EFFECTS OF VARIATIONS IN TREE CANOPY OPENNESS, PREY ABUNDANCE, AND ABIOTIC FACTORS ON BAT ACTIVITY IN THE NANTAHALA NATIONAL FOREST

A thesis presented to the faculty of the Graduate School of
Western Carolina University in partial fulfillment of the
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ABSTRACT

EFFECTS OF VARIATIONS IN TREE CANOPY OPENNESS, PREY ABUNDANCE, AND ABIOTIC FACTORS ON BAT ACTIVITY IN THE NANTAHALA NATIONAL FOREST

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Western Carolina University (December 2018)

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Early successional habitat is known to be a source of foraging habitat for bats, and studies have shown that bat activity is higher in disturbed and open vegetation structures. This study analyzed the importance of early successional habitat, created by forest management activities, on bat foraging behavior in the mixed hardwood forest of the Nantahala National Forest Cheoah Ranger District, Graham County, North Carolina. The objective was to determine the effects of variations in forest canopy opening aggregation (aggregated or dispersed) on bat foraging habitat selection. I hypothesized that 1) bat activity would be higher in dispersed canopy openings, 2) open-adapted bats would be more active in opening interior, while clutter-adapted bats would be more active in forest interior between openings, 3) bat activity would be positively correlated with prey abundance, 4) bat activity would be higher above the tree canopy than below at site centers, and 5) bat activity would be negatively correlated with elevation. Simultaneous samples were collected via Anabat SD2 (Titley Scientific, Columbia, MO) acoustical bat detectors from two canopy opening treatments, one aggregated and one dispersed. Results suggest that 1) both clutter and open adapted bats were more active in dispersed openings and within openings compared to the forest corridors between them; 2) bats are equally active above and below the canopy; 3) activity is positively correlated with prey abundance, specifically with Lepidoptera, Diptera, and Coleoptera; and 4) activity is negatively correlated with increasing elevation. These results provide information for better forest management applications to improve bat foraging habitat. For example, this study demonstrates that dispersed canopy openings may provide better foraging habitat than aggregated openings for both open-adapted and clutter-adapted bat species.

CHAPTER 1: INTRODUCTION

Natural or anthropogenic disturbances that cause loss of forest canopy create early successional habitat (ESH). Many species of plants and animals depend on ESH; for example, Collins and Pickett (1987) demonstrated that shade intolerant plant species grow better in areas of recent disturbance, Stoleson (2013) demonstrated that certain bird species use ESH as post-breeding habitat, and Grindal and Brigham (1997) demonstrated that bats use ESH as foraging habitat. Interest in ESH management has risen in recent years due to the decline in ESH caused by farmland abandonment, as well as shifts in forest management practices caused by public opposition to forest clear-cuts (Askins 2001). Timber harvest is one of the most effective ways to create early successional habitats in managed forest ecosystems; however, in order to restore biodiversity, it is important that we understand the factors that contribute to suitability of ESH (Thompson and DeGraaf 2001). For example, this study explores how aspects of timber harvest management such as size and aggregation influence bat foraging activity.

Forestry and logging influence bat roosting sites and foraging habitat (Hayes 2003). To date, research on forest-dwelling bats has focused predominantly on characterizing roosts and roost-switching behavior (Lacki et al. 2001). Foraging has been studied less often, even though it is presumed that prey selection is one of the primary driving factors of bat activity (Agosta et al. 2003). Early successional habitat created by forest management activities is known to be foraging habitat for bats; activity is higher in disturbed and open vegetation than in adjacent mature forest (Loeb and O’Keefe 2006). Both vertical and horizontal edges of forests are important sites for foraging (Menzel et al. 2005; Hayes and Gruver 2000; Kalcounis et al. 1999), although foraging preference also is related to certain tree species and forest openness

(Kalcounis et al. 1999). In addition, forest corridors connecting suitable habitats are valuable for some species of bats (Murray and Kurta 2004; Verboom and Spoelstra 1999).

Differences in maneuverability and ability to detect and avoid clutter can influence a bat's ability to exploit habitats (Kalcounis et al. 1999). In general, bats with small bodies and low wing aspect ratios are better adapted for maneuvering in higher levels of clutter than bats with large bodies and high wing aspect ratios. Species with high wing aspect ratios, high wing loads, and low frequency, narrow-band echolocation calls (open-adapted bats) tend to forage in more open environments (Norgerg and Rayner 1987). In the Southern Appalachians, these include big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and silver haired bats (*Lasionycteris noctivagans*). Species with low wing aspect ratios, low wing loads, and high frequency, broad-band echolocation calls (clutter-adapted bats) tend to forage in more cluttered environments; in the Southern Appalachians these include species in the genus *Myotis*, tri-colored bats (*Perimyotis subflavus*), and evening bats (*Nycticeius humeralis*) (Norgerg and Rayner 1987).

Prey abundances can also be influenced by forest canopy disturbance, and can drive bat activity in specific environments and influence dietary selection (Didham et al. 1996). Diets of many species vary both seasonally and geographically, which is not surprising considering the morphological variation among bat species (Brigham and Saunders 1990). In North America, almost all species are insectivorous, feeding on multiple orders of insects. One question is whether foraging is opportunistic or selective; however, due to the difficulty and limitations of sampling methods for prey there are few prey-selection studies (Whitaker 1994). Swift et al. (1985) determined that bat diets consist mainly of Diptera (Nematocera) and Trichoptera. Other research has shown that big brown bats and evening bats tend to have diets high in coleopterans, long-eared bats (*Corynorhinus* spp.) have diets high in lepidopterans, and species of *Myotis* have diets with high concentrations of dipterans (Whitaker 1988).

Proximity to abiotic resources may also play a role in bat roosting and foraging habitat. For example, Evelyn et al. (2004) suggest that bats are more likely to roost in areas closer to water. Elevation, as well as changes in temperature, also influences bat activity, as bats move to areas that minimize thermoregulatory costs. Other factors such as cloud cover and wind strength have been shown to influence bat activity (Verboom and Spoelstra 1999).

In this study, I analyzed how logging and the subsequent creation of early successional habitat (ESH) influence bat activity. Forest dwelling animals such as bats may depend on ESH for shelter or food, and thus depend on canopy disturbances that produce openings of shrubland or thicket habitat (Litvaitis et. al. 1999; Askins, 2001). Some bat species avoid areas of high structural complexity; therefore, bats may forage in canopy openings where maneuverability is easier (Brigham et. al. 1997). Furthermore, proximity and size of ESH may influence habitat use by bats (Hunter et. al. 2001). I aimed to compare bat activity between aggregated (ESH that is close to other ESH) and dispersed (ESH that is farther away from other ESH) canopy openings created by forest management to determine optimal foraging habitat for both open-adapted and clutter-adapted bat species. I hypothesized: 1) bat activity would be greatest in dispersed openings when compared to aggregated openings, due to the increased potential foraging habitat created between mature forests and early successional habitat; 2) open-adapted bats would be most active in opening interiors, and clutter-adapted bats would be most active in forests between openings; 3) open-adapted bats would be most active above the canopy in forest interiors between openings, and clutter-adapted bats would be most active below the canopy in forest interiors between openings; 4) bat activity would be positively correlated with prey abundance; and 5) bat activity would be negatively correlated with increasing elevation and positively correlated with mean nightly temperatures. This research will provide information for better forest management applications to improve bat foraging habitat; specifically, how canopy opening aggregation influences bat foraging habitat.

