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# Effect of Forest Opening Characteristics, Prey Abundance, and Environmental Factors on Bat Activity in the Southern Appalachians

Jonathan Daniel Brooks
*Clemson University*, jbrook9@clemson.edu

EFFECT OF FOREST OPENING CHARACTERISTICS, PREY ABUNDANCE, AND
ENVIRONMENTAL FACTORS ON BAT ACTIVITY IN THE
SOUTHERN APPALACHIANS

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Patrick D. Gerard
Susan C. Loeb

ABSTRACT

Early successional habitat (ESH) is important for many wildlife species. Over the past century, land use changes have caused ESH to decline in hardwood forests of the eastern United States. The decline of ESH and ESH dependent wildlife has caused concern among land managers and scientists. Bats, which utilize ESH for foraging, are also a conservation concern, however little information is available on how ESH restoration affects bats. My objective was to determine how opening size, presence of edge, prey abundance, vegetation structure, and environmental factors affect bat activity in forest openings. In June-August 2014 and May-August 2015, I placed Anabat SD2 bat detectors at the interior and edge of small (0.2-1.6 ha), medium (2.1-5.6 ha), and large (6.2-18.5 ha) forest openings in the Nantahala National Forest Cheoah Ranger District, Graham County, North Carolina. Call files recorded were filtered using AnalookW and identified to species using Kaleidoscope Pro. Townes-style Malaise insect traps were paired with each bat detector and insects captured were counted and identified to order. iButton temperature loggers were also paired with each bat detector and used to determine mean nightly temperature. Vegetation surveys were conducted to quantify vegetation structure. Difference in insect abundance, bat activity, and bat species richness were tested using mixed effects general linear models. Opening size and presence of edge did not affect total insect abundance, however there was a positive effect of live and dead tree basal area and mean nightly temperature. Overall bat activity was significantly higher at opening edges compared to opening interiors, was positively related to mean nightly temperature, and was negatively related to vegetation structure. Activity of open-

adapted species was also negatively related to vegetation structure. These results suggest that opening size and prey abundance do not affect bat activity in the southern Appalachian Mountains, however vegetation structure and environmental factors are important. Open-adapted bats may select foraging patches with less vegetation structure because they can forage more efficiently in these environments, whereas clutter-adapted bats can forage efficiently in both cluttered and open environments. When creating ESH, land managers should maintain an open vegetation structure to benefit open-adapted bat species, focus on creating openings at lower elevations, and configure openings to maximize edge relative to opening area.

DEDICATION

I would like to dedicate this thesis to those who have walked along side me during my journey through life. To Greg Murray and Kathy Winnett-Murray, for inspiring me to pursue a career in conservation and for their continued support both professionally and personally. To Richard Frost, for believing in me and teaching me to do the same. I am so grateful for our conversations together and your thoughtful questions. Finally, to my mom and dad, whose love, support, and encouragement mean so much to me. I am so blessed to have you both as parents.

# ACKNOWLEDGEMENTS

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CHAPTER ONE


EFFECT OF FOREST OPENING CHARACTERISTICS, PREY ABUNDANCE, AND
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INTRODUCTION

Early successional habitat (ESH) is an important habitat type which is receiving

increased attention from scientists and land managers (Askins 2001, DeGraaf and

Yamasaki 2003, Swanson et al. 2011, King and Schlossberg 2014). ESHs are areas that

have been disturbed within approximately the past decade, have a relatively open canopy

structure, and have a vegetation community dominated by herbaceous plants and shrubs

(Greenberg et al. 2011a). Other terms used to describe this habitat type include forest

openings, stand initiation stage, and young forest communities (Oliver 1980, DeGraaf

and Yamasaki 2003, Greenberg et al. 2011a).

ESHs are created by natural disturbances such as wind storms, ice storms,

wildfire, insect epidemics, and disease, or by anthropogenic disturbances, such as logging

and prescribed burning (Rogers 1996, Lorimer 2001, Trani et al. 2001, DeGraaf and

Yamasaki 2003, Lorimer and White 2003, Swanson et al. 2011, Greenberg et al. 2011a).

After the arrival of Europeans in North America, large areas of land were cleared for

agriculture and timber harvest which created an abundance of ESH (Askins 2001,

Lorimer 2001, Trani et al. 2001, Lorimer and White 2003). Starting in the first half of the

20th century, natural disturbance, especially wildfire, was suppressed and abandoned farm

land was allowed to regenerate to mature forest (Trani et al. 2001, Askins 2001, Lorimer

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2001, DeGraaf and Yamasaki 2003). The changes in land use patterns over the past century have led to the decline of ESH in hardwood forests of the eastern United States (Lorimer 2001, Askins 2001, Trani et al. 2001, Lorimer and White 2003, DeGraaf and Yamasaki 2003, Shifley and Thompson 2011). For example, abundance of ESH declined from 33% in 1968-1976 to 17% by 1989-1999 in 11 states in the northeastern U.S. (Brooks 2003) and declined from 24% in 1967 to 8% in 2008 in Indiana (Shifley and Thompson 2011).

The decline of ESH is concerning because ESH is critical habitat for many species. For example, the abundance of shade-intolerant herbs and fruiting plants, important sources of food for both birds and mammals, are greater in recently disturbed forests (Greenberg et al. 2007, Elliott et al. 2011, Greenberg et al. 2011b). Reptiles also utilize ESH for basking (McLeod and Gates 1998, Greenberg et al. 2007) and >128 species of bird are known to be associated with ESH, many of which are in decline or are species of conservation concern (Hunter et al. 2001). Areas of recently disturbed forest are also important habitats for many terrestrial mammals (Kirkland 1990, Urban and Swihart 2011).

Bats also use ESH, or forest openings, for foraging (Loeb and O'Keefe 2011). Bats are a serious conservation concern because their populations are declining due to a number of threats. Currently, white-nose syndrome (WNS) is the most significant cause of bat morality in North America (O'Shea et al. 2016) with infected populations declining as much as 75%-90% in species such as little brown bats (*Myotis lucifugus*), northern long-eared bats (*M. septentrionalis*), Indiana bats (*M. sodalis*), and tri-colored bats

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(*Perimyotis subflavus*) (Turner et al. 2011). Wind energy is also a threat to bats (O'Shea et al. 2016). Large numbers of bat fatalities have been documented at industrial wind energy facilities (Arnett et al. 2008) and an estimated 600,000 bats were killed in 2012 due to interactions with wind turbines in the United States (Hayes 2013). Migratory tree-roosting species such as hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) are the most frequent fatalities (Arnett et al. 2008). The threats posed by WNS and wind energy are in addition to ongoing threats faced by bats such as habitat loss and fragmentation, intentional killing, and environmental contaminants (O'Shea et al. 2016).

Although creating ESH may harm bats by eliminating roost trees and fragmenting the forest, it may also benefit bats by creating foraging habitat. A number of studies have shown that bat activity is higher in stands with more open vegetation structure (Brigham et al. 1997, Yates and Muzika 2006, Erickson and West 2003, Owen et al. 2004, Loeb and O'Keefe 2006, Betts 2009, Brooks 2009, Bender et al. 2015). However, only a limited number of studies have examined the effect of forest opening size on bat activity. Grindal and Brigham (1998) used bat detectors to monitor bat activity in timber harvests ranging in size from 0.5-1.5 ha. They found that bat activity did not differ significantly across opening sizes. However, the range of opening sizes sampled was small compared to the range of forest opening sizes found in managed forests which can be 0.2-20.0 ha. In West Virginia, little brown bats, big brown bats (*Eptesicus fuscus*), eastern red bats (*L. borealis*), and hoary bats are more likely to be detected in larger canopy gaps (Ford et al.

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2005). Edges between mature forest and ESH also appear to be important foraging habitat for bats (Hein et al. 2009, Morris et al. 2010).

Two factors affecting bat foraging habitat selection are wing morphology and echolocation call structure. Wing morphology can be described using wing aspect ratio (wing span$^2$/wing area) and wing load (wing area/weight) (Norberg and Rayner 1987). Bats with high wing aspect ratios (long narrow wings) and high wing loads (high force on wings) are adapted for straight line, long distance flight. These species also tend to have low frequency, narrow band echolocation calls which allow them to perceive objects at greater distances (Aldridge and Rautenbach 1987). Species with high wing aspect ratios, high wing loads, and low frequency, narrow band echolocation calls tend to forage in more open environments and are referred to as "open-adapted" species. Open-adapted species in the Southern Appalachians include big brown bats, eastern red bats, hoary bats, and silver-haired bats (Norberg and Rayner 1987). Alternatively, bats with low wing aspect ratios (short broad wings) and low wing loads (low force on wings) are adapted for short distance, agile flight (Norberg and Rayner 1987). These species tend to have high frequency, broad band echolocation calls which allow them to perceive their surroundings in greater detail (Aldridge and Rautenbach 1987). Species with low wing aspect ratios, low wing loads, and high frequency, broad band echolocation calls tend to forage in more cluttered environments and are referred to as "clutter-adapted" species. Clutter-adapted species in eastern North America include species in the genus *Myotis*, tri-colored bats, and evening bats (*Nycticeius humeralis*).

Although wing morphology and echolocation call structure may affect bat response to opening size and presence of edge, other factors such as prey abundance and the abiotic environment may also have a significant effect on foraging patch selection. Results of studies examining the relationship between bat activity and prey abundance are mixed. Morris et al. (2010) found that overall bat activity, eastern red bat activity, and hoary bat activity were positively correlated with Lepidoptera abundance. However, Grindal and Brigham (1998) did not find a clear relationship between bat activity and insect abundance. Bats are also more likely to be found near water (Krusic et al. 1996, Brooks 2009) and at lower elevations (Grindal and Brigham 1999).

My objective was to determine how opening size, presence of edge, prey abundance, and abiotic environmental factors affect bat activity in forest openings. I hypothesized that: 1) open-adapted bats (big brown bats, silver-haired bats, hoary bats, and eastern red bats) would be more active in large openings than in small openings, 2) clutter-adapted species (tri-colored bats, *Myotis* spp.) would not respond to differences in opening size, 3) activity of open-adapted bats would be greater at opening interiors, 4) activity of clutter-adapted bats would be greater at opening edges, 5) overall bat activity and activity of individual species would be higher in openings with greater insect abundance, 6) activity of open-adapted species would be greater in openings with more open vegetation structures, 7) activity of clutter-adapted species would be greater in openings with more cluttered vegetation structure, 8) overall bat activity and activity of individual species would be greater at lower elevations, 9) overall bat activity and activity

of individual species would be greater near water, and 10) overall bat activity and activity of all species would be greater on warmer nights.

METHODS

*Study area*

My study took place in the Nantahala National Forest Cheoah Ranger District, Graham County, North Carolina (Figure 1). The Cheoah Ranger District is located in the southern Appalachian Mountains which are characterized by ridge and valley topography with high mountain peaks. The dominant vegetation type is mixed hardwood forest interspersed with pine stands and mountain balds. Common tree species include oaks (*Quercus*), maples (*Acer*), poplars (*Liriodendron*), hickories (*Carya*), and pines (*Pinus*). In May-August in 2014 and 2015, the average monthly temperature was 21.4°C and average monthly precipitation was 91.1 mm. Elevation in the Cheoah Ranger District ranges from 530 m to 1,658 m.

