2016.
15. Griffitts, R.E., L.E. Dodd, and M.J. Lacki. The activity of *Myotis sodalis* and *Myotis septentrionalis* changes on the landscape of Mammoth Cave National Park following the arrival of White-nose Syndrome. *Mammoth Cave National Park's 11th Research Symposium*, Mammoth Cave, KY, 18-20 April 2016.
16. Griffitts, R.E., L.E. Dodd, and M.J. Lacki. Effects of prescribed fire on bat activity following the arrival of White-Nose Syndrome. *Annual Meeting of Southeastern Bat Diversity Network and Colloquium on the Conservation of Mammals in the Eastern United States*, Lake Guntersville, AL, 18-19 February 2016.
17. Griffitts, R.E., and L.E. Dodd. Effects of White-Nose Syndrome on bat activity across the

landscape of Mammoth Cave National Park. *Annual Meeting of the Kentucky Bat Working Group (Invited),* Natural Bridge State Park, KY, 5 November 2015.

18. L.E. Dodd, M.J. Lacki, N.S. Skowronski, M.B. Dickinson, and L.K. Rieske. Long-term impacts of prescribed fire on bat and insect activity at Mammoth Cave National Park. *5th Fire in Eastern Oak Forests Conference (Invited),* Tuscaloosa, AL, 27-29 May 2015. Available at: https://vimeo.com/oakfirescience.

Scientific Posters:

1. Dodd, L.E., M.J. Lacki, N.S. Skowronski, M.B. Dickinson, and L.K. Rieske. Synthesis of a long-term research project elucidating the spatial relationships between imperiled bats and local fire management practices in the wake of White-nose Syndrome. *97th Annual Meeting of the National Academy of Science's Travel Research Board*, Washington D.C., 9 January 2018.
2. Fulton, S.A., and L.E. Dodd. Relating bat and insect communities in the context of White-nose Syndrome and prescribed fire. *47th Annual North American Symposium on Bat Research*, Knoxville, TN, 18-21 Oct 2017.
3. Dodd, L.E., S.A. Fulton, R.E. Griffitts, and L.K. Rieske. Insect community responses to prescribed fire and White-nose Syndrome in eastern deciduous forests. *North American Forest Insect Work Conference,* Washington, D.C., 31 May – 3 June 2016.
4. Fulton, S.A., and L.E. Dodd. Using next-generation sequencing to investigate dietary preferences of bats in the wake of White-Nose Syndrome. *Annual Meeting of Southeastern Bat Diversity Network and Colloquium on the Conservation of Mammals in the Eastern United States,* Lake Guntersville, AL, 18-19 February 2016.
5. Fulton, S., L.K. Rieske, and L.E. Dodd. Assessing dietary changes of bats in the wake of White-nose Syndrome. *Annual Meeting of the Kentucky Academy of Science,* Highland Heights, KY, 13-14 November 2015.
6. Griffitts, R.E., and L.E. Dodd. Bat activity after prescribed fires at Mammoth Cave National Park. *Annual Meeting of the Kentucky Academy of Science,* Highland Heights, KY, 13-14 November 2015.
7. Dodd, L.E., A.G. Skiles, and L.K. Rieske. Simulating effects of fire on gypsy moth caterpillars fed improved American chestnut. *57th Annual Southern Forest Insect Work Conference,* Fayetteville, AR, 21-24 July 2015.
8. Fulton, S.A., L.E. Dodd, and L.K. Rieske. Is bigger really better? Assessing caloric value of lepidopterans as bat prey. *57th Annual Southern Forest Insect Work Conference,* Fayetteville, AR, 21-24 July 2015.

Other Outreach / Media:

1. Participated in PBS New Hour's Student Reporting Labs, "Students Join Efforts to Save Mammoth Cave's Bats," Summer 2017. Accessible at: https://studentreportinglabs.org/americathebeautiful/saving-mammoth-caves-bats/
2. Organized lab outreach at Mammoth Cave National Park's Annual Bat Night, Included demonstration tables for trapping of nocturnal insects, 27 August 2016.
3. Presentation given to the Midway Environmental Action Forum, "Bat Ecology and Conservation," 21 April 2016, Midway Presbyterian Church, Midway, KY.

4. Outreach at Mammoth Cave National Park's Annual Bat Night, Included demonstration tables for bat echolocation and trapping of nocturnal insects, 29 August 2015.
5. Interviewed for "Arthro-Pod," an entomology-focused podcast produced by the University of Nebraska – Lincoln, "Episode 13: Bat-Insect Interactions with Dr. Luke Dodd," 9 July 2015. Accessible at: http://arthro-pod.blogspot.com/2015/07/arthro-pod-episode-13-bat-insect.html

Appendix C. Metadata

Data Types

To assess bat activity at MACA, we recorded echolocation calls of bats and also collected morphometric data from captured bats. We stored all raw recorded echolocation materials as either zero-crossing data (Anabat II) or full-spectrum data (Songmeter SM3), as per the capabilities of detector types. We stored all raw echolocation calls in folders sorted according to date and location recorded. For acoustic data used to address Objective 1 in this report, we produced Microsoft Excel spreadsheets that have assigned spatial and temporal descriptors for each file / data row, alongside identifications generated using automatic classification software. The workbook file contains a metadata tab describing these data. For morphometric data used to address Objective 1 in this report, the resultant Microsoft Excel spreadsheets followed data entry guidelines of the Kentucky Department of Fish and Wildlife Resources and US Fish and Wildlife Services. Capture data have been submitted according to respective permitting requirements.

To assess insect activity and use by bats at MACA, we recorded insect count data from traps, and resultant Microsoft Excel spreadsheets are further distinguished on the basis of the analysis (i.e., ANOVA / master data, AIC modeling, dbRDA, and nutritional geometry). In all instances, data for both bats and insects are temporally and spatially tagged so that predator and prey are aligned into a single data line. The workbook file contains a metadata tab describing these data. Additional measurements for bomb calorimetry and DNA-based analyses are species- and specimen-specific, and each have dedicated workbooks. All workbooks contain metadata tabs describing these data.

Finally, for the data collected in relation to Objective 3 in this report, the resultant measurements from assays are arranged according to the 2×2 study design, with beginning and ending growth rates for both CADI and LYDI responses aligned for calculation of treatment effects. This final objective has a dedicated workbook. The workbook file contains a metadata tab describing these data.

Data Storage and Backup

Data are stored on a laptop hard drive, backed up on an external USB drive, and will be backed up on an EKU server at the completion of #14-1-05-22. Following precedence of JFSP #14-0-05-7, we will deposit all three workbooks described above within the permanent archive within two years of the completion of the grant (i.e., by 31 December 2020). As of April 2018 two additional articles in preparation that are to be submitted summer of 2019. Any additional publications or products resulting from #14-1-05-22 after April 2019 will be placed in the JFSP archive as well.

Data Access

Following precedence of JFSP #14-0-05-7, we will make our data available to others once we have received the full benefit of the data for publication in the primary literature. Raw data and metadata will be made public through consultation with MACA and the NPS. We also plan to include a citation of the data location in all research articles. We will request repositories to not release these data to the public until it is either published, or two years have passed since the project end-date.