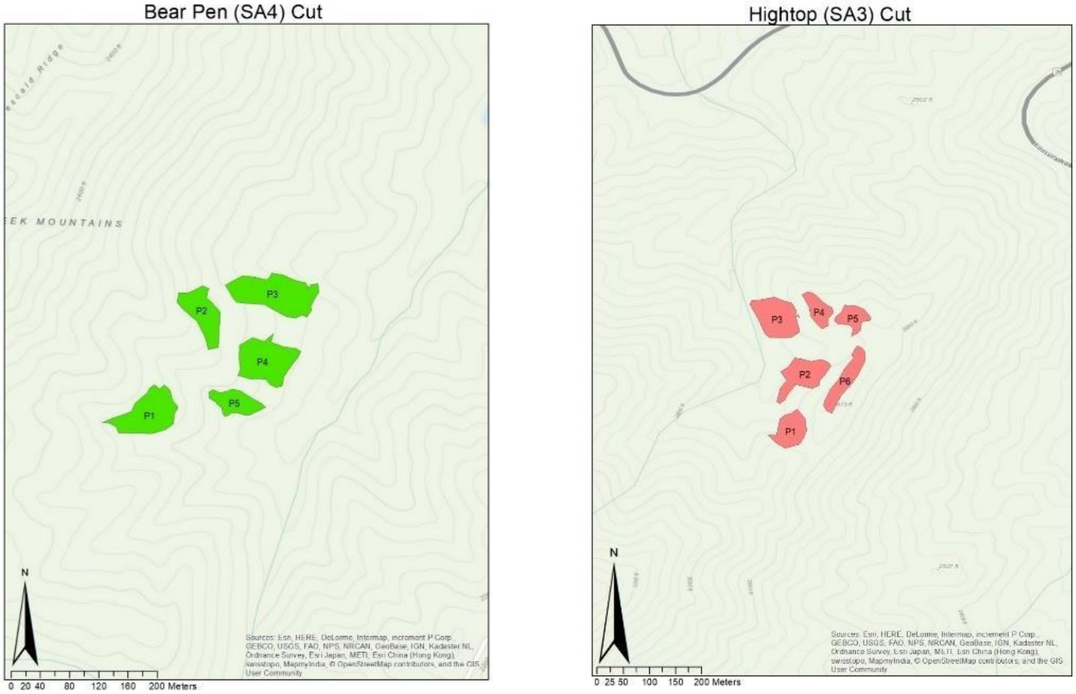
CHAPTER 2: METHODS

Study Area

The study took place near Fontana Lake in the Nantahala National Forest Cheoah Ranger District, Graham County, North Carolina. Sampling was conducted from May 22nd, 2017 to August 4th, 2017 in four sites, each containing five one-acre openings, near Round Mountain Gap (Latitude: 35.435100 Longitude: -83.783271). Openings in two sites were aggregated (SA3, SA4; Figure 1), and openings in two sites were dispersed (SD1, SD3; Figure 2). All twenty openings were created before sampling began by cutting timber to one foot above ground and leaving it lay. The size of each forest opening was mapped using a Trimble GPS unit to determine area and distance from opening center to nearest opening center (Table 1). The forest type at the study site is mixed hardwood interspersed with pine stands, characterized by ridge and valley topography, and includes the common tree species *Quercus, Acer, Liriodendron, Carya,* and *Pinus.* Elevation in the Cheoah Ranger District ranges from 530 meters to 1,658 meters. Maximum elevation at Round Mountain Gap is 781 meters.

Table 1. Elevation and area for sample locations. “SD” and “SA” within Cut ID represent either a dispersed or aggregate site, with the following number representing from which site the sample was taken. “P’ or “F” represents either a patch or forest sample location, with the following number representing from which patch or forest the sample was taken. “CC” or “SC” represents either a canopy center or site center sample location within its respective site. For example, Cut ID SD1P1 is dispersed site 1 patch 1.

Dispersed Cut ID	Elevation (m)	Area (m^2)	Aggregate Cut ID	Elevation (m)	Area (m^2)
SD1P1	604.4	4178.4	SA4P1	631.7	3790.3
SD1P2	611.7	4246.9	SA4P2	631.5	1519.1
SD1P3	576.6	4195.8	SA4P3	595.8	4947.0
SD1P4	590.3	4203.2	SA4P4	598.6	3933.8
SD1P5	592.6	4136.5	SA4P5	596.2	1752.3
SD1F1	596.5	4653.9	SA4F1	645.3	4158.7
SD1F2	580.9	2985.2	SA4F2	613.3	959.4
SD1F3	608.4	5419.4	SA4F3	596.8	4231.4
SD1F4	603.2	2485.7	SA4F4	597.1	1461.8
SD1F5	622.4	3566.6	SA4F5	610.5	2673.9
SD1SC	601.4	12664.6	SA4SC	620.9	5459.8
SD1CC	601.4	12664.6	SA4CC	620.9	5459.8
SD3P1	649.0	4097.1	SA3P1	854.0	2683.5
SD3P2	623.0	4222.7	SA3P2	843.4	3557.7
SD3P3	618.0	4633.7	SA3P3	833.3	4329.7
SD3P4	606.6	4649.2	SA3P4	856.7	1762.8
SD3P5	611.1	4115.3	SA3P5	861.4	1755.5
SD3F1	618.7	5044.0	SA3F1	850.1	1899.7
SD3F2	624.8	11565.9	SA3F2	861.7	1286.0
SD3F3	616.9	5167.9	SA3F3	857.4	1027.4
SD3F4	606.9	1165.0	SA3F4	859.5	1877.1
SD3F5	618.4	1002.8	SA3F5	832.7	3062.8
SD3SC	635.2	12729.0	SA3SC	844.3	3803.4
SD3CC	635.2	12729.0	SA3CC	844.3	3803.4



Bear Pen (SA4) Cut

Hightop (SA3) Cut

Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

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Figure 1. Map of aggregate site SA4 representing openings 1-5 (Inter-opening distance is 19.1m to 44.3m), and site SA3 representing openings 1-6 (Inter-opening distance is 7.9m to 19.1m) At this site a 6th opening was mistakenly cut, therefore opening P1 was not used, and P6 was used as P1.