*Study design*

I sampled 33 forest openings in 2014-2015, however one opening was dropped from the analysis due to equipment failure. All openings had an open canopy structure and were dominated by shrubs, herbaceous plants, and bare ground. Openings included timber harvests, southern pine beetle (*Dendroctonus frontalis*) treatments, prescribed burns, and wildlife openings. Timber harvests were classified by the U.S. Forest Service as either shelterwood establishment or two-age shelterwood establishment harvests and were completed <5 years prior to sampling. Southern pine beetle treatments were areas of forest which were clear cut, burned, and replanted with shortleaf pine (*P.echinata*) to

regenerate areas of forest affected by the beetle. These openings were ≤11 years old. Wildlife openings were clearings maintained for the benefit of wildlife through regular mowing. Prescribed burns were completed <7 years prior to sampling.

I classified openings based on their size as small (0.2-1.6 ha), medium (2.1-5.6 ha), or large (6.2-18.5 ha). In each sampling period, I selected one small, medium, and large opening to be sampled simultaneously. The three openings were chosen to minimize travel time between openings and are considered a block. The average distance between openings was 1.1 km with a range of 0.01-12.4 km.

*Acoustic Sampling*

All data were collected June 4-August 2, 2014 and May 22-August 13, 2015. I used Anabat SD2 (Titley Scientific, Columbia, MO) acoustical bat detectors to measure bat activity in each opening. The microphone was enclosed in a weatherproof housing mounted atop a 3.7 m pole and connected to the detector, which was enclosed in a waterproof container at the base of the pole, via a 6.10 m cable. The microphone housing was fabricated using PVC couplings and a 3.8 cm swept-45° PVC elbow into which the front of the microphone was placed. The opening of the elbow was angled approximately 45° above horizontal and was oriented toward the interior of the opening. Prior to the start of each field season, the sensitivities of the Anabat SD2 detectors were equalized to a detector with an internal sensitivity setting of 30 using the Anabat Equalizer (Titley Scientific, Columbia, MO).

I placed two Anabat SD2 detectors in each opening. One detector was positioned 5 m into the opening from the boundary between the forest and the opening. The other

detector was placed 70 m into the opening or at the opening center, whichever was closer.

Because the edge effect for bats extends 40 m into forest openings (Jantzen and Fenton 2013) placing detectors 70 m into the opening or at the opening center was sufficient to avoid edge effects. Detectors within an opening were >20 m from each other to prevent both detectors from simultaneously recording the same bat.  Each detector was programed to begin recording 15 min prior to sunset and stop recording 15 min after sunrise. Bat activity was monitored for at least three nights in each opening. I discarded data collected on nights with heavy rain or when rain lasted more than 30 min. An iButton temperature logger (Embedded Data Systems, Lawrenceburg, KY) was also placed on a Malaise insect trap (see below) approximately 5 m from each detector. The temperature loggers recorded ambient temperature at 10 min intervals throughout the night.

Call files were downloaded from the SD2 detector using CFCread (Titley Scientific, Columbia, MO) with a division ratio of eight, smooth of 50, and max TBC of 5 sec. I used an automated filter algorithm (noise filter) in AnalookW (Titley Scientific, Columbia, MO) to remove files that did not contain bat calls. Files that passed the noise filter were manually reviewed to confirm the presence of bat calls in each file. Each file that contained at least one bat call was considered a bat pass and I used these files as a measure of overall bat activity. Files that passed the noise filter were then run through a more rigorous filter (ID filter) which removed files with <5 call pulses or that were of otherwise low quality. Files passing this filter were also manually reviewed to ensure that they contained only search phase calls.  These files were then input into Kaleidoscope

Pro Version 3.1.0 (Wildlife Acoustics, Maynard, MA) for species identification. Settings used in Kaleidoscope Pro can be found in Table 1. Species assignments made by Kaleidoscope were manually reviewed and identifications were corrected if necessary. If I did not agree with the identification assigned by Kaleidoscope but could not confidently identify the species, I dropped the file from the analysis. Identified files were counted to determine species level activity. Because it can be difficult to differentiate between some species, even with the use of an automated classifier, I grouped big brown bats and silver-haired bats, eastern red bats and evening bats, and *Myotis* spp. Although eastern red bats tend to be more open-adapted and evening bats tend to be more clutter-adapted, evening bats are rare at our study location and would not contribute significantly to activity of this group (O'Keefe et al. 2009, Loeb personal communication).

*Insect Sampling*

A Townes-style Malaise insect trap was paired with each bat detector. The traps were positioned approximately 5 m from the bat detector as terrain and vegetation allowed. Insect traps paired with bat detectors at opening edges were also positioned approximately 5 m from the edge. A small LED headlamp was hung on the collection head of each trap. As close to recording start time as possible, collection bottles filled ~1/8 full of 80% ethanol were attached to the traps and the LED headlamps were illuminated. The bottles were removed from the insect traps the following morning as close to recording stop time as possible. At least two nights of insect trapping were completed at each location sampled. Insects collected were transferred to storage containers with 80% ethanol. The specimens were counted and identified to order with

the aid of a dissecting scope. I classified insects based on keys found in Tripplehorn and Johnson (2005). I analyzed both the total abundance of insects and the abundance of the five insect orders commonly preyed upon by bats: Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (Whitaker 2004).

*Habitat and Landscape Characteristics*

Vegetation surveys were conducted within 5 m radius (78.5 m$^2$) plots centered on each bat detector at the interior and edge of each opening. Within each plot, I counted the number of trees <1 m, 1-2 m, and >2 m in height. Percent cover of shrubs <0.5 m, 0.5-1.5 m, and >1.5 m and percent cover of herbaceous plants <1 m, 1-2 m, and >2 m were visually estimated to the nearest 5%. The percentage of bare ground was also visually estimated and basal area of live and dead trees was determined using a ten-factor prism. All estimates of cover were conducted by the same person to eliminate variation due to multiple observers.

The position of each bat detector was recorded using a Trimble GeoExplorer 2008 GPS with TerraSync software (Trimble, Sunnyvale, CA). The GPS had a horizontal accuracy of <2 m. The GPS files were post-processed using Pathfinder Pro 5.60 (Trimble, Sunnyvale, CA) and were imported into ArcMap 10.1 (ESRI, Redlands, CA). The elevation of each point was extracted using a digital elevation model (U.S. Geological Survey 2013). Distance to the nearest permanent water source was also determined in ArcMap using the National Hydrography Dataset (U.S. Geological Survey 2014).

*Statistical analysis*

All analyses were conducted using SAS University Edition (SAS Institute, Cary, NC). Principle components analysis was used to reduce the number of variables in the vegetation data (PROC PRINCOMP). I used the cumulative proportion of variation explained by each component to aid in selecting relevant components. Selected components were used as covariates in subsequent analyses.

I tested for differences in mean total insect abundance using mixed effects general linear models (PROC GLIMMIX). Fixed effects were opening size (small, medium, large), location (interior, edge), and size*location. Random effects were block, block*size, and location(block*size). The block effect incorporated both the sampling block and the year in which the block was sampled by assigning a unique value to each block across both years. Vegetation principle components, elevation, distance to water, and mean nightly temperature were used as covariates. I assumed a Poisson distribution with a log link function and used an offset to account for differences in sampling period length. I used a significance level of $\alpha=0.10$ for rejecting the null hypothesis. To assess whether the data met model assumptions, a plot of the residuals was examined. Significant fixed effects were assessed using a Fisher's Least Significant Difference test to determine which treatment levels were significantly different. A pairwise correlation analysis was conducted between each insect order to determine if these abundances were correlated (PROC CORR).

To determine if the noise and ID filters removed files consistently across all opening sizes and locations, the number of files passing each filter was subtracted from the number of files input into the filter. I then tested for differences in the mean number

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of calls removed by each filter using a mixed effects general linear model. Fixed effects were size, location, and size*location and random effects were block, block*size, and location(block*size). Covariates included in the models were the vegetation principle components, elevation, distance to water, and temperature. I assumed a Poisson distribution with a log link function and used an offset to account for differences in the length of night. I used a significance level of $\alpha=0.10$ for rejecting the null hypothesis. Differences in treatment levels for fixed effects were determined using a Fisher's Least Significant Difference test.

To test for differences in overall bat activity and species-level bat activity, I used a mixed effects general linear model with size, location, and size*location as fixed effects and block, block*size, and location(block*size) as random effects. Vegetation principle components, elevation, distance to water, temperature, and total insect abundance were used as covariates. I assumed a Poisson distribution and used an offset to account for differences in sampling period length. I used a significance level of $\alpha=0.10$ for rejecting the null hypothesis. The residuals plot was examined to determine if the data met the model assumptions. Differences in treatment levels for fixed effects were determined using a Fisher's Least Significant Difference test.

To test for differences in bat species richness I also used a mixed effects general linear model with size, location, and size*location as fixed effects and block, block*size, and location(block*size) as random effects, but I assumed a multinomial distribution with a cumulative logit link function. Because of issues with model convergence, I used four categories of species richness: zero species/species group, one species/species groups,

two species/species groups, and ≥3 species/species groups. Vegetation principle

components, elevation, distance to water, temperature, and total insect abundance were

used as covariates. I used a significance level of $\alpha$=0.10 for rejecting the null hypothesis

and used odds ratios to interpret model results.

RESULTS

I sampled a total of 32 openings over the two years of the study: 20 openings in

2014 and 27 openings in 2015. Of the 27 openings sampled in 2015, 15 were resampled

from 2014. Sampling effort for each opening size category can be found in Table 2.

*Vegetation structure*

I selected the first five principle components which explained 67% of the total

variation observed in the data (Table 3). Component one represented overall structural

complexity, component two represented shrub cover, component three represented

herbaceous plant cover, component four represented live and dead tree basal area, and

component five represented tall trees and shrubs.

*Insect abundance*

A total of 27,243 insects were identified in 2014 and 48,863 insects were

identified in 2015. Insect abundance was highest in small openings followed by large and

medium openings in both years (Table 4). In 2014, total insect abundance was higher at

opening edges than opening interiors across all opening sizes, but in 2015 total insect

abundance was only higher at opening edges in small and large opening. However,

differences in mean total insect abundance among opening sizes or between interior and

edge were not statistically significant (Table 5). Mean total insect abundance was

positively related to basal area (component 4) and mean nightly temperature, and negatively related to elevation.

In 2014, Diptera was the most abundant order followed by Lepidoptera, Hymenoptera, Hemiptera, Coleoptera, and Collembola (Table 6). In 2015, Diptera was again the most abundant order followed by Lepidoptera, Hemiptera, Hymenoptera, Thysanoptera, and Coleoptera. Coleoptera, Diptera, and Hemiptera were most abundant in small openings in 2014 and Hymenoptera and Lepidoptera were most abundant in medium openings (Fig. 2.a). In 2015, Diptera, Hemiptera, and Lepidoptera were most abundant in small openings and Coleoptera and Hymenoptera were most abundant in large openings (Fig. 2.b). Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera were more abundant at opening edges than interiors in 2014 and 2015 (Fig.3.a, b).

Neither opening size nor location had a significant effect on mean abundance of Diptera, Lepidoptera, Hymenoptera, Hemiptera, or Coleoptera, although the abundance of these five insect orders were positively related to mean nightly temperature (Table 5). The abundance of several insect orders were also related to vegetation structure. For example, Diptera abundance was positively related to basal area (component 4), Lepidoptera and Coleptera abundance was negatively related to shrub cover (component 2), and Hemipteran abundance was negatively related to vegetation structural complexity (component 1) and shrub cover (component 2) but positively related to basal area (component 4). Further, the abundance of Diptera, Lepidoptera, and Hemiptera were negatively related to elevation. The abundance of Diptera, Lepidoptera, Hymenoptera, Hemiptera, and Coleoptera were correlated with one another (Table 7).

