Mammoth Cave Research Symposia
10th Research Symposium 2013

Feb 14th, 2:00 PM

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Recommended Citation

Luke E. Dodd, Nicholas S. Skowronski, Matthew B. Dickinson, Michael J. Lacki, and Lynne K. Rieske, "Using LiDAR to Link Forest Canopy Structure with Bat Activity and Insect Occurrence: Preliminary Findings" (February 14, 2013). *Mammoth Cave Research Symposia.* Paper 13.
http://digitalcommons.wku.edu/mc_reserch_symp/10th_Research_Symposium_2013/Day_one/13

Using LiDAR to Link Forest Canopy Structure with Bat Activity and Insect Occurrence: Preliminary Findings

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Abstract

Bats are an imperiled, yet ecologically-important group of vertebrate predators. Our ongoing research focuses on testing hypotheses about the relationships between the effects of fire on canopy structure and insect prey availability, and how these factors relate to use of foraging space by bats during the pre- and post-hibernation periods at Mammoth Cave National Park (MCNP). LiDAR-derived data (October 2010) were intersected with spatially explicit sampling of bat and insect populations (2010-2011) in order to characterize relationships between canopy structure, insect abundance, and bat activity. A canonical correspondence analysis for bat data suggested that forest canopy structure has a strong relationship with bat activity, particularly for species that echolocate at higher frequencies. Less variation was accounted for in a canonical correspondence analysis of insect occurrence. Even so, this analysis still demonstrated that variation in forest canopy structure influences the insect community at MCNP, albeit in varied ways for specific orders of insects.

Introduction

Remote sensing techniques such as light-detection and ranging (LiDAR) have expanded the scale and scope of ecological studies, allowing for more effective management of an expanding number of wildlife species (Vierling et al. 2008, Hudak et al. 2009). As bats are an imperiled and ecologically-important group of vertebrate predators, our study was initiated to relate the relative activity of these predators with the occurrence of their insect prey across the gradient of forest conditions found at Mammoth Cave National Park (MCNP). This ongoing project focuses on testing hypotheses about the relationships between the effects of fire on insect prey availability and canopy structure, and how these factors relate to use of foraging space by bats during the pre- and post-hibernation periods at MCNP. Aboveground habitat quality pre- and post-hibernation is critical because bats must go into hibernation with sufficient fat reserves and often leave hibernation in poor condition. A better understanding of the spatial and temporal patterns associated with bat foraging is important given the recent arrival of White-nose Syndrome (WNS) at MCNP.

Methods

Mammoth Cave National Park encompasses 23,000 ha in Barren, Hart, and Edmonson counties on the edge of the Crawford-Mammoth Cave Uplands of the Interior Plateau of Kentucky (Woods et al. 2002). We developed three-dimensional canopy height models across the entirety of MCNP in October of 2010 using discrete-return scanning LiDAR (>4 pulses / m^2). We processed these data using “Toolbox for LiDAR data Filtering and Forest studies” software (Chen et al. 2007). The output from this processing included high resolution digital elevation models, canopy height models, as well as three-dimensional canopy height profiles (Skowronski et al. 2007). These canopy height profiles allowed assessment of the density of vegetation throughout the forest canopy (Figure 1).