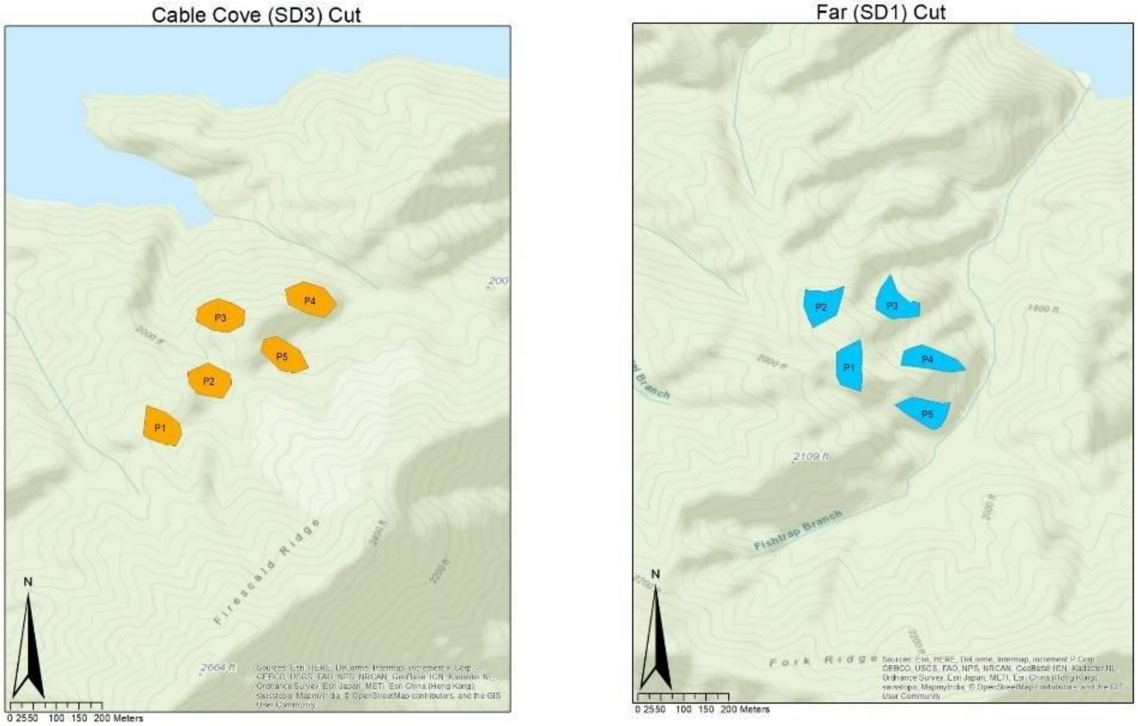

Figure 2. Map of dispersed site SD3 representing openings 1-5 (Inter-opening distance is 48.0m to 73.0m) and dispersed site SD1 representing openings 1-5 (Inter-opening distance is 61.1m to 67.6m).

Bat Acoustical Sampling

Twenty forest openings and twenty forest-between-openings were sampled May-August 2017 (Figure 1 & Figure 2). Sample locations were randomized and samples were taken simultaneously for half of two opening treatments, one aggregated and one dispersed, over three consecutive nights, using ten Anabat SD2 (Titley Scientific, Columbia, MO) acoustical bat detectors. These ultrasonic detectors have proven valuable for monitoring echolocation calls and can provide information on when and where bats are most active (Russo and Jones 2003). Acoustic surveying was conducted at the center of the openings and the center of the intact forest between openings for five locations at each aggregated and dispersed site (Figure 3). After the three-night sampling period, all Anabats were moved to the other half of both sites for additional sampling, before moving on to sample other sites. Additionally, at one of the site centers, Anabats were placed both above and below the tree canopy for comparison between ground level and canopy surveys. After the three-day sampling period, the canopy Anabat was moved to the center of the other site, either aggregated or dispersed, at the start of the second sampling period. This process was repeated for each aggregated/dispersed pair of research sites.

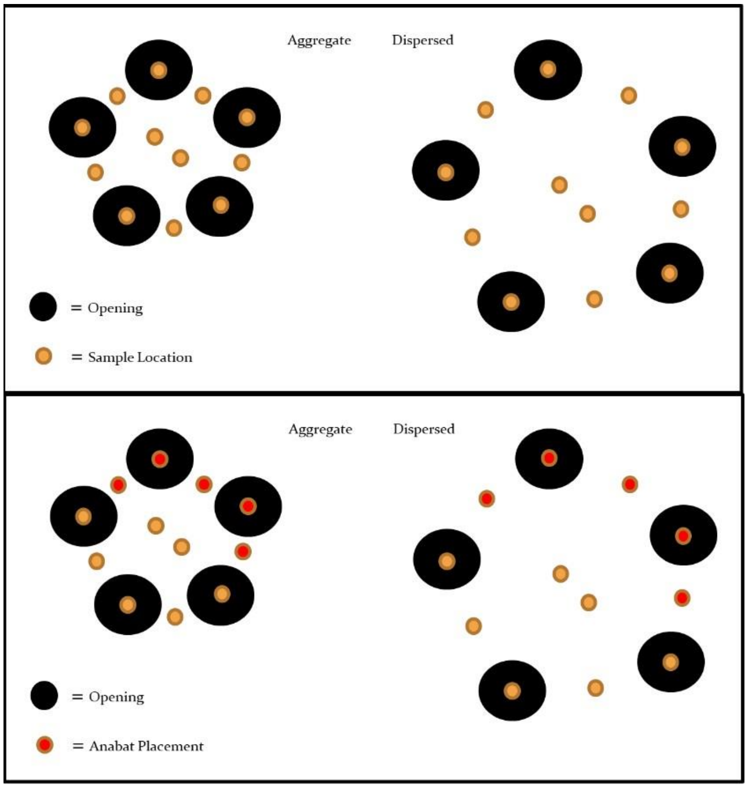

Figure 3. Aggregate and Dispersed site setup (top) and example of Anabat placement (bottom). Sample locations for Anabats were chosen at random. After three nights of sampling Anabats were moved to the remaining sample locations. Locations in the center of sites were either ground level or canopy level.

The Anabat microphone was housed in a PVC coupling and a 3.8 cm swept-45° PVC elbow attached atop a pole 1.8m from the ground. The opening of the elbow was angled 45° above horizontal and the microphone was attached via 1.83m cable to the recording device housed in a waterproof container at the base of the pole. For opening interior and ground level forest interior, the microphone was 1.83m from the ground. For forest canopy, the microphone was 18.3m above the ground via a telescoping fiberglass pole. Each detector was programmed to begin recording 15 minutes prior to sunset and stop recording 15 minutes after sunrise.

Prey Abundance Sampling

For each recording night, prey abundance data were collected via Malaise traps. As previous research has found varying degrees of correlation between bat activity and insect abundance (Grindal & Brigham 1998), and prey abundance surveys are time-consuming, insects collected from this survey were identified to Order. Three Malaise traps were paired at random with three Anabats for both an aggregate and dispersed site during sampling periods, placed 1m from the base of the Anabat. The traps were set out 15 minutes before sunset and collected 15 minutes after sunrise each recording day. Because all traps could not be set nor collected within the 15-minute window, the order in which traps were set or collected was randomized for each sampling day. An LED was placed above the trap and illuminated at the start of the collection time. All insects were trapped in a solution of 70% ethanol. Upon collection, all insects were identified to Order. For Diptera, Lepidoptera, Hemiptera, Hymenoptera, and Coleoptera, dry mass was measured, and insects were dried in a fume hood until there was no recorded change in weight.

Abiotic Factors

The amount of edge and area of forest openings were mapped using a Trimble ProXH GPS unit (ESRI ArcPad 7.01). Snags were quantified within a 30m radius of each detector, noting percent cover of remaining bark, the condition of bark, and any openings within the snag that may be a potential roosting site. GPS data were loaded into ArcGIS 10.5.1 (ESRI 2011), and distance from opening center to nearest opening center, elevation, and area for each opening were extracted. Percent canopy cover was estimated at each sampling location using a camera with fish-eye lens and Gap Light Analyzer software (Frazer et al. 1999). Average nightly temperatures and average nightly precipitation were recorded from the closest weather station located at Fontana Dam (Table 2).