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*Bat activity*

A total of 52,063 files were recorded (28,098 in 2014, 23,965 in 2015), of which 15,523 were identified as bat calls (6,668 in 2014, 8,855 in 2015) and 7,565 (3,191 in 2014, 4,374 in 2015) were able to be identified to species. The mean number of calls removed by the noise filter did not vary with opening size or location within the opening, however the mean number of calls removed did increase significantly with mean nightly temperature (Table 8). The mean number of calls removed by the ID filter was significantly higher at opening edges than opening interiors and was negatively related to vegetation structure and positively related to mean nightly temperature.

In 2014, overall bat activity was highest in large openings followed by small and medium openings (Table 9). In 2015, overall activity was highest in small openings followed by large and medium openings. Overall bat activity was higher at opening edges than interiors in both years and this difference was statistically significant (Table 10). There was also a significant negative effect of vegetation structural complexity (component 1) and a positive effect of mean nightly temperature on overall bat activity.

Big brown/silver-haired bats were the most frequently detected species group in 2014 followed by tri-colored bats, eastern red/evening bats, *Myotis* spp., and hoary bats (Table 11). Eastern red/evening bats were the most frequently detected species group in 2015 followed by big brown/silver-haired bats, tri-colored bats, hoary bats, and *Myotis* spp. In 2014, big brown/silver-haired bats and eastern red/evening bats occurred at 100% of sites surveyed. Tri-colored bats occurred at 81.6% of sites, *Myotis* spp. occurred at 39.5% of sites, and hoary bats occurred at 13.2% of sites. In 2015, eastern red/evening

bats occurred at 98.2% of sites surveyed, big brown/silver-haired bats occurred at 90.7% of sites, tri-colored bats occurred at 75.9% of sites, *Myotis* spp. occurred at 38.9% of sites, and hoary bats occurred at 22.2% of sites.

Big brown/silver-haired bat activity was highest in large openings in 2014 (Fig. 4.a) and highest in small openings in 2015 (Fig. 4.b). Big brown/silver-haired bat activity was greater at opening interiors than opening edges in both 2014 and 2015 (Fig 5.a, b). However, mean nightly activity did not differ significantly across opening sizes or between interiors and edges (Table 10). There was a significant negative relationship between big brown/silver-haired bat activity and structural complexity, shrub cover, elevation, and mean nightly temperature (Table 10)

Eastern red/evening bat activity was highest in small openings and lowest in large openings in 2014 (Fig. 4.a) and was highest in small openings and lowest in medium openings in 2015 (Fig. 4.b). Activity was also greater at opening edges than opening interiors in both 2014 and 2015 (Fig. 5.a, b). There was no significant effect of opening size or presence of edge on eastern red/evening bat activity, however there was a significant size*location effect (Table 10). Eastern red/evening bat activity was significantly higher at medium edges than at interior and edges of small openings and interiors of medium and large openings (Table 12, Fig. 6). Eastern red/evening bat activity was positively related to mean nightly temperature but was negatively related to structural complexity (component 1), herbaceous plant cover (component 3), and elevation (Table 9).

Hoary bat activity was highest in small openings and lowest in medium openings in 2014 (Fig. 4.a). In 2015, hoary bat activity was highest in small openings and lowest in large openings (Fig. 4.b). Hoary bat activity was greater at opening interiors in 2014 (Fig. 5.a) and at opening edges in 2015 (Fig. 5.b). Mean activity was not significantly different across opening size or interiors and edges, however mean activity was positively related to total insect abundance (Table 10). The residual plot showed evidence of a high frequency of zero counts indicating model assumptions may not have been met.

*Myotis* spp. activity was highest in large openings and lowest in medium openings both in 2014 and 2015 (Fig. 4.a, b). Activity was greater at opening interiors than at opening edges in both years (Fig. 5.a, b). There was no significant difference in mean *Myotis* spp. activity across opening sizes or interiors and edges (Table 10). However, mean activity was positively related to herbaceous cover (component 3). The residual plot showed evidence of a high frequency of zero counts indicating model assumptions may not have been met.

Tri-colored bat activity was highest in large openings and lowest in medium openings in 2014 (Fig. 4.a) and was highest in small openings and lowest in medium openings in 2015 (Fig. 4.b). Activity was greater at opening interiors than at opening edges in 2014, but was greater at opening interiors in 2015 (Fig. 5.a, b). Mean tri-colored bat activity did not vary significantly across opening sizes or interiors and edges, however there was a significant positive relationship with mean nightly temperature (Table 10).

Species richness observed in forest openings ranged from zero to five species/species groups. Bat species richness was highest in small openings and lowest in medium openings in both 2014 and 2015 (Table 13), however this difference was not statistically significant (Table 14). In 2014, species richness was higher at edges than interiors in small and medium openings, and higher at interiors than edges in large openings. In 2015, bat species richness was higher at opening edges across all opening sizes. However, none of the differences in mean species richness across opening sizes or interiors and edge were statistically significant. There was a significant effect of overall vegetation structure (component 1) and a significant positive of temperature on bat species richness. The odds of observing fewer bat species increased by 1.32 with a one unit increase of component one and the odds of observing fewer bat species decreased by 0.77 with a one unit increase of temperature.

DISCUSSION

In general, opening size was not a significant factor explaining bat activity. However, similar to other studies, overall bat activity was higher at the edges of forest openings compared to forest opening interiors in the southern Appalachian Mountains (Hein et al. 2009, Morris et al. 2010, Jantzen and Fenton 2013). In contrast, bat activity was not related to insect abundance, but vegetation structure was important for overall activity and the activity of many species groups. Further, overall activity and that of several species or species groups were related to environmental conditions such as temperature and elevation.

The lack of response by bats and insects to opening size suggests that other factors may be more important in determining use of ESH patches by bats and insects in the Southern Appalachians. Grindal and Brigham (1998) also did not observe a response by bats or insects to openings ranging in size from 0.5 to 1.5 ha. Ford et al. (2005) surveyed openings with mean canopy gap diameters ranging from 16.6 m to 35.1 m (~0.02-0.10 ha) and found that big brown bats, eastern red bats, hoary bats, and little brown bats were more likely to occur in larger openings. The smallest opening that I surveyed was 0.2 ha which is twice as large as the largest opening surveyed by Ford et al. (2005) which may explain why I did not observe a difference in activity among opening sizes.

Although opening size was not an important factor for predicting bat activity or insect abundance, presence of edge was important in determining overall bat activity. Greater overall bat activity at edges is not surprising given the results of other studies. For example, open-adapted and clutter-adapted species show a preference for opening edges in the Coastal Plain of North Carolina (Hein et al. 2009, Morris et al. 2010) and in Ontario, Canada (Jantzen and Fenton 2013). Activity at opening edges may be greater because edges provide bats with protection from wind (Verboom and Spoelstra 1999), abundant prey (Whitaker et al. 2000), refuge from predators (Walsh and Harris 1996, Lima and O'Keefe 2013), and navigational landmarks (Verboom et al. 1999). However, the lack of response by individual species or species groups is not consistent with these studies. This lack of response at the species group level may have been due to a greater proportion of low quality calls recorded at opening edges, thus reducing the number of

calls for some, or perhaps all, species or species groups at edges. Dense vegetation is known to reduce call detection (Parsons 1996, Patriquin and Barclay 2003). I tried to reduce the effect of clutter on detection by placing my detectors 5 m from the tall, dense vegetation of the forest interior, elevating the detector microphones 3.7 m above the ground, and orienting detector microphones towards the opening center. However, this appeared to have not been sufficient to completely eliminate the effects of clutter on call quality.

Vegetation structure was also a significant factor in determining bat activity. Similar to previous studies, bat response to vegetation structure was generally related to wing morphology and echolocation call structure (Norberg and Rayner 1987, Aldridge and Rautenbach 1987, Erickson and West 2003, Patriquin et al. 2003, Owen et al. 2004, Ford et al. 2005, Loeb and O'Keefe 2006, Brooks 2009, Mehr et al. 2012, Bender et al. 2015). The negative response of overall bat activity to vegetation structure was likely driven by big brown/silver-haired bats and eastern-red/evening bats which made up a large proportion of the calls identified. In contrast, hoary bats, an open adapted species, did not respond to vegetation structure. This may have been due to the low number of detections of hoary bats rather than the actual effect of vegetation structure. Alternatively, hoary bats may not have responded to vegetation structure because they were foraging well above the vegetation (Brigham et al. 1997).

Abiotic environmental factors were also useful in predicting bat activity. Although there were some exceptions among bat species/species groups and insect orders, in general, bat activity and insect abundance were positively related to

temperature and negatively related to elevation. Separating the effects of temperature and elevation is difficult as they are often correlated. Grindal and Bridgham (1999) also found that bat activity was greater at lower elevations in southern British Columbia and sex ratios in bats at higher elevations are often male-biased (Cryan et al. 2000, Ford et al. 2002). Higher insect abundance and reduced thermoregulation costs at lower elevations may increase reproductive success of females that roost at lower elevations, resulting in higher activity levels. The negative relationship between temperature and big brown/silver-haired bat activity is more difficult to explain. One explanation is that big brown/silver-haired bats must acquire more prey on colder nights to offset thermoregulation cost, but this explanation ignores behaviors such as torpor which conserve body heat.

Although elevation and temperature were useful for explaining bat activity, distance to water was not. A number of studies have found that bat activity is higher closer to water (Menzel et al. 2005, Ford et al. 2006, Brooks 2009), but other studies have found only a limited effect of distance from water on bat occupancy (Yates and Muzika 2006, Hein et al. 2009). One explanation for the lack of response to water in my study is that water is such a ubiquitous resource in the Southern Appalachians that there is no need for bats to aggregate around it. The average distance of my sites to water was 147.7 m and ranged from 5.7 m to 508.7 m despite making an effort to avoid openings near water. However, bat activity may be greater closer to water in landscapes where water is scarcer or in drier years.

The positive relationship between bat species richness and temperature was likely due to greater bat and insect activity on warmer nights. The higher activity levels on warmer nights made detecting rare species, such as *Myotis* spp. and hoary bats, more likely. However, it was surprising that species richness was lower at sites with higher structural complexity. I would have expected species richness to be higher in openings with more vegetation structure because the rare *Myotis* spp. are more likely to occur there. The negative relationship between species richness and vegetation structure may have resulted from lower rates of detection for high-frequency bat calls in openings with more vegetation structure.

I was not able to account for potential differences in detection among opening sizes or between edges and interiors using standard techniques (e.g. Mackenzie 2006) because of the split-plot design of this study. Results from studies which do not incorporate differences in detection should be interpreted cautiously (MacKenzie et al. 2002). A number of factors can affect detection in studies using acoustical detectors including vegetation structure and call intensity (Patriquin and Barclay 2003, Sleep and Brigham 2003, Duchamp et al. 2006). I attempted to control for differences in detection in my experimental design. Bat detectors were placed in areas with the most open vegetation structure available and microphones were elevated above vegetation. I also limited comparisons to within species/species groups which have similar call structure. However, there was evidence that detection may have affected my results. For example, significantly more calls were removed by the ID filter from detectors at opening edges than at opening interiors.