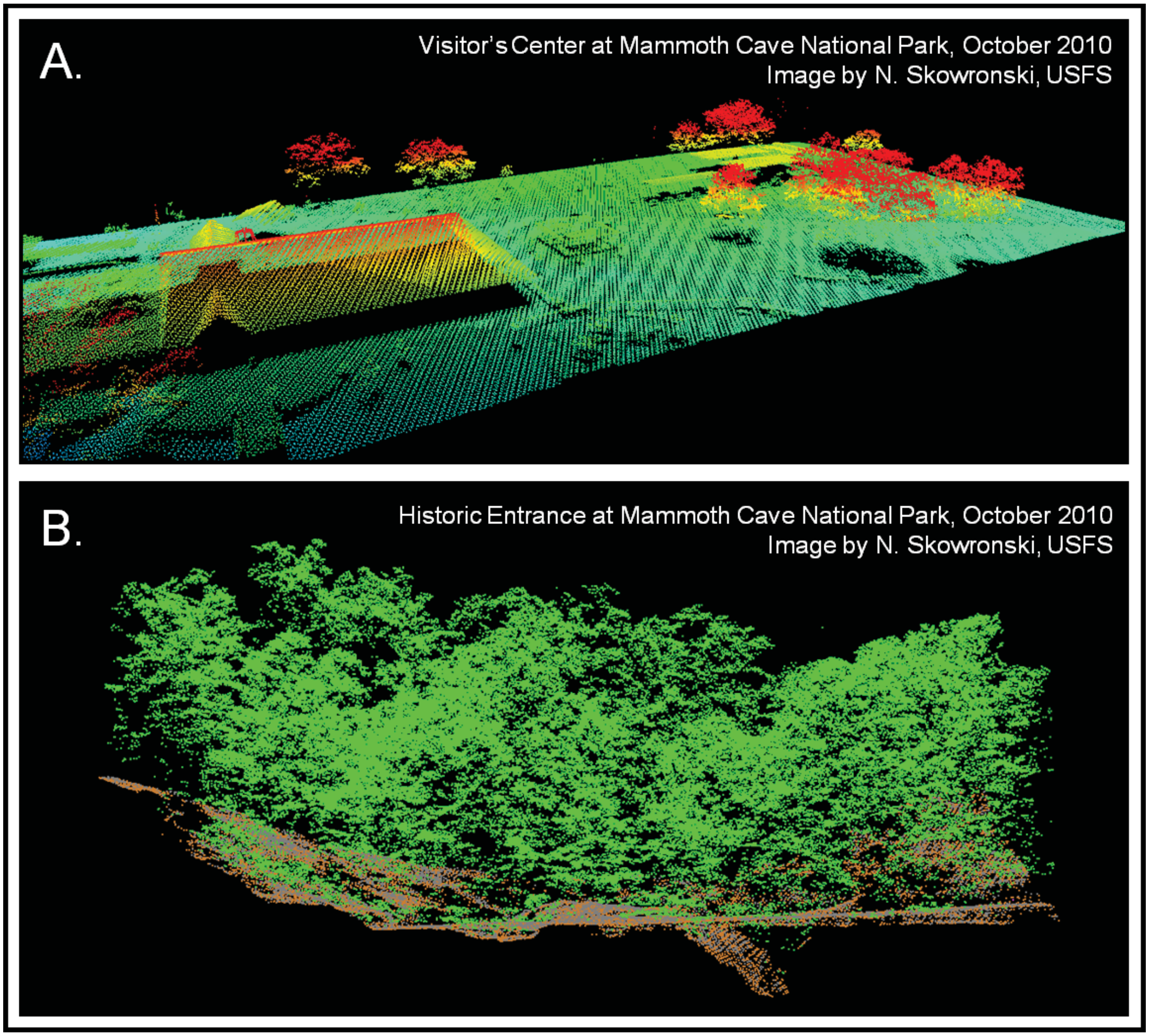

Figure 1: LiDAR-derived images demonstrating three-dimensional data derived for Mammoth Cave National Park.

LiDAR-derived data were intersected with spatially explicit sampling of bat and insect populations in order to characterize relationships between canopy structure, insect occurrence, and bat activity.
We conducted surveys for bat activity and nocturnal insect occurrence from September 2010 through October 2011 using acoustic detectors and blacklight traps, respectively. These surveys took place across an array of upland and riverine habitats that covered a range of forest canopy heights. Transects were used for both techniques, which entailed multiple survey points (all ≥ 100 m apart). We surveyed transects in tandem so that monitoring took place at a burned land parcel simultaneous with an unburned land parcel.

We assessed bat activity using the Anabat II system (Titley Electronics, Colombia, Missouri) powered by a 12 V gel-cell battery and housed in plastic containers to protect equipment from inclement weather (O'Ferrell 1998). Acoustic surveys spanned multiple (2-3) nights to account for nightly variation (n = 4 acoustic detectors / transect). Despite standard placement and operation, the potential existed for microphone sensitivity to vary over time, as well as between units, so we regularly calibrated acoustic detectors using an ultrasonic insect repeller (Britzke 2004). Analysis of acoustic data collected between sunset and sunrise was carried out using Echoclass v.1.1, an automated software package for acoustic identification developed by the U.S. Army Engineer Research and Development Center and provided by the U.S. Fish and Wildlife Service (USFWS 2012). With this software, echolocation pulses are isolated into high frequency (> 34 kHz) and low frequency (≤ 34 kHz) categories (E. Britzke, U.S. Army Engineer Research and Development Center, pers. comm.). The resulting response variables we considered for bat activity were the numbers of echolocation files and pulses within the high and low-frequency categories, on a per night basis. The number of feeding buzzes isolated per night from echolocation data was considered as an additional response variable indicative of foraging activity by bats.