Table 2. Abiotic Factors for Aggregate and Dispersed Sites

Cut ID	% Canopy Cover	Snags	% Bark	Openings	Precipitation	Temp Low
SD1P1	84.9	2	98	2	0.14	62
SD1P2	96.6	6	79	3	0.06	56
SD1P3	65.3	0	0	0	0.06	56
SD1P4	94.2	1	95	11	0.14	62
SD1P5	79.2	10	88	4	0.14	62
SD1F1	17.4	2	43	2	0.14	62
SD1F2	20.6	1	95	0	0.06	56
SD1F3	16.5	0	0	0	0.06	56
SD1F4	30.4	2	98	1	0.14	62
SD1F5	17.7	9	87	2	0.14	62
SD1SC	16.4	2	48	0	0.06	56
SD1CC	16.4	2	48	0	0.06	56
SD3P1	84.5	4	93	18	0	51
SD3P2	99.0	11	56	6	0.34	60
SD3P3	99.0	4	48	4	0.04	53
SD3P4	61.1	2	98	7	0	51
SD3P5	94.9	3	12	14	0.34	60
SD3F1	20.0	7	96	3	0.04	53

SD3F2	20.2	5	85	2	0.04	53
SD3F3	19.5	10	49	15	0	51
SD3F4	20.1	5	73	14	0.04	53
SD3F5	24.7	15	71	2	0.34	60
SD3SC	22.4	0	0	0	0.04	53
SD3CC	22.4	0	0	0	0.04	53
SA4P1	89.6	0	0	0	0	51
SA4P2	85.6	3	68	3	0.04	53
SA4P3	81.9	1	80	1	0.04	53
SA4P4	96.6	1	50	7	0.34	60
SA4P5	90.6	7	47	2	0.04	53
SA4F1	14.7	1	80	1	0	51
SA4F2	38.6	2	55	15	0.34	60
SA4F3	14.1	0	0	0	0.04	53
SA4F4	23.1	2	63	2	0.34	60
SA4F5	17.0	5	95	10	0.04	53
SA4SC	37.7	4	90	1	0	51
SA4CC	37.7	4	90	1	0	51
SA3P1	98.5	1	95	1	0.14	62
SA3P2	23.1	3	68	3	0.06	56
SA3P3	96.8	8	31	10	0.06	56
SA3P4	96.6	1	80	1	0.14	62
SA3P5	81.2	3	52	3	0.14	62
SA3F1	16.0	0	0	0	0.06	56
SA3F2	17.9	1	95	0	0.14	62
SA3F3	18.9	2	95	2	0.06	56
SA3F4	15.2	2	8	2	0.14	62
SA3F5	20.4	1	40	1	0.06	56
SA3SC	12.3	1	80	4	0.14	62
SA3CC	12.3	1	80	4	0.14	61

Data Analysis

Anabat samples were analyzed with Analook W and automatic identification software (Titley Scientific, Columbia, MO). Data files were filtered in Analook W and were manually reviewed to confirm presence of bat passes. Acoustic files were analyzed using Kaleidoscope (US Fish and Wildlife Service), and the passes contained within each file were identified to species. One file represents all bat passes for one specific night for one recording device, where pulses are the number of bat calls within a given pass. Activity data from the acoustic surveys for the opening and forest-between-opening, as well from aggregate and dispersed openings, were analyzed using a two-way Analysis of Variance (ANOVA) to compare differences in mean number of bat passes. Data for this analysis were transformed by adding 10 to each datum to remove zeros in order to perform a log transform. Means of bat activity for tree canopy and ground level samples at site centers were compared between aggregate and dispersed sites with a T-test. The relationship between activity and insect richness and abundance was tested by Pearson Correlation Coefficients. Bat species detected were separated into two groups based on wing morphology: clutter adapted or open adapted. Number of passes for these groups was compared between opening and forest treatments with a Fishers exact test, blocked by sampling period. Relationships between environmental variables and insect abundance and diversity was measured with Canonical Correlation Analysis. A Principle Components Analysis (PCA) was performed on abiotic data, including opening area, elevation, mean nightly temperature, mean nightly precipitation, and snag data, to examine relationships among these variables (PC-ORD).

CHAPTER 3: RESULTS

Differences in Habitat Use by Bats

In total, 2,228 bat passes were recorded between 8th June and 27th July. When using pulses (the number of calls within a given pass) as a measure of activity, bat activity was higher in openings than in the forest between openings ($p = 0.01$) and was marginally higher in dispersed compared to aggregated openings ($p = 0.06$) (Figure 4; Table 3). When using passes as a measure of activity, bat activity was higher in openings than in the adjacent forest between openings ($p = 0.01$) and was marginally higher in dispersed compared to aggregated openings ($p = 0.09$) (Figure 5; Table 4). Figure 6 a-e represents a Fishers exact test used to determine the probability of passes of a clutter or open adapted bat in either a patch or forest. Without blocking for sample period, the probability of occurrence of a clutter or open adapted bat was significantly higher in openings than in forests for both groupings of species ($p=0.017$; Figure 6 a). When blocking by sample period, blocks 1 (6/8/17 – 6/10/17) and 2 (6/25/17 – 6/27/17) were found to be not statistically significant with a p value approximating 1, due to a lack of clutter and open adapted bats detected in forest samples (Figures 6 b, c). For block 3 (7/8/17 – 7/10/17; Figure 6 d) and block 4 (7/25/17 – 7/27/17; Figure 6 e), the probability of a bat pass for either an open or clutter adapted bat was found to be independent of sample location ($p = 0.09$ and $p = 0.29$ respectively). For all blocks, most passes were open adapted bats in openings, with clutter adapted bats occurring in openings less often. For all blocks, open adapted species' passes were detected in relatively even abundances; however, a greater number of passes of clutter adapted species in block 3 & 4 compared to blocks 1 & 2 suggests a seasonal shift in habitat use by clutter adapted species. Very few passes occurred in forest samples for either grouping of species; therefore, a t-test comparing activity above and below the tree canopy was not performed.