Another outcome of this study is further documenting the devastating effect of WNS, which was first detected in western North Carolina in the winter of 2011-2012 and has resulted in significant declines in Indiana bat, northern long-eared bat, little brown bat, and tri-colored bat capture rates since 2013 in the adjacent Great Smoky Mountains National Park (O'Keefe et al. 2015). Although direct comparisons between acoustical datasets are not possible because of differences in detection, broad trends can be inferred. Little brown bats were the most commonly detected species in acoustical studies conducted in West Virginia prior to the arrival of WNS, making up 15-25% of calls recorded (Owen et al. 2004, Ford et al. 2005). In my study, calls from *Myotis* spp. comprised less than 2% of the passes recorded.

The results of this study indicate that restoring ESH may create foraging opportunities for bats, especially open-adapted species. However, these species require an open vegetation structure. For forest openings to benefit these species, managers should maintain open vegetation structures. Managers should also consider restoring ESH at lower elevations where bat activity is higher. Although the size of ESH patches does not seem to affect bat activity, edges may be important locations. Configuring patches to maximize the amount of edge relative to the patch area may further benefit bats.

TABLES

Table 1 – Settings used in Kaleidoscope Pro 3.1.0 to assign species to calls recorded.

| Options Group | Option | Value |
|---|---|---|
| Filter | Filter noise files | Selected |
| | Keep noise files | Not selected |
| | Signal of interest kHz min | 15 |
| | Signal of interest kHz max | 120 |
| | Signal of interest ms min | 2 |
| | Signal of interest ms max | 500 |
| | Minimum number of calls | 5 |
| | Advanced signal enhancement | Selected |
| Classifier | Classifier | Bats of North American 3.1.0 |
| | Accuracy | 0 Balance (Neutral) |
| | Species | EPFU, LABO, LACI, LANO, MYLE, MYLU, MYSE, MYSO, NYHU, PESU |

Table 2 – Number of (a) detector hours and (b) insect trap hours sampled at the interior and edge of small, medium, and large openings in the Nantahala National Forest, NC May-August 2014-2015.

a)

| Size | Total | | Interior | | Edge | |
|---|---|---|---|---|---|---|
| | 2014 | 2015 | 2014 | 2015 | 2014 | 2015 |
| Small | 526.6 | 553.1 | 243.4 | 287.4 | 283.2 | 265.7 |
| Medium | 406.8 | 574.8 | 173.5 | 287.4 | 233.3 | 287.4 |
| Large | 536.5 | 564.5 | 262.9 | 277.1 | 273.6 | 287.4 |

b)

| Size | Total | | Interior | | Edge | |
|---|---|---|---|---|---|---|
| | 2014 | 2015 | 2014 | 2015 | 2014 | 2015 |
| Small | 392.4 | 509.8 | 189.5 | 254.6 | 202.9 | 255.2 |
| Medium | 398.9 | 497.4 | 200.9 | 256.4 | 198.0 | 241.0 |
| Large | 415.4 | 511.6 | 214.3 | 255.6 | 201.1 | 256.0 |

Table 3 – Results of the principle components analysis on the vegetation survey data collected at each location where bat activity and insect abundance were sampled in the Nantahala National Forest, NC May-August 2014-2015. The table shows eigenvalues for each principle components as well as the cumulative variation explained by the component.

| | Component 1 Structural complexity | Component 2 Shrub cover | Component 3 Herbaceous cover | Component 4 Basal area | Component 5 Tall trees & shrub |
|---|---|---|---|---|---|
| Trees <1 m | 0.071 | -0.576 | 0.052 | 0.023 | 0.124 |
| Trees 1-2 m | 0.405 | 0.054 | 0.189 | -0.134 | 0.131 |
| Trees >2 m | 0.408 | 0.026 | 0.148 | -0.301 | 0.310 |
| Shrubs <0.5 m | 0.380 | 0.284 | -0.060 | -0.141 | -0.253 |
| Shrubs 0.5-1.5 m | 0.350 | 0.323 | -0.007 | 0.125 | -0.199 |
| Shrubs > 1.5 m | 0.054 | 0.119 | -0.275 | 0.324 | 0.789 |
| Herbaceous <1 m | -0.455 | 0.061 | -0.320 | -0.171 | -0.126 |
| Herbaceous 1-2 m | -0.295 | 0.228 | 0.480 | 0.211 | 0.078 |
| Herbaceous >2 m | -0.230 | 0.173 | 0.557 | -0.010 | 0.211 |
| Bare ground | 0.138 | -0.607 | 0.114 | 0.091 | -0.061 |
| Live basal area ($m^2 \cdot ha^{-1}$) | 0.133 | 0.065 | -0.245 | 0.700 | -0.120 |
| Dead basal area ($m^2 \cdot ha^{-1}$) | 0.105 | -0.087 | 0.380 | 0.422 | -0.249 |
| Variation | 0.25 | 0.14 | 0.11 | 0.09 | 0.09 |
| Cumulative variation | 0.25 | 0.40 | 0.50 | 0.59 | 0.67 |

Table 4 – Number of insects captured per trap hour at the interior and edge of small, medium, and large forest openings in the Nantahala National Forest, NC May-August 2014-2015.

| Size | Total | | Interior | | Edge | |
|---|---|---|---|---|---|---|
| | 2014 | 2015 | 2014 | 2015 | 2014 | 2015 |
| Small | 27.7 | 45.5 | 15.7 | 40.6 | 38.8 | 50.4 |
| Medium | 16.3 | 24.1 | 14.9 | 24.3 | 17.7 | 24.0 |
| Large | 23.8 | 26.7 | 16.1 | 22.1 | 31.9 | 31.3 |

Table 5 – Results of mixed effects general linear models for total insect abundance and five insect orders commonly preyed upon by bats in the Nantahala National Forest, NC May-August 2014-2015.

| Effect | Df | F | P | Coefficient |
|---|---|---|---|---|
| *Total* | | | | |
| Size | 67.09 | 0.91 | 0.418 | - |
| Location | 69.46 | 0.13 | 0.723 | - |
| Size*location | 65.05 | 0.21 | 0.814 | - |
| Component 1 | 76.06 | 7.77 | 0.100 | -0.094 |
| Component 2 | 78.85 | 2.33 | 0.131 | -0.121 |
| Component 3 | 73.81 | 0.09 | 0.761 | 0.023 |
| Component 4 | 77.19 | 5.39 | 0.023 | 0.198 |
| Component 5 | 79.16 | 0.89 | 0.348 | -0.085 |
| Elevation | 79.20 | 2.87 | 0.094 | -0.001 |
| Water distance | 79.66 | 1.01 | 0.319 | -0.001 |
| Temperature | 174.00 | 1552.19 | <0.001 | 0.163 |
| *Diptera* | | | | |
| Size | 66.74 | 1.05 | 0.355 | - |
| Location | 69.47 | 0.27 | 0.605 | - |
| Size*location | 64.50 | 0.43 | 0.651 | - |
| Component 1 | 76.16 | 1.77 | 0.188 | -0.086 |
| Component 2 | 77.23 | 1.46 | 0.230 | 0.110 |
| Component 3 | 74.14 | 0.17 | 0.682 | 0.034 |
| Component 4 | 77.46 | 6.09 | 0.016 | 0.241 |
| Component 5 | 78.75 | 1.07 | 0.305 | -0.106 |
| Elevation | 77.97 | 3.04 | 0.085 | -0.001 |
| Water distance | 78.77 | 1.09 | 0.301 | -0.002 |
| Temperature | 174.00 | 1286.87 | <0.001 | 0.166 |

## Lepidoptera

| | | | | |
|---|---|---|---|---|
| Size | 29.42 | 1.91 | 0.166 | - |
| Location | 53.15 | 0.12 | 0.728 | - |
| Size*location | 37.88 | 0.74 | 0.483 | - |
| Component 1 | 45.14 | 0.02 | 0.879 | 0.008 |
| Component 2 | 60.50 | 13.50 | <0.001 | -0.244 |
| Component 3 | 70.73 | 1.12 | 0.293 | -0.069 |
| Component 4 | 70.49 | 0.06 | 0.811 | 0.018 |
| Component 5 | 69.58 | 2.31 | 0.133 | -0.116 |
| Elevation | 50.61 | 4.94 | 0.031 | -0.001 |
| Water distance | 53.53 | 1.71 | 0.197 | -0.002 |
| Temperature | 174.00 | 81.53 | <0.001 | 0.135 |

## Hymenoptera

| | | | | |
|---|---|---|---|---|
| Size | 28.14 | 0.31 | 0.737 | - |
| Location | 52.53 | 2.30 | 0.136 | - |
| Size*location | 37.63 | 0.46 | 0.634 | - |
| Component 1 | 42.02 | 0.78 | 0.383 | -0.052 |
| Component 2 | 62.36 | 1.32 | 0.256 | -0.092 |
| Component 3 | 65.72 | 0.11 | 0.746 | -0.024 |
| Component 4 | 66.53 | 0.67 | 0.415 | 0.070 |
| Component 5 | 64.06 | 0.70 | 0.406 | 0.074 |
| Elevation | 41.33 | 0.38 | 0.542 | -0.0003 |
| Water distance | 46.82 | 0.24 | 0.626 | 0.0007 |
| Temperature | 174 | 42.03 | <0.001 | 0.115 |

## Hemiptera

| | | | | |
|---|---|---|---|---|
| Size | 30.44 | 0.15 | 0.858 | - |
| Location | 54.71 | 0.02 | 0.898 | - |
| Size*location | 39.63 | 0.16 | 0.856 | - |
| Component 1 | 47.60 | 15.84 | <0.001 | -0.290 |
| Component 2 | 65.75 | 3.05 | 0.086 | -0.168 |
| Component 3 | 57.84 | 0.67 | 0.417 | 0.069 |
| Component 4 | 62.55 | 2.89 | 0.094 | 0.168 |
| Component 5 | 67.78 | 1.31 | 0.256 | -0.122 |
| Elevation | 48.03 | 2.95 | 0.092 | -0.001 |
| Water distance | 56.47 | 3.31 | 0.074 | -0.003 |
| Temperature | 174.00 | 183.06 | <0.001 | 0.271 |

*Coleoptera*

| | | | | |
|---|---|---|---|---|
| Size | 26.53 | 0.76 | 0.477 | - |
| Location | 59.62 | 0.00 | 0.972 | - |
| Size*location | 42.83 | 0.21 | 0.808 | - |
| Component 1 | 44.77 | 2.54 | 0.118 | -0.098 |
| Component 2 | 55.99 | 4.37 | 0.041 | -0.165 |
| Component 3 | 76.15 | 0.31 | 0.580 | -0.044 |
| Component 4 | 69.64 | 2.73 | 0.103 | 0.144 |
| Component 5 | 60.76 | 0.46 | 0.499 | -0.062 |
| Elevation | 49.43 | 2.42 | 0.126 | -0.0009 |
| Water Distance | 49.93 | 0.55 | 0.463 | -0.001 |
| Temperature | 174 | 99.20 | <0.001 | 0.247 |

Table 6 – Number of insects per trap hour by Order and percentage of all insects captured in Malaise traps in the Nantahala National Forest, NC May-August 2014-2015.

| Order | 2014 | | 2015 | |
|---|---|---|---|---|
| | Count | Percent | Count | Percent |
| Coleoptera | 0.62 | 2.8 | 1.07 | 3.3 |
| Collembola | 0.34 | 1.5 | 0.29 | 0.9 |
| Diptera | 18.01 | 79.8 | 22.86 | 71.1 |
| Ephemeroptera | <0.01 | 0 | 0.00 | 0.0 |
| Hemiptera | 0.86 | 3.8 | 2.19 | 6.8 |
| Hymenoptera | 0.96 | 4.2 | 1.84 | 5.7 |
| Lepidoptera | 1.32 | 5.8 | 2.44 | 7.6 |
| Mecoptera | 0.01 | <0.1 | <0.01 | <0.1 |
| Neuroptera | 0.04 | 0.2 | 0.07 | 0.2 |
| Odonata | 0.00 | 0.0 | <0.01 | <0.1 |
| Orthoptera | 0.04 | 0.2 | 0.06 | 0.2 |
| Plecoptera | 0.01 | <0.1 | 0.03 | 0.1 |
| Psocoptera | 0.07 | 0.3 | 0.17 | 0.5 |
| Thysanoptera | 0.29 | 1.3 | 1.11 | 3.4 |
| Trichoptera | 0.03 | 0.1 | 0.04 | 0.1 |