We assessed insect occurrence using 10-W blacklight traps (Universal Light Trap, Bioquip Products, Gardena, California). A single survey night for insects was conducted in the same land parcels as that for concurrent acoustic surveys (n = 4 traps / transect). As per recommendations of Yela and Holyoak (1997) for sampling Lepidoptera, survey were conducted on nights with temperatures ≥ 16° C at sunset, no precipitation, and low wind speeds. We suspended blacklight traps 2.5-m aboveground prior to sunset and operated traps throughout the entire night. A dichlorvos-based 'pest strip' (ca. 2×6-cm) was placed within each blacklight trap to subdue specimens. Insects were identified using keys (Covell 2005, Triplehorn and Johnson 2005) and reference collections at the University of Kentucky. Insects ≥10 mm in length were identified to the lowest taxon practical. Response variables were numbers per night for the most abundant orders we recorded: Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera.

We used canonical correspondence analysis (CCA) to explore relationships between forest canopy structure and bats and insects separately. Variables describing density of vegetation throughout the forest canopy follow those developed by Lesak et al. (2011) and were based on a 15-m radius around each faunal survey point. These forest canopy variables describe the relative density of vegetation in the understory, midstory, and overstory (referred to as "canopy" in Lesak et al. 2011), and the relative proportions of these strata in relation to one another (i.e., ratios of midstory to overstory, understory to midstory, and understory to overstory). We generated a gap index for each faunal survey point; this variable was a proportional expression of the absence of vegetation >3 m in height. This index thus considered the lack of taller vegetation (or "gap") within a 15-m radius around each faunal sampling point. Data were analyzed in PC-ORD v.4.25 following standard ordination techniques (McCune and Grace 2002) using default settings; Monte Carlo tests of significance were run for 300 iterations. Relationships within and between faunal and LiDAR-derived data were explored using biplots.

Results

Bat surveys were carried out over 114 nights during August-October of 2010 and April-October of 2011, yielding a total of 769 detector-nights. These data were collected prior to the detection of WNS at MCNP. The CCA of bat activity with forest canopy structure was significant (Table 1), and explained over 47% of the variation in acoustic data. High-frequency

Table 1: Summary of canonical correspondence analyses relating both bat activity and insect occurrence to forest canopy variables for Mammoth Cave National Park.

Summary Statistic	**Bat CCA**	**Insect CCA**
Total Variance ("Inertia") of Response Variables	0.82	1.03
Eigenvalue for First Axis	**0.390**	**0.108**
Variance Explained by First Axis (%)	47.4	10.5
Monte-Carlo Test of Correlations in First Axis (P-value)	0.001	0.05
Eigenvalue for Second Axis	**0.002**	**0.022**
Variance Explained by Second Axis (%)	0.3	2.1
Monte-Carlo Test of Correlations in Second Axis (P-value)	0.10	0.61

and low-frequency variables were broadly separated in multivariate space (Figure 2). A closer association was observed between the high frequency variables than between the low frequency variables. Variation in high frequency variables was more closely associated with variation of forest canopy variables than was variation in low frequency variables. The proportion of overstory, proportion of midstory, and gap index had the strongest relationships with bat activity. In contrast, the ratio of understory to overstory strata had the weakest relationship. High frequency bat activity was positively associated with an increased proportion of vegetation density in the overstory and midstory. Low frequency bat activity was less associated with forest canopy variables; however, low frequency pulses closely aligned with gap index, indicating a weak positive association between these variables. The incidence of feeding buzzes did not have a strong association with forest canopy variables.