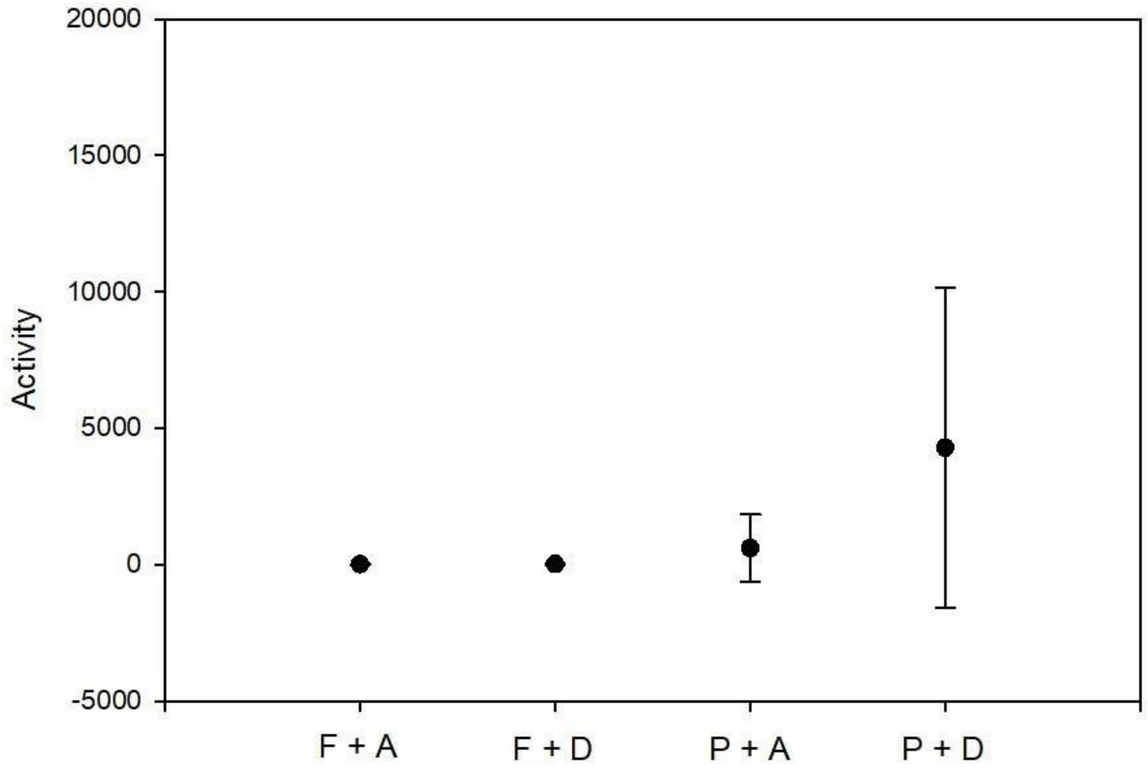

Figure 4. Mean and Standard Error of pulses as a measure of bat activity in Forest/Opening (p = 0.01) and Aggregated/Dispersed (p = 0.06). F + A and F + D represent Forest and either Aggregated or Dispersed samples. P + A and P + D represent Patch Opening and either Aggregated of Dispersed samples.

Table 3: ANOVA Summary of Pulses as a Measure of Bat Activity comparing forest/opening and aggregate/dispersed

Source	DF	Sums of Square	Mean Square	F Value	P Value
Plot Type	1	59153536.23	59153536.23	6.59	0.0145
Aggregation Type	1	33890969.03	33890969.03	3.78	0.0598
Interaction	1	33710796.03	33710796.03	3.76	0.0604

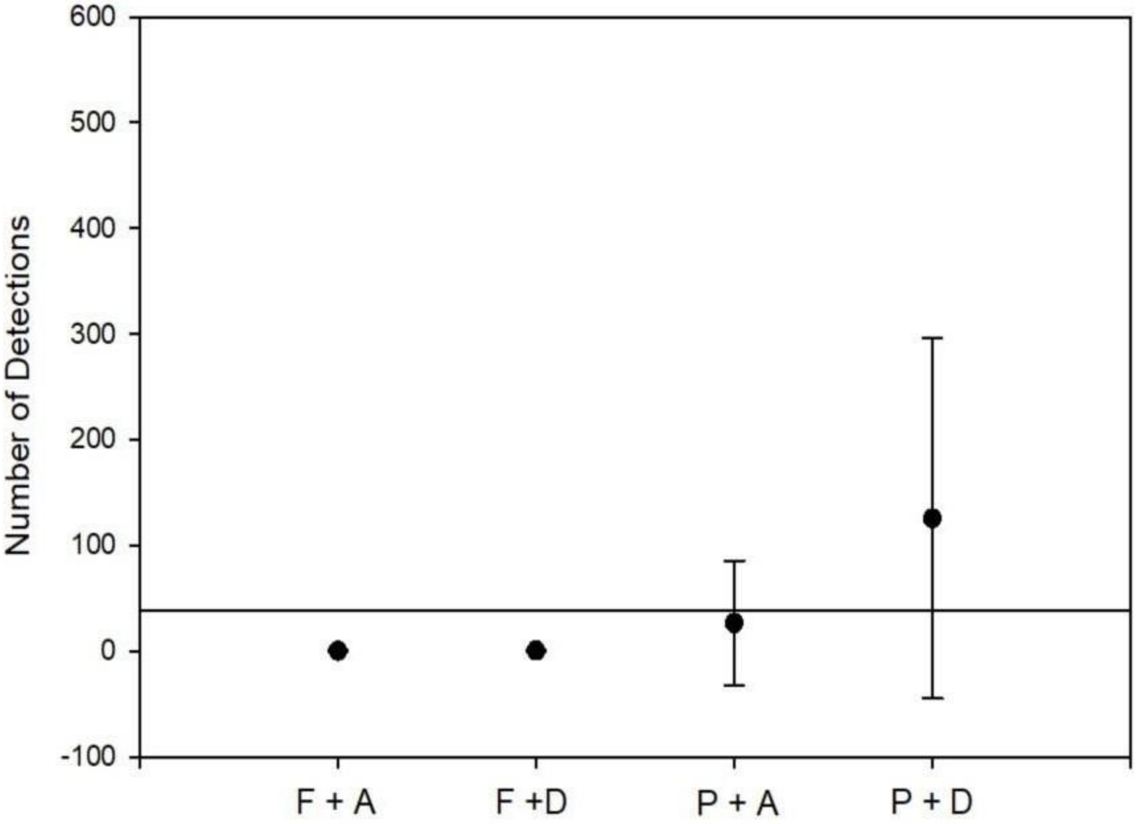

Figure 5. Mean and Standard Error of bat passes in Forest/Opening (p = 0.01) and Aggregate/Dispersed (p = 0.09). The solid line represents the mean number of passes. F + A and F + D represent Forest and either Aggregated or Dispersed samples. P + A and P + D represent Patch Opening and either Aggregated of Dispersed samples.

Table 4. ANOVA Summary of Passes as a Measure of Bat Activity comparing forest/opening and aggregate/dispersed

Source	DF	Sums of Squares	Mean Square	F Value	P Value
Plot Type	1	57153.6	57153.6	7.02	0.0119
Aggregation Type	1	24601.6	24601.6	3.02	0.0906
Interaction	1	24403.6	24403.6	3	0.0919