Table 7 – Pearson correlation coefficient and p-values for Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera abundance in the Nantahala National Forest, NC May-August 2014-2015. The upper value for each comparison is the Pearson correlation coefficient and the lower value is the *P*-value.

|  | Coleoptera | Diptera | Hemiptera | Hymenoptera | Lepidoptera |
|---|---|---|---|---|---|
| Coleoptera |  | 0.41 | 0.30 | 0.74 | 0.51 |
|  |  | <0.001 | <0.001 | <0.001 | <0.001 |
| Diptera | 0.41 |  | 0.70 | 0.40 | 0.55 |
|  | <0.001 |  | <0.001 | <0.001 | <0.001 |
| Hemiptera | 0.30 | 0.71 |  | 0.30 | 0.51 |
|  | <0.001 | <0.001 |  | <0.001 | <0.001 |
| Hymenoptera | 0.74 | 0.40 | 0.30 |  | 0.43 |
|  | <0.001 | <0.001 | <0.001 |  | <0.001 |
| Lepidoptera | 0.52 | 0.55 | 0.51 | 0.42 |  |
|  | <0.001 | <0.001 | <0.001 | <0.001 |  |

Table 8 – Mixed effects general linear model results for mean number of files removed by the noise and ID filters for calls collected in interior and edges of small, medium, and large forest openings in the Nantahala National Forest, NC May-August 2014-2015.

*Noise filter*

| Effect | Df | F | P | Coefficient |
|---|---|---|---|---|
| Size | 30.05 | 0.88 | 0.427 | - |
| Location | 58.44 | 0.00 | 0.962 | - |
| Size*location | 43.88 | 1.79 | 0.179 | - |
| Component 1 | 42.80 | 0.32 | 0.572 | -0.055 |
| Component 2 | 60.83 | 1.09 | 0.300 | 0.141 |
| Component 3 | 61.87 | 1.71 | 0.196 | -0.162 |
| Component 4 | 67.53 | 0.88 | 0.352 | -0.131 |
| Component 5 | 66.45 | 0.00 | 0.963 | 0.007 |
| Elevation | 40.30 | 1.90 | 0.176 | -0.001 |
| Water distance | 47.93 | 1.08 | 0.304 | -0.002 |
| Temperature | 273.00 | 38.98 | <0.001 | 0.104 |

*ID filter*

| Effect | Df | F | P | Coefficient |
|---|---|---|---|---|
| Size | 45.51 | 0.29 | 0.752 | - |
| Location | 59.48 | 2.84 | 0.097 | - |
| Size*location | 41.36 | 0.72 | 0.494 | - |
| Component 1 | 61.50 | 13.24 | 0.001 | -0.235 |
| Component 2 | 66.61 | 0.03 | 0.860 | -0.014 |
| Component 3 | 73.21 | 1.54 | 0.219 | -0.100 |
| Component 4 | 74.22 | 0.94 | 0.336 | 0.082 |
| Component 5 | 75.09 | 1.99 | 0.163 | 0.132 |
| Elevation | 45.25 | 2.30 | 0.137 | -0.001 |
| Water distance | 56.20 | 0.35 | 0.556 | -0.0008 |
| Temperature | 271.00 | 142.86 | <0.001 | 0.115 |

Table 9 – Overall bat activity per detector hour at the interior and edge of small, medium, and large openings in the Nantahala National Forest, NC May-August 2014-2015.

| Size | Total | | Interior | | Edge | |
|---|---|---|---|---|---|---|
| | 2014 | 2015 | 2014 | 2015 | 2014 | 2015 |
| Small | 5.23 | 8.42 | 4.75 | 7.59 | 5.64 | 9.32 |
| Medium | 1.87 | 3.15 | 1.73 | 1.88 | 1.97 | 4.41 |
| Large | 5.88 | 4.23 | 5.70 | 3.65 | 6.06 | 4.79 |

Table 10 – Results of mixed effects linear models for overall bat activity and species/species group activity at the interior and edge of small, medium, and large openings in the Nantahala National Forest, NC May-August 2014-2015.

| Effect | Df | F | P | Coefficient |
|---|---|---|---|---|
| *Overall* | | | | |
| Size | 43.75 | 0.44 | 0.648 | - |
| Location | 54.63 | 3.18 | 0.080 | - |
| Size*location | 37.01 | 1.43 | 0.253 | - |
| Component 1 | 59.35 | 21.74 | <0.001 | -0.290 |
| Component 2 | 63.45 | 1.99 | 0.164 | -0.104 |
| Component 3 | 69.98 | 2.67 | 0.107 | -0.122 |
| Component 4 | 71.04 | 2.40 | 0.1261 | 0.126 |
| Component 5 | 71.60 | 2.16 | 0.1462 | 0.133 |
| Elevation | 43.40 | 2.40 | 0.126 | -0.002 |
| Water distance | 54.52 | 0.21 | 0.650 | 0.0006 |
| Temperature | 154.00 | 97.77 | <0.001 | 0.108 |
| Insect abundance | 154.00 | 1.76 | 0.187 | 0.0009 |
| *Big brown/silver-haired bats* | | | | |
| Size | 31.64 | 0.96 | 0.394 | - |
| Location | 55.98 | 0.01 | 0.926 | - |
| Size*locaton | 38.27 | 1.23 | 0.303 | - |
| Component 1 | 58.74 | 5.71 | 0.020 | -0.291 |
| Component 2 | 57.98 | 5.71 | 0.033 | -0.326 |
| Component 3 | 48.62 | 0.49 | 0.486 | 0.093 |
| Component 4 | 75.99 | 0.19 | 0.662 | 0.071 |
| Component 5 | 70.62 | 0.04 | 0.844 | 0.034 |
| Elevation | 48.66 | 4.11 | 0.048 | -0.002 |
| Water distance | 60.39 | 0.51 | 0.479 | 0.002 |
| Temperature | 154.00 | 12.85 | <0.001 | -0.093 |
| Insect abundance | 154.00 | 0.45 | 0.502 | 0.002 |

*Eastern red/evening bats*

| | | | | |
|---|---|---|---|---|
| Size | 32.35 | 0.62 | 0.546 | - |
| Location | 56.71 | 2.16 | 0.147 | - |
| Size*location | 38.07 | 2.87 | 0.069 | - |
| Component 1 | 53.35 | 15.34 | <0.001 | -0.412 |
| Component 2 | 61.33 | 1.19 | 0.279 | -0.149 |
| Component 3 | 81.60 | 7.57 | 0.007 | -0.360 |
| Component 4 | 70.85 | 0.27 | 0.6073 | 0.072 |
| Component 5 | 72.95 | 0.39 | 0.536 | 0.095 |
| Elevation | 46.91 | 10.00 | 0.003 | -0.003 |
| Water distance | 50.87 | 0.12 | 0.730 | 0.0008 |
| Temperature | 154.00 | 94.38 | <0.001 | 0.244 |
| Insect abundance | 154.00 | 2.09 | 0.150 | -0.002 |

*Hoary bat*

| | | | | |
|---|---|---|---|---|
| Size | 103.6 | 0.07 | 0.936 | - |
| Location | 24.41 | 0.03 | 0.857 | - |
| Size*location | 21.43 | 0.08 | 0.923 | - |
| Component 1 | 100.60 | 0.78 | 0.381 | -0.670 |
| Component 2 | 37.19 | 1.24 | 0.272 | -0.838 |
| Component 3 | 51.90 | 0.18 | 0.674 | -0.726 |
| Component 4 | 39.85 | 0.76 | 0.390 | -0.726 |
| Component 5 | 68.77 | 1.54 | 0.218 | 1.074 |
| Elevation | 74.12 | 0.73 | 0.395 | 0.004 |
| Water distance | 95.52 | 0.54 | 0.463 | -0.010 |
| Temperature | 154.00 | 0.08 | 0.774 | -0.051 |
| Insect abundance | 52.30 | 6.20 | 0.016 | 0.026 |

*Myotis* spp.

| | | | | |
|---|---|---|---|---|
| Size | 40.46 | 0.08 | 0.924 | - |
| Location | 87.64 | 1.71 | 0.195 | - |
| Size*location | 52.34 | 0.79 | 0.458 | - |
| Component 1 | 49.94 | 0.54 | 0.464 | -0.121 |
| Component 2 | 52.39 | 0.03 | 0.869 | -0.035 |
| Component 3 | 40.88 | 3.80 | 0.058 | 0.415 |
| Component 4 | 48.65 | 1.96 | 0.168 | 0.317 |
| Component 5 | 64.04 | 0.52 | 0.472 | 0.191 |
| Elevation | 57.41 | 0.17 | 0.681 | 0.0006 |
| Water distance | 68.98 | 1.21 | 0.274 | -0.005 |
| Temperature | 154.00 | 0.84 | 0.360 | -0.073 |
| Insect abundance | 154.00 | 1.07 | 0.303 | -0.006 |

*Tri-colored bat*

| | | | | |
|---|---|---|---|---|
| Size | 36.05 | 0.37 | 0.692 | - |
| Location | 54.44 | 0.32 | 0.576 | - |
| Size*location | 37.34 | 1.84 | 0.174 | - |
| Component 1 | 58.56 | 0.57 | 0.452 | -0.112 |
| Component 2 | 62.41 | 2.09 | 0.153 | -0.248 |
| Component 3 | 72.71 | 0.73 | 0.394 | 0.155 |
| Component 4 | 68.60 | 0.78 | 0.380 | 0.173 |
| Component 5 | 104.00 | 1.45 | 0.232 | -0.348 |
| Elevation | 61.30 | 2.50 | 0.119 | -0.004 |
| Water distance | 46.95 | 1.91 | 0.174 | -0.005 |
| Temperature | 154.00 | 84.33 | <0.001 | 0.400 |
| Insect abundance | 154.00 | 1.07 | 0.302 | 0.001 |

Table 11 – Total number of calls per detector hour by species group and year as well as percentage of calls identified to species from bat detectors placed in small, medium, and large forest openings in the Nantahala National Forest, NC May-August 2014-2015.

| Species | 2014 | | 2015 | |
|---|---|---|---|---|
| | Passes | Percent | Passes | Percent |
| Big brown/silver-haired | 1.08 | 49.8% | 0.86 | 33.2% |
| Eastern red/evening | 0.50 | 23.1% | 1.13 | 43.7% |
| Hoary | 0.03 | 1.6% | 0.03 | 1.2% |
| *Myotis* spp. | 0.04 | 1.7% | 0.03 | 1.0% |
| Tri-colored | 0.52 | 23.8% | 0.54 | 20.8% |

Table 12 –Significant interactions for eastern red bat activity in forest openings in the Nantahala National Forest, NC May-August 2014-2015.