Insect surveys were carried out over 41 nights concurrent with acoustic surveys, yielding a total of 205 trap-nights. The CCA of insect occurrence with forest canopy structure was significant (Table 1), and explained over 10% of the variation in the insect data. Abundance of various insect orders separated out in multivariate space (Figure 3). Abundance of Diptera and

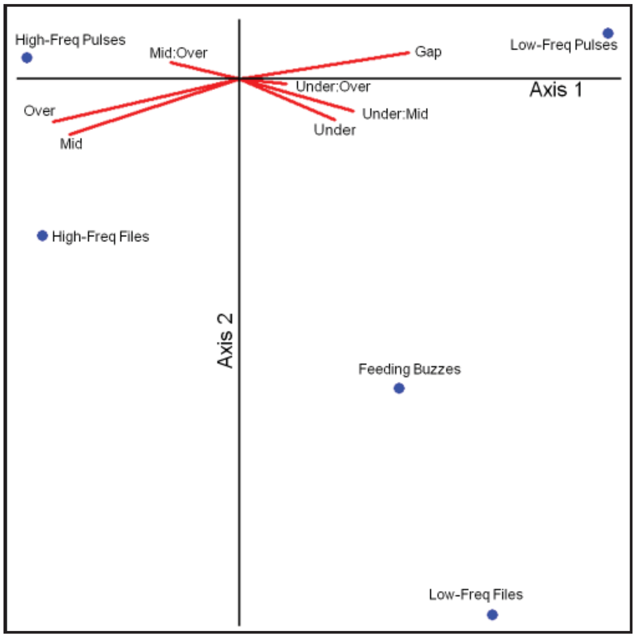

Figure 2: A biplot based on a canonical correspondence analysis of bat activity and forest canopy variables for Mammoth Cave National Park (using LC scores). The ordination shows the relative relationships between bat activity variables (circles) and forest canopy variables (vectors). Abbreviated forest canopy variables are: gap index (gap), relative proportion of midstory (mid), relative proportion of overstory (over), relative proportion of understory (under), ratio of relative proportion of midstory to relative proportion of overstory (mid:over), ratio of relative proportion of understory to relative proportion of midstory (under:mid), and ratio of the relative proportion of understory to relative proportion of overstory (under:over).

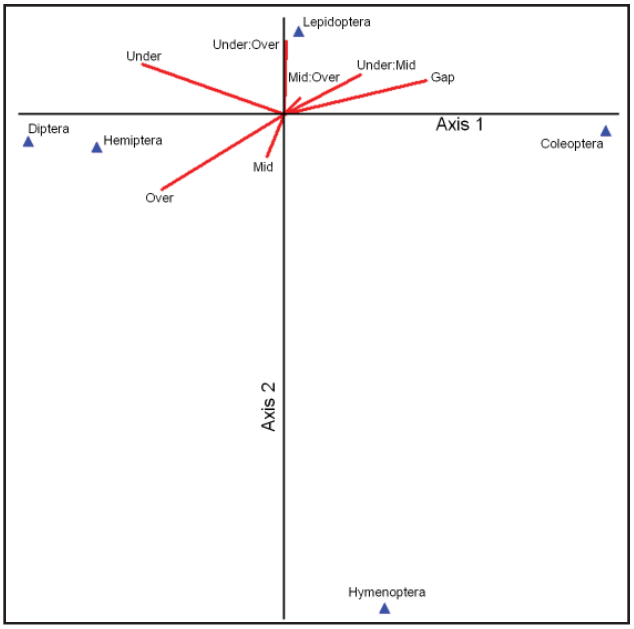

Figure 3: A biplot based on a canonical correspondence analysis of insect abundance and forest canopy variables for Mammoth Cave National Park (using LC scores). The ordination shows the relative relationships between insect abundance variables (triangles) and forest canopy variables (vectors). Abbreviated forest canopy variables are: gap index (gap), relative proportion of midstory (mid), relative proportion of overstory (over), relative proportion of understory (under), ratio of relative proportion of midstory to relative proportion of overstory (mid:over), ratio of relative proportion of understory to relative proportion of midstory (under:mid), and ratio of the relative proportion of understory to relative proportion of overstory (under:over).