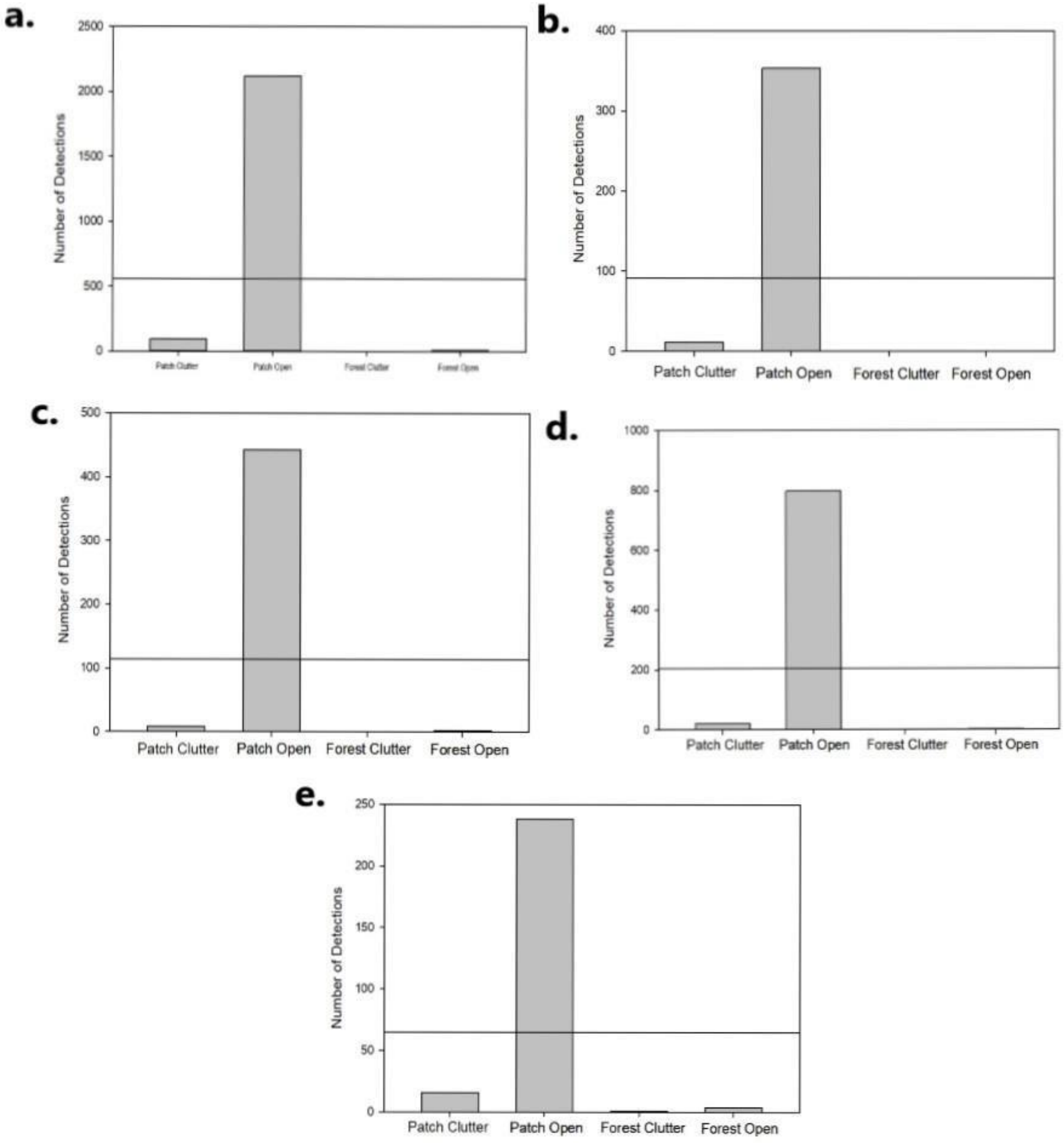

Figure 6 a-e: Fishers exact test used to determine the probability of occurrence of a clutter or open adapted bat in either a patch or forest. Figure 5-a represents all passes throughout the study, while Figure 5 b-e represent Blocks 1 – 4. Figure 5-b represents samples taken from 6/8/17 – 6/10/17 (Block 1), Figure 5-c represents samples taken from 6/25/17 – 6/27/17 (Block 2), Figure 5-d represents samples taken from 7/8/17 – 7/10/17 (Block 3), and Figure 5-e represents samples taken from 6/25/17 – 6/27/17 (Block 4).

Prey Abundance and Bat Activity

In total, 21,203 insects in twenty-three orders were collected over the duration of the study (Table 5). Weak correlations were found between the number of bat pulses and insect diversity (r = -0.017; Figure 7). When broken down by the five orders commonly preyed on by bats, positive correlations were found between number of pulses and abundance of Lepidoptera (r = 0.61), Diptera (r = 0.51) and Coleoptera (r = 0.55) and no correlations were found between number of pulses and abundance of Hemiptera (r = 0.001) or Hymenoptera (r = 0.19) (Figure 8 a-e; Table 6). A positive correlation was found between the number of bat pulses and insect abundance (r = 0.62; Figure 8 f; Table 6). When using bat passes instead of pulses, no or weak negative correlations were found between insect abundance, insect diversity, and abundance of the five orders of insects commonly preyed on by bats (Table 7).

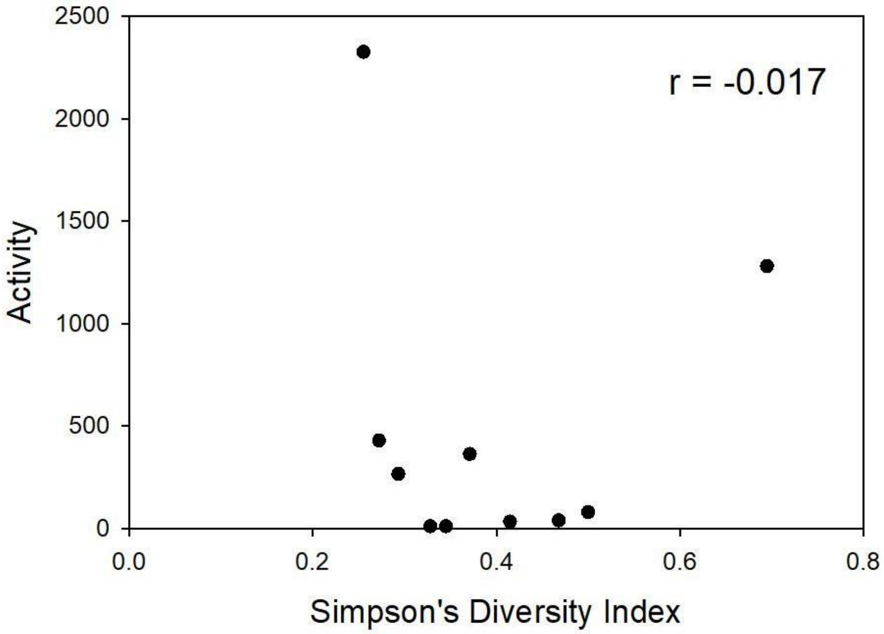

Figure 7. Scatter plot of bat activity and insect Simpson’s Diversity Index (r = -0.017).

Table 5. Abundance of insects by Order. Cumulative dry weights for Diptera, Lepidoptera, Hemiptera, Hymenoptera, and Coleoptera

Insect Order	Abundance	Dry Weight (g)
Acari	84	-
Achatinoidea	1	-
Araneae	65	-
Blattaria	10	-
Coleoptera	798	1.518
Collembola	99	-
Diplura	794	-
Diptera	10757	1.644
Hemiptera	1017	0.620
Hymenoptera	1819	2.224
Isoptera	2	-
Lepidoptera	2281	2.951
Mantodea	1	-
Metastigmata	10	-
Neuroptera	9	-
Odonata	25	-
Opiliones	14	-
Orthoptera	60	-
Phasmatodea	2	-
Pseudoscorpiones	2	-
Psocoptera	27	-
Thysanoptera	3324	-
Trichoptera	1	-