| Interaction effect | Estimate | df | t | p |
|---|---|---|---|---|
| Large interior, medium edge | -0.8681 | 50.15 | -1.92 | 0.060 |
| Medium interior, medium edge | -1.036 | 50.55 | -2.72 | 0.009 |
| Medium edge, small interior | 0.952 | 46.20 | 1.87 | 0.067 |
| Medium interior, small edge | 1.033 | 43.67 | 2.06 | 0.045 |

Table 13 – Mean bat species richness at the interior and edge of small, medium, and large openings in the Nantahala National Forest, NC May-August 2014-2015.

| Size | Total | | Interior | | Edge | |
|---|---|---|---|---|---|---|
| | 2014 | 2015 | 2014 | 2015 | 2014 | 2015 |
| Small | 2.7 | 2.9 | 2.4 | 2.7 | 3.0 | 3.0 |
| Medium | 1.8 | 2.0 | 1.6 | 1.9 | 1.9 | 2.1 |
| Large | 2.2 | 2.4 | 2.4 | 2.3 | 2.0 | 2.6 |

Table 14 – Results of mixed effects general linear models for species richness   recorded in small, medium, and large forest openings in the Nantahala National Forest, NC May-August 2014-2015.

| Effect | DF | F | P | Coefficient | Odds Ratio |
|---|---|---|---|---|---|
| Size | 32.78 | 0.34 | 0.715 | - | - |
| Location | 153.00 | 1.30 | 0.255 | - | - |
| Size*location | 153.00 | 0.61 | 0.547 | - | - |
| Component 1 | 57.08 | 2.90 | 0.094 | 0.278 | 1.321 |
| Component 2 | 46.75 | 2.40 | 0.128 | 0.301 | 1.351 |
| Component 3 | 107.00 | 0.62 | 0.434 | -0.177 | 0.838 |
| Component 4 | 79.92 | 0.13 | 0.716 | 0.077 | 1.080 |
| Component 5 | 65.45 | 0.35 | 0.558 | -0.134 | 0.874 |
| Elevation | 28.80 | 1.09 | 0.305 | 0.001 | 1.001 |
| Distance to water | 43.55 | 2.73 | 0.106 | 0.006 | 1.006 |
| Temperature | 78.32 | 8.69 | 0.004 | -0.260 | 0.771 |
| Insect abundance | 153.00 | 1.79 | 0.183 | -0.013 | 0.987 |