Hemiptera were closely associated with one another and separate from abundance of Coleoptera and abundance of Lepidoptera. The latter two orders were also separated from one another. Abundance of Hymenoptera was widely separated from other variables, and consequently had little weight on the analysis. The proportion of understory, proportion of overstory, and gap index had the strongest relationships with insect abundance, whereas the ratio of midstory to overstory strata had the weakest relationship. Abundance of Diptera and Hemiptera were positively associated with an increased proportion of vegetation density in both the overstory and understory. Abundance of Coleoptera was distantly associated with gap index. Abundance of Lepidoptera was less associated with the first axis, but closely aligned with the ratio of understory to overstory strata.

Discussion

These analyses are a first step towards elucidating the role that forest canopy structure plays in determining aboveground habitat use by bats at MCNP. Our data suggest that forest structure has a strong relationship with bat activity, particularly for species that echolocate at higher frequencies. This finding largely agrees with observations that show bats that echolocate at higher frequencies tend to be more capable of flight in "cluttered" habitats that possess an increased density of vegetation (Barclay and Brigham 1991, Swartz et al. 2003). Conversely, we found a reduced association between low frequency bat activity and forest canopy variables. This outcome is consistent with the use of open "uncluttered" foraging space by low-frequency echolocating bats in other habitats (Aldridge and Rautenbach 1987, Saunders and Barclay 1992), and with data that demonstrate North American bats which use low frequency echolocation also possess wing morphologies suited for flight in habitats with decreased clutter (Bogdanowicz et al. 1999, Lacki et al. 2007). The association we observed between low frequency bat activity and an increased gap index, while weak, further supports these patterns in habitat use.

While less variation was accounted for in the CCA of insect occurrence, those data still demonstrate that variation in forest canopy structure influences the insect community at MCNP. Multiple insect orders were positively related with an increased density of vegetation in the understory strata (Diptera, Hemiptera, and Lepidoptera). The associations between specific insect orders and canopy conditions are complex, however, given: 1) the ordination positions of forest canopy variables relating to the upper strata, and 2) the wide ecological and taxonomic diversity seen across these common insect orders. Regardless, affiliations between insect groups and specific strata in the forest canopy likely relates to varied abundance and utilization of host resources (Ober and Hayes 2008, Dodd et al. 2012). The orders of prey most consistently consumed by North American bats (Coleoptera, Diptera, and Lepidoptera; Lacki et al. 2007) separated from one another in our ordination. This suggests broad differences in forest canopy conditions where these insect orders are most common. Since the relative consumption of these orders of prey does vary across bat species, it will be important to determine in future analyses whether any affiliations between insects and cluttered foraging spaces may translate to increased availability of preferred prey for specific species groups of bats (i.e., those tending to use either high or low frequency echolocation).

Despite the link between cluttered forest canopies and high frequency bat activity, we did not see a strong association between feeding buzzes and any forest canopy variable. We offer several possible explanations. First, high-frequency bats may actively move through cluttered space, but may not feed extensively in these canopy conditions due to reduced foraging success (Bogdanowicz et al. 1999, Swartz et al. 2003). Second, some high-frequency bats (i.e., the northern myotis, *Myotis septentrionalis*), are capable of feeding in cluttered habitats by gleaning insects from the surface of vegetation, where feeding activity is based on insects located by passive listening and not echolocation (Faure et al. 1993, Ratcliffe and Dawson 2003). Third, the feeding buzz variable considered in our analysis incorporated both high and low frequency echolocation pulses. Thus, potential relationships between forest canopy variables and a variable representing foraging success for bats that echolocate at either high or low frequencies may have been masked. Regardless, our findings indicate that forest canopy structure influences activity of bats. The extent to which feeding behavior of insectivorous bats is influenced by canopy structure, however, remains less clear. Based on our findings we postulate that canopy structure may be of less importance for feeding success of insectivorous bats than previously hypothesized (Hayes and Loeb 2007). Further studies are needed to confirm or refute this possibility.

Acknowledgements

The authors thank T. Culbertson, K. Rose, and J. Winters for technical assistance. This research was supported by a grant from the USDA Joint Fire Sciences Program and by the College of Agriculture at the University of Kentucky. The information reported in this paper (No. 13-09-026) is part of a project of the Kentucky Agricultural Experiment Station and is published with the approval of the Director.

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