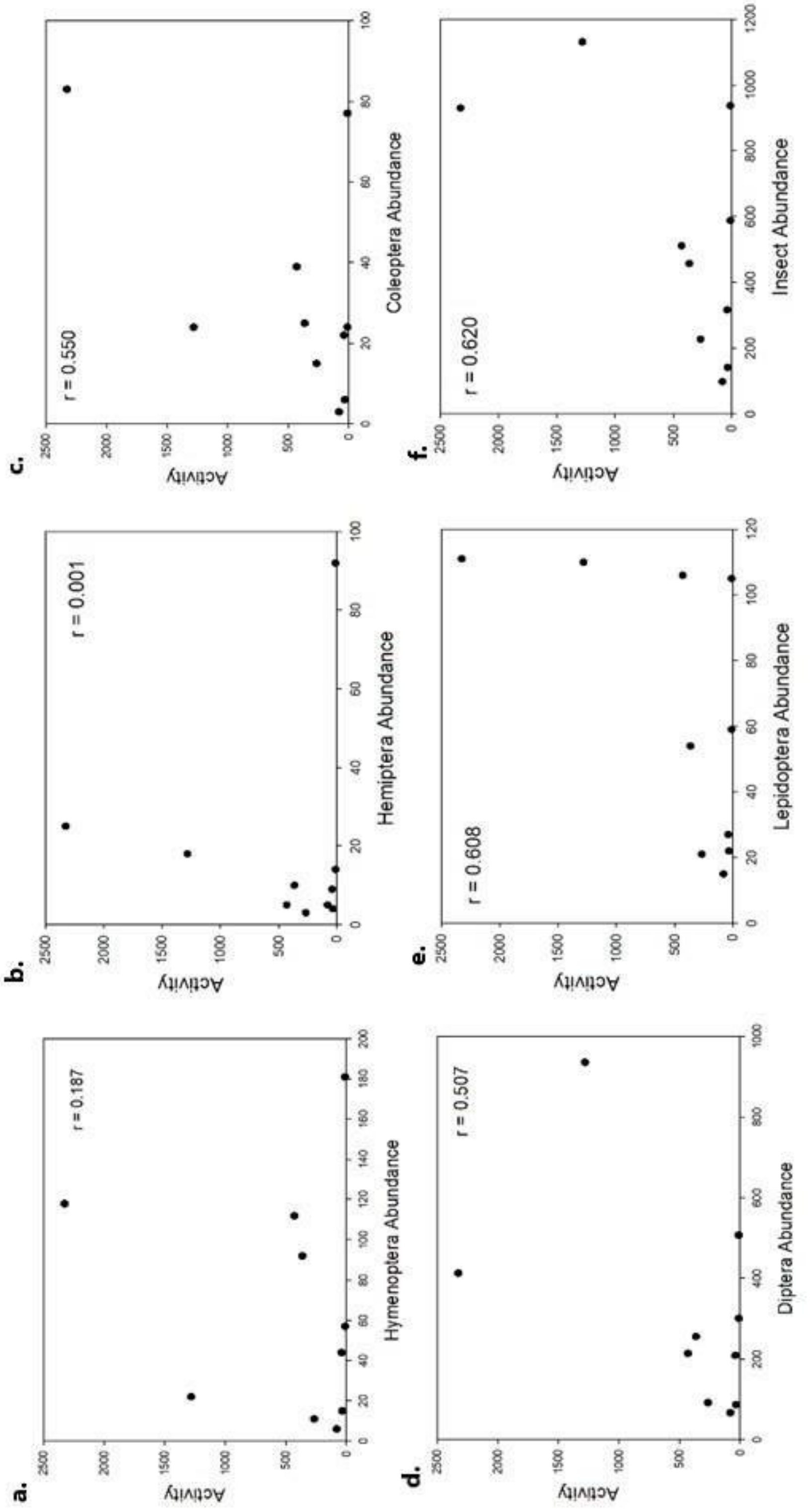

Figure 8 a-f: Scatter plot of Pearson Correlations relating bat pulses with insect variables.

Table 6. Pearson Correlation Coefficients of Pulses and Insect Variables

Activity	Simpsons	Diptera	Lepidoptera	Hemiptera	Coleoptera	Hymenoptera	Abundance
2326	0.255	413	111	25	83	118	930
430	0.272	214	106	5	39	112	511
266	0.293	92	21	3	15	11	227
11	0.328	301	105	14	77	181	588
11	0.345	507	59	92	24	57	937
364	0.371	256	54	10	25	92	457
34	0.415	87	22	4	6	15	141
40	0.468	209	27	9	22	44	316
80	0.5	67	15	5	3	6	98
1281	0.695	936	110	18	24	22	1131
Correlation	**-0.017**	**0.507**	**0.608**	**0.001**	**0.550**	**0.188**	**0.620**

Table 7. Pearson Correlation Coefficients of Passes and Insect Variables

Passes	Diptera	Hemiptera	Coleoptera	Lepidoptera	Hymenoptera	Simpsons	Abundance
528	209	9	22	27	44	0.468	316
2	507	14	77	59	181	0.345	937
22	150	5	7	15	39	0.491	222
81	87	6	10	25	17	0.347	157
160	114	113	22	64	45	0.216	389
1	333	11	23	8	86	0.563	306
2	1252	110	82	107	208	0.396	3750
14	67	5	3	15	6	0.5	195
41	256	10	25	54	92	0.371	457
Correlation	**-0.250**	**-0.042**	**-0.204**	**-0.131**	**-0.314**	**-0.033**	**-0.228**

Abiotic Factors

Canonical correlation analysis revealed that abundances of orders of insects differed with respect to environmental variables (Figure 9). Of the environmental variables, precipitation and canopy cover (CCO1), and elevation and temperature (CCO2) explained the most variation (29.1% and 14.2% respectively), with Hemiptera more likely found in wet high elevation sites and Coleoptera and Hymenoptera in dry low elevation sites. Precipitation, percent canopy cover, temperature and elevation were negatively correlated with their axes (Table 8). Pearson Correlation analysis found no correlation between bat activity and precipitation (r = -0.03) and a weak negative correlation between bat activity and elevation (r = -0.30 Figure 10).

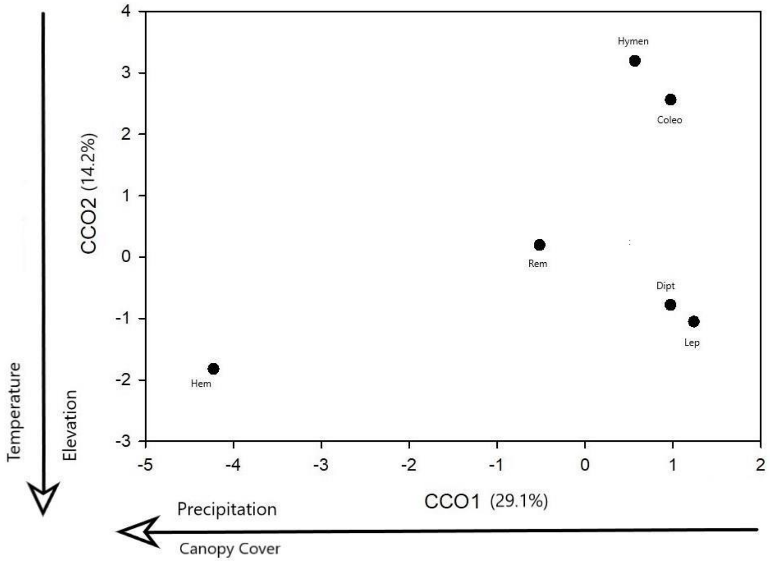

Figure 9. Canonical Correlation of environmental variables and insect abundance for sample locations. Distribution of insect orders on the first two canonical correlation axes and percent variation explained. Hemiptera (Hem), Hymenoptera (Hymen), Coleoptera (Coleo), Diptera (Dipt), Lepidoptera (Lep), and remaining orders of insects (Rem). Precipitation, canopy cover, temperature, and elevation are negatively correlated with their axes.

Table 8. Correlations and Biplot scores for environmental variables.