FIGURES

Figure 1 – Map of the Nantahala National Forest Cheoah Ranger District, Graham County, NC. The Cheoah Ranger Districted is in the southern Appalachian Mountains adjacent to the Great Smoky Mountain National Park. Black dots indicate the location of openings sampled.
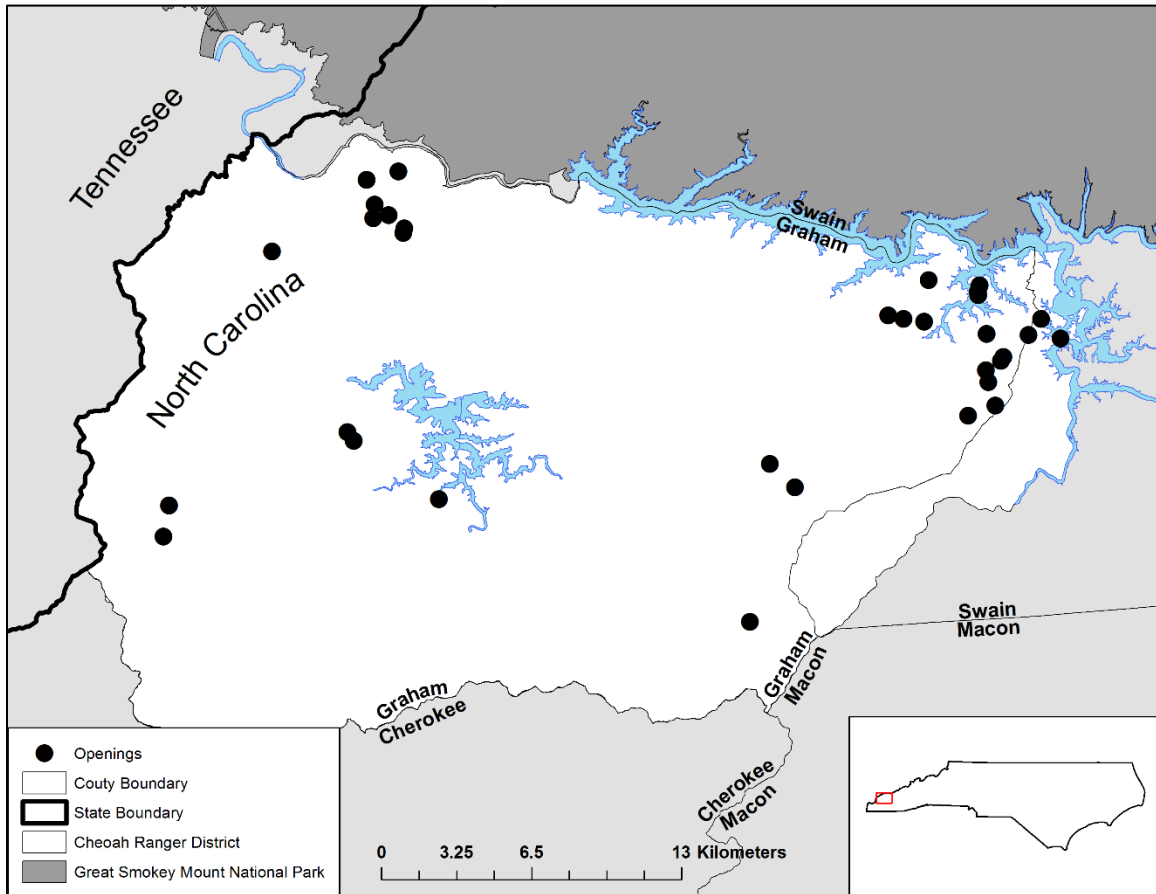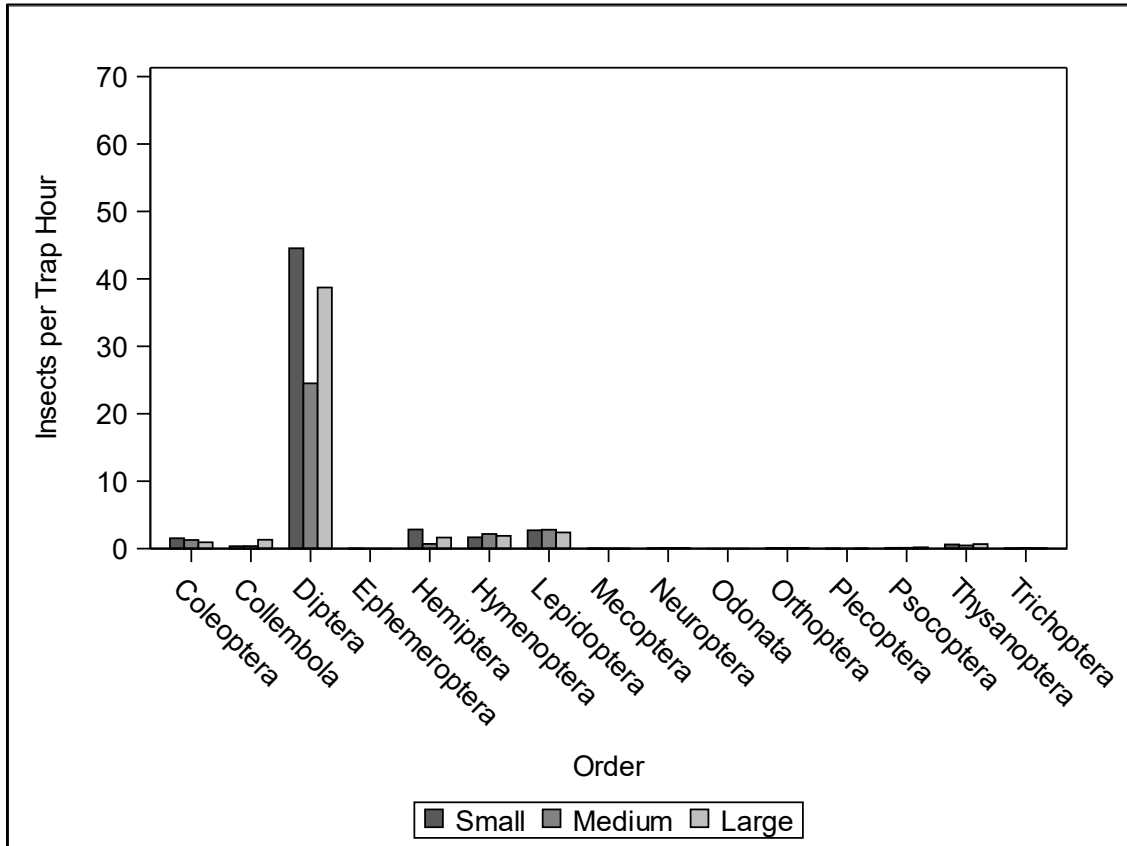
Figure 2 – Number of insects per trap hour collected in small, medium, and large forest openings in the Nantahala National Forest, NC in (a) June-August 2014 and (b) May-August 2015.
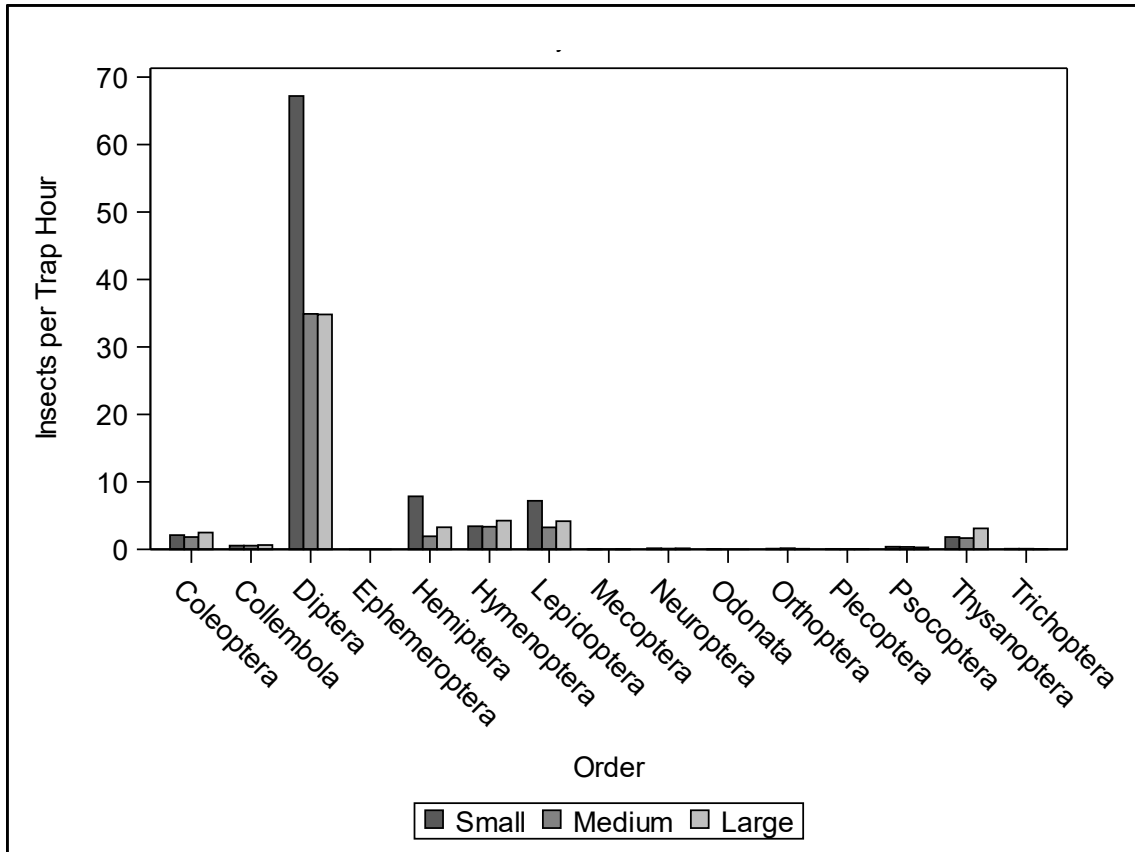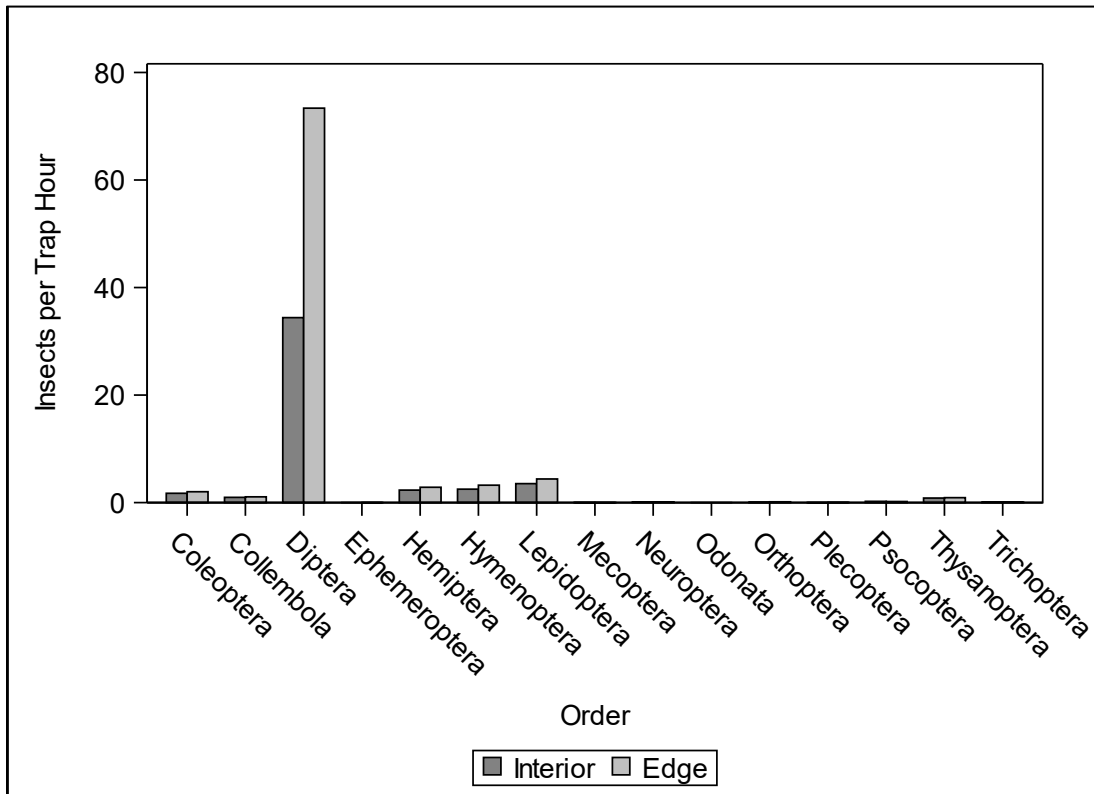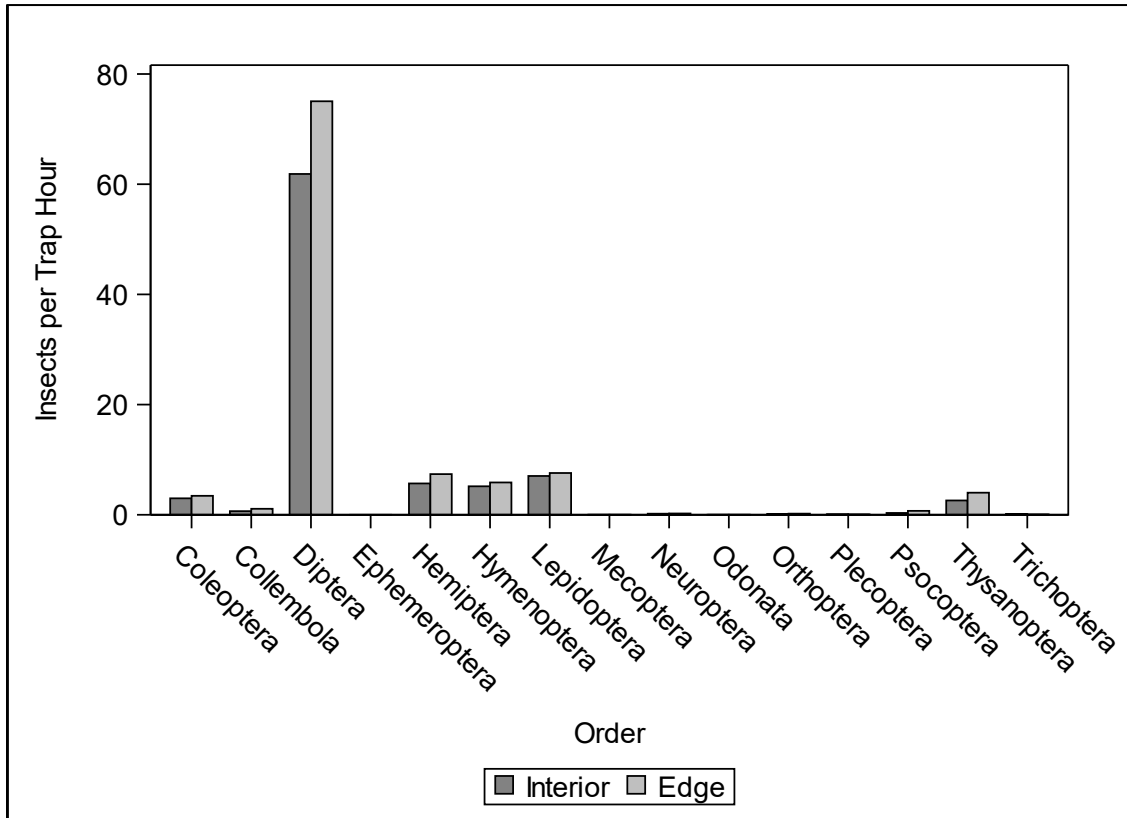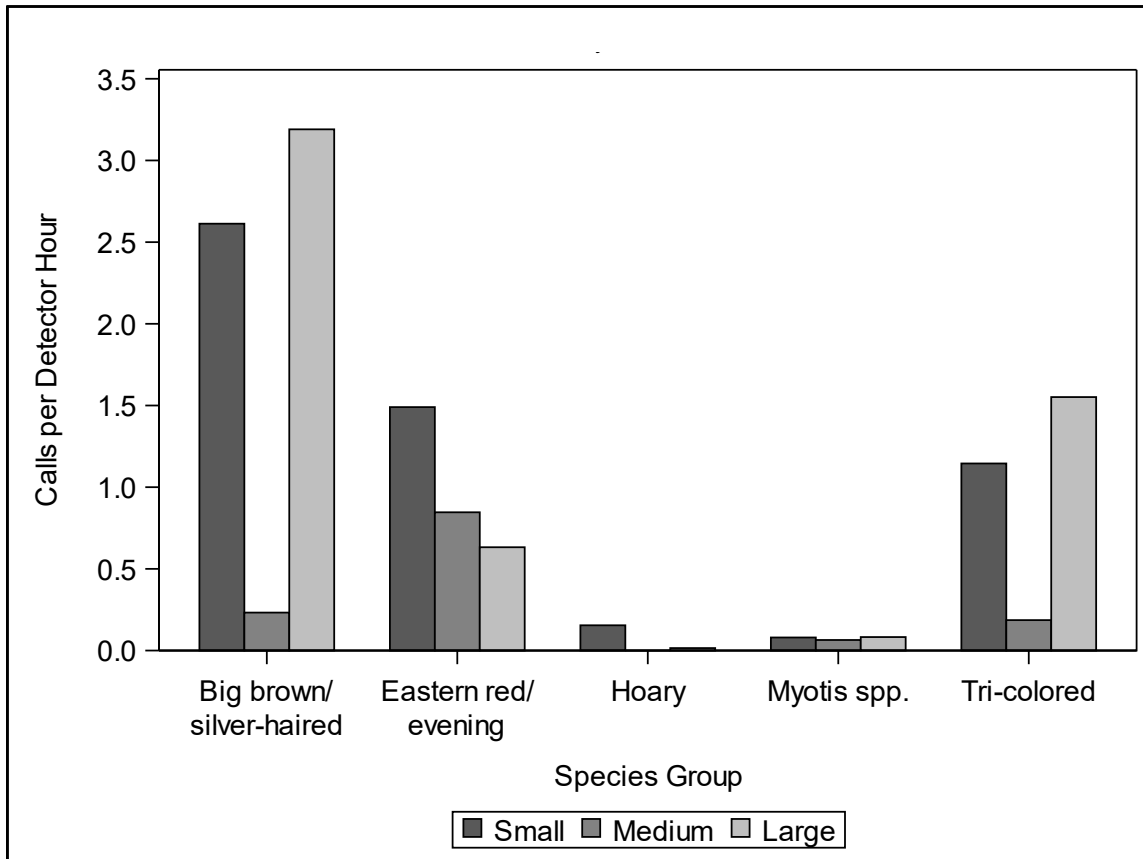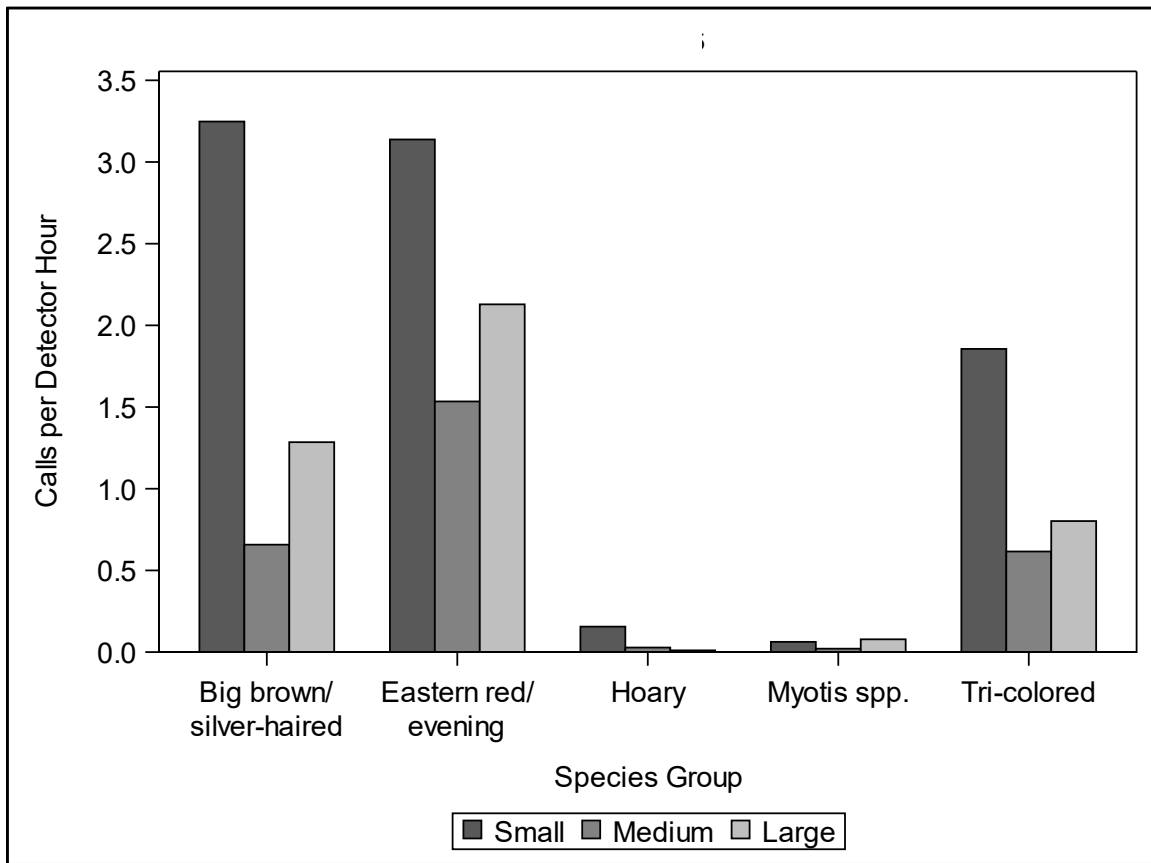
a)

b)