	Correlations			Biplot Scores		
Variable	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Elev	0.274	-0.528	-0.051	0.047	-0.064	-0.004
Area	-0.165	-0.047	-0.3	-0.029	-0.006	-0.023
% Cover	-0.701	0.226	-0.515	-0.122	0.027	-0.039
Snag	-0.239	-0.353	-0.3	-0.042	-0.043	-0.023
Bark	0.374	-0.017	-0.156	0.065	-0.002	-0.012
Open	-0.502	0.226	-0.04	-0.087	0.027	-0.003
Precip	-0.778	0.076	0.466	-0.135	0.009	0.035
Temp	-0.128	-0.48	0.139	-0.022	-0.058	0.011

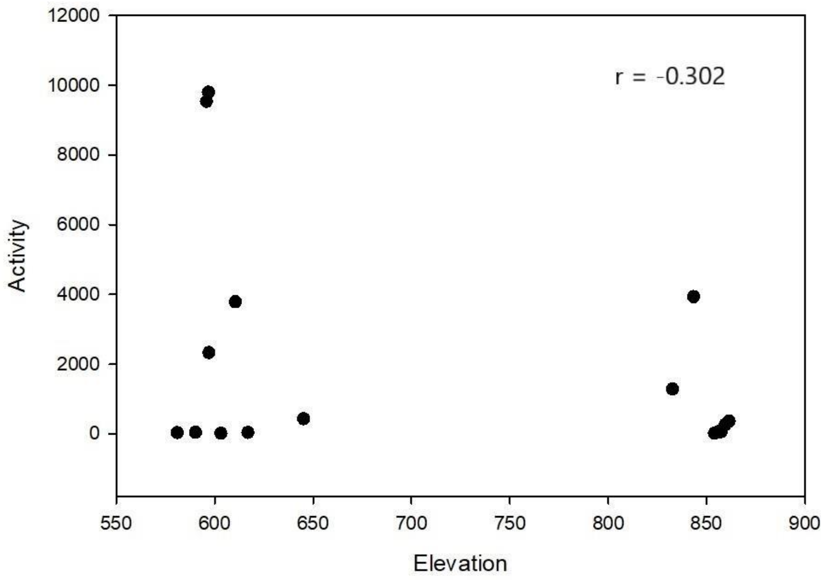

Figure 10. Scatter plot of Pearson Correlations relating bat activity and elevation (r = -0.302).

CHAPTER 4: DISCUSSION

A greater number of bat pulses in openings compared to surrounding uncut forest suggests that early successional habitat (ESH) may be good foraging habitat for bats. Further, in contrast to the hypothesis that clutter adapted bats would be less responsive to canopy variations than open adapted bats, more passes of both clutter and open adapted species in openings rather than intact forest suggests ESH is important for both groups of species. O'Keefe et al. (2014) and Kalcounis et al. (1999) have shown that forest type, forest structure, and within stand variation play important roles in determining foraging habitat by bats, and Loeb and O'Keefe (2006) demonstrated that areas of sparse vegetation are the best predictor for open adapted species, as well as some clutter adapted species such as the northern long-eared bat *Myotis septentrionalis*. Additionally, Patriquin and Barclay (2003) found that open adapted species, as well as the clutter adapted species *Myotis lucifugus,* preferentially foraged in areas of sparse vegetation. Patriquin and Barclay also found that forest type significantly influenced foraging activity of clutter adapted species. Therefore, forest type and degree of vegetative clutter may play just as important of a role as wing morphology in predicting foraging habitat preference of clutter adapted species.

One question in this study was how bats use the open space above tree canopies between patches of ESH. Kalcounis et al. (1999) addressed this question and found that activity of both open adapted and clutter adapted species was higher above the tree canopy than below. In this study, not enough passes were recorded to perform statistical analysis, suggesting that ESH is the primary foraging habitat for both groups of bats.

In this study, I hypothesized that bat activity would be greatest in dispersed openings when compared to aggregated openings, due to the increased potential foraging habitat created between mature forests and early successional habitat. Indeed, a greater number of bat passes and bat pulses was recorded in dispersed sites than in aggregated sites. Results from an ANOVA comparing aggregation were marginally significant ($p = 0.07$), suggesting that some aspect of aggregation may be influencing bat activity. Previous research in this area has shown that, in contrast to opening size, opening shape and amount of edge can influence foraging activity (Brooks et al. 2017, Jantzen, M., & Fenton, M. 2013). Here, average area:edge and area:distance ratios of aggregated sites was 14.5:1 and 112.8:1 respectively, and average area:edge and area:distance ratios of dispersed sites was 15.9:1 and 60.5:1 respectively, suggesting that although all openings had relatively similar amounts of edge, dispersed sites were more discrete. One hypothesis for differences in activity between aggregated and dispersed sites may be how bats perceive the landscape; i.e., aggregated openings may appear as one large ESH rather than discrete clusters of ESH. In studying how bat activity changes along a gradient from mature forest to the center of an ESH opening, Jantzen and Fenton (2013) determined that bat activity is highest in openings within 20m of a forest edge, regardless of wing morphology. If bats perceive highly aggregated openings as containing less edge habitat, optimal foraging habitat in these sites may be limited relative to dispersed ESH.

The total number of insects captured (21,203) from June 8th – July 27th at Round Mountain Gap was consistent with previous insect surveys conducted in this area (Brooks et al. 2017). Although no correlation was found between insect diversity and bat activity, insect abundance and bat activity were positively correlated, suggesting that bats use ESH that are abundant in specific types of insects. Diet analyses (Valdez & Shea 2014, Morton & Khun 2003, and Agosta & Morton 2003) have demonstrated that Lepidoptera, Diptera, Coleoptera, and Hemiptera can account for large portions of a bats diet. Indeed, of the five insect orders commonly preyed upon by bats (Swift et al. 1985), Lepidoptera, Diptera, and Coleoptera abundances were positively correlated with bat pulses, while Hemiptera and Hymenoptera were not correlated with pulses. However, using number of passes as a measure of activity, no or weak negative correlations were found between bat passes and all five of the orders of insects commonly preyed upon by bats. One explanation for the difference in results when comparing pulses and passes to insect abundance is that when compared to navigation, foraging behavior requires echolocation of greater pulse duration to track non-stationary objects. Therefore, using pulses relating to feeding behavior as a measure of activity may provide more information about foraging behavior when compared to bat passes.

Insect communities differed by site and were related to environmental variables. Of the environmental variables measured, elevation, temperature, precipitation, and canopy cover explained the most variation in the data with respect to insect communities. Abundances of Hemiptera were greater at wet high elevation sites, while abundances of Hymenoptera and Coleoptera were greater at dry low elevation sites; these results are similar to previous findings at Round Mountain Gap (Brooks et al. 2017). As it was correlated with certain insect species, bat activity might also be expected to correlate with environmental variables. Indeed, bat activity decreased with increasing elevation. Kusch & Schmitz (2013) also found that climatic variables such as temperature and precipitation can influence foraging habitat partitioning among bat species, and Verboom & Spoelstra (1999) demonstrated that wind strength is correlated with distance bats are willing to travel to foraging habitat. Our results suggest that in combination with insect abundance, environmental variables such as elevation may be good predictors for bat activity.

Implications and Future Directions

This study draws attention to early successional habitat as an important component in creating habitat heterogeneity. In the Northeastern United States, approximately half of bird and mammal species rely on some combination of early, mid, and late-successional habitats (Fuller & DeStefano, 2003, Litvaitis et al. 1999). For example, the clutter adapted bat species *Myotis lucifugus*, as well as the black bear *Ursus americanus* and white-tailed deer *Odocoileus virginianus*, are known to be facultative users of early successional habitats (Litvaitis 2003). One goal of this research was to provide information for forest management practices favorable to bats. Results indicate that dispersed timber harvests may provide better foraging habitat for bats than aggregated sites, and that considerations should be made for insect communities, as well as environmental variables such as elevation. For example, dispersed logging sites at dry, low elevation sites may provide good foraging habitat for bats. Future research should include canopy openings of varying size and aggregation, further analysis of prey availability over environmental gradients such as elevation, and greater partitioning of specific bat species, to better understand how creation of early successional habitat impacts foraging behavior.

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