Figure 3 – Number of insects per trap hour collected at the edges and interiors of forest openings in the Nantahala National Forest, NC in (a) June-August 2014 and (b) May-August 2015.

a)

b)

Figure 4 – Number of bat passes per detector hour recorded in small, medium, and large forest openings in the Nantahala National Forest, NC (a) June-August 2014 and (b) May-August 2015.
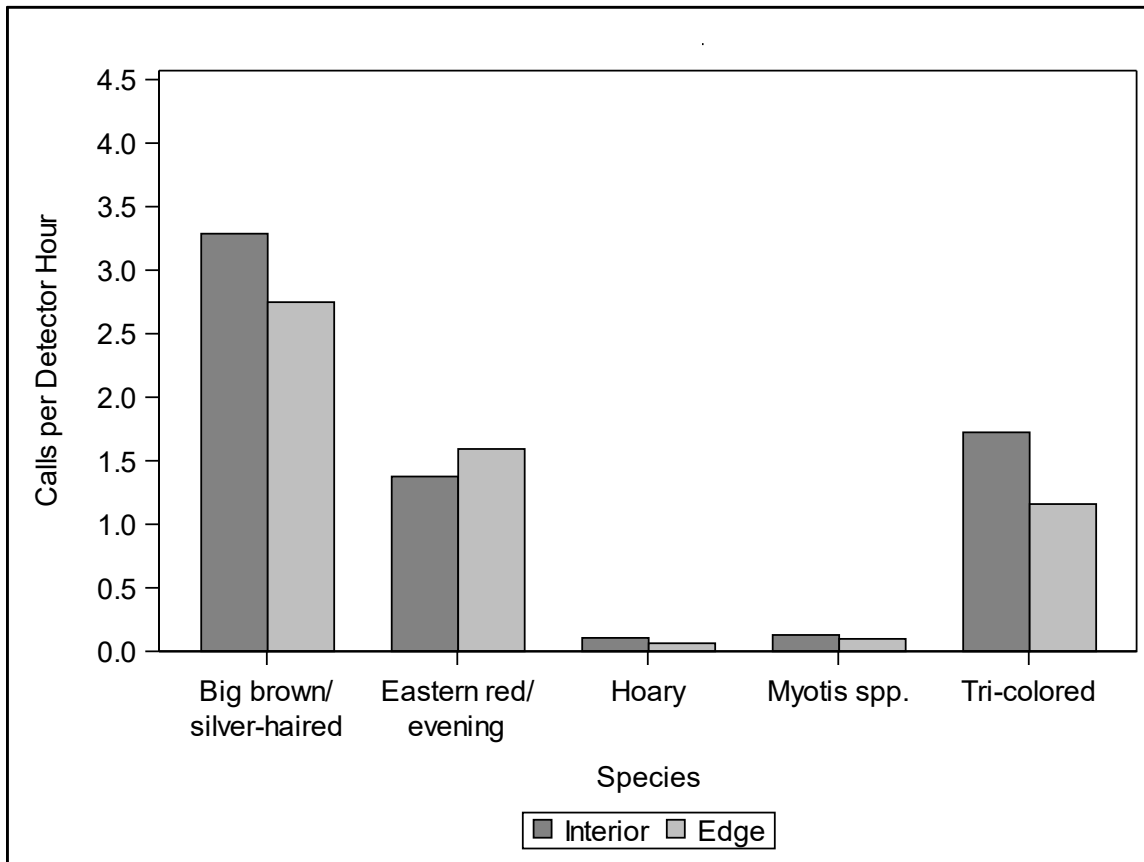
a)

b)

Figure 5 – Number of passes per detector hour collected at the interior and edge of forest openings in the Nantahala National Forest, NC in (a) June-August 2014 and (b) May-August 2015.
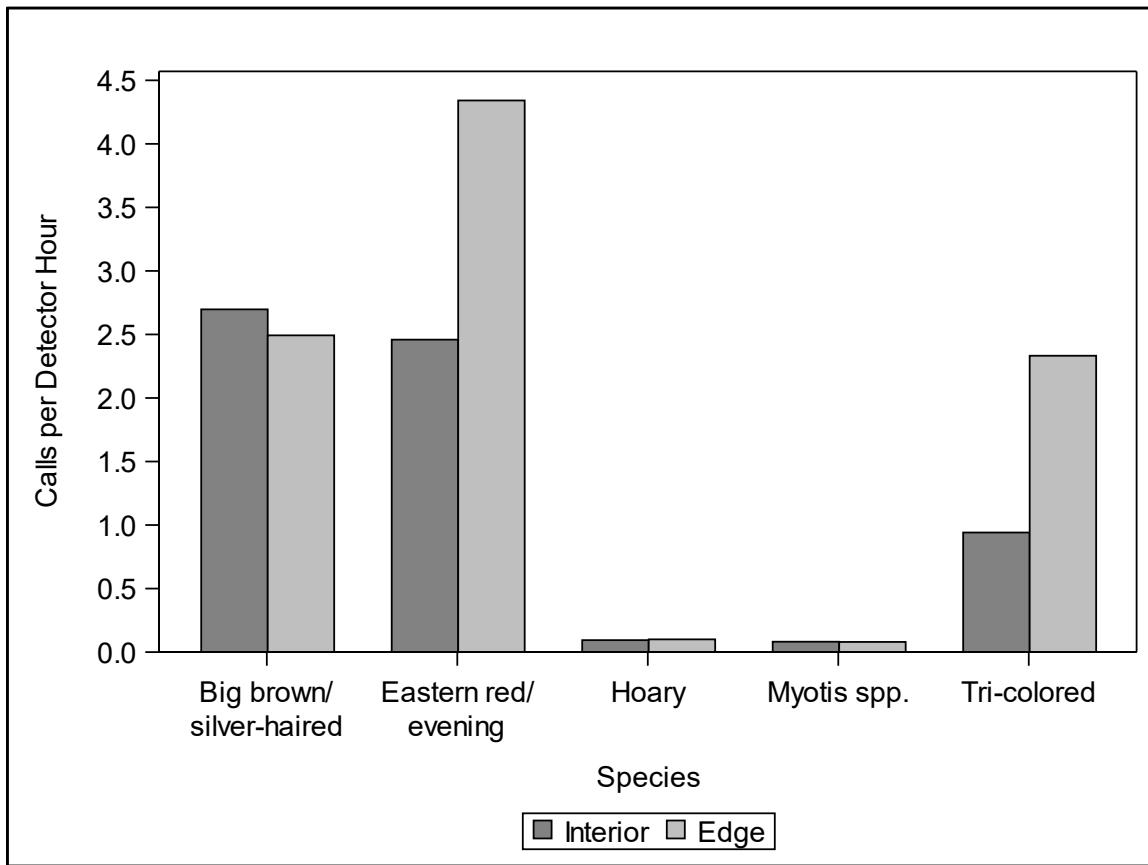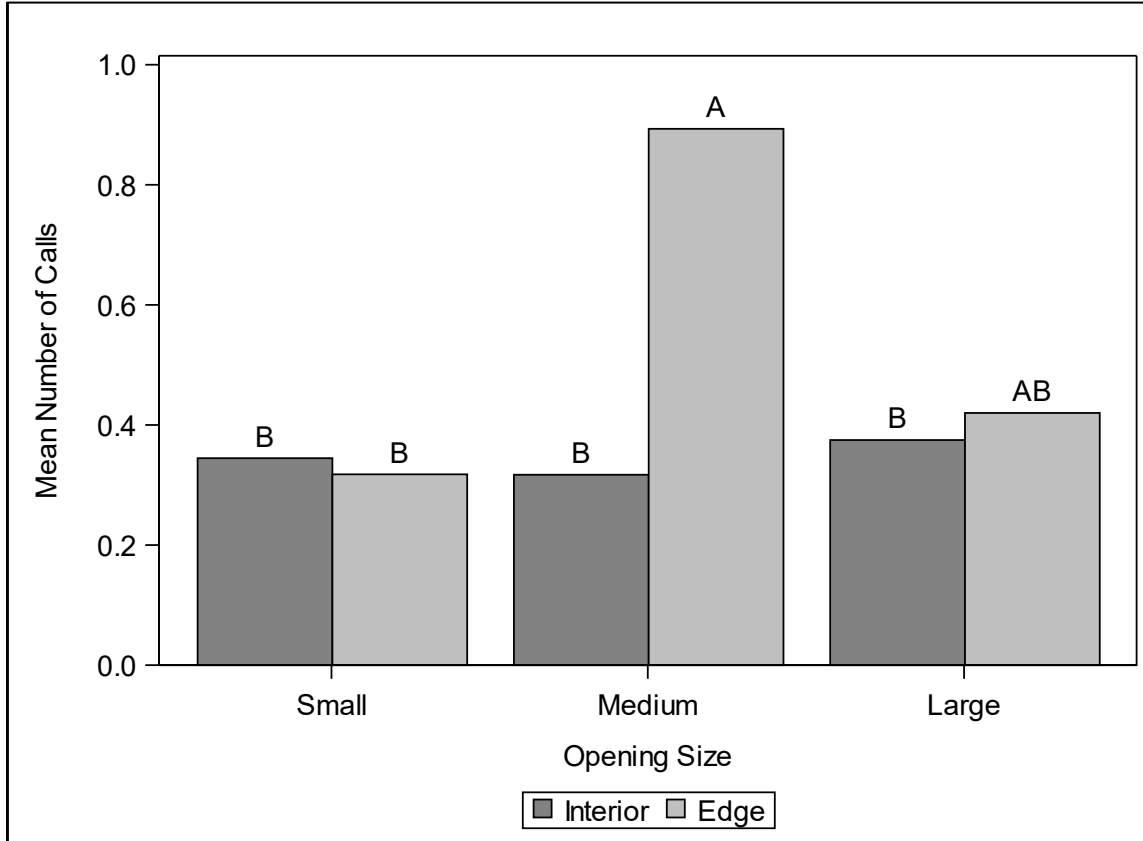
a)

b)

Figure 6 – Mean number of eastern red/evening bat passes by opening size and location within opening in the Nantahala National Forest, NC May-August 2014-2015. Bars with different letters are significantly different (α=0.10).

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