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Within a species' distribution, there is often a core population that constitutes the majority of individuals. When threats to a species are present, the core populations within the species distribution usually receive the majority of the conservation effort. However, when core populations are threatened, peripheral populations of a species distribution may be critical for conservation. Warmer temperatures along the Atlantic coastal plain may allow peripheral bat populations to remain active through the winter, thereby lowering the probability that they will migrate to hibernacula or wintering sites. Wintering at hibernacula and migrations to wintering sites are both associated with high mortality in multiple bat species because of White Nose Syndrome (WNS) and fatalities at wind farms, respectively. The objective of this study was to determine if, during the winter, peripheral populations of bats in the North Carolina coastal plain are more active than non-peripheral populations. I established four Song Meter recording stations along a 295 kilometer north-south transect in the coastal plain (peripheral sites) and two Song Meter recording stations in the piedmont (non-peripheral sites) of North Carolina I recorded activity every night from sunset to sunrise, during the years 2012-2014. At all sites in both regions (piedmont and coastal plain) there was lower bat activity in the winter compared with the summer. However, winter was the only season where region was a significant predictor, on its own, of bat activity, whereby the coastal plain had higher bat activity in the winter when compared to the piedmont. Moreover, the probability of recording bats during the winter was higher on the coastal plain when

compared to the piedmont. In addition, I was able to conservatively identify a subset of my recordings to species. In general, the same species of bats were present in the summer and the winter on the coastal plain.   Importantly, bats species that have seen high mortality from WNS, including *Myotis septentrionalis* and *Perimyotis subflavus*, were active during the winter in the coastal plain. Increased winter activity of WNS impacted species in peripheral North Carolina populations means these individuals could never come into contact with *Pseudogymnoascus destructans (Pd*; the fungus characteristic of WNS*)* spores or could increase their survival should they be infected with *Pd*. I also found that migratory tree bat species are using the coastal plain and piedmont regions differently with the piedmont likely being used as a stopover point along a migratory route and the coastal plain likely being used as a wintering ground. Of the migratory tree bats, *Lasiurus borealis* remained present year-round on the coastal plain. On the other hand, *Lasiurus cinereus* and *Lasionycteris noctivagans* appeared to migrate, in some cases to the coastal plain. Migration by *Lasiurus cinereus* and *Lasionycteris noctivagans* could lead to mortality from wind turbines. My study demonstrates important seasonal differences in activity between coastal plain (peripheral) and piedmont (non-peripheral) populations of bats in the Atlantic coastal plain and underscores the conservation importance of the winter activity of peripheral bat populations.

YEAR-ROUND ACTIVITY OF PERIPHERAL BAT POPULATIONS IN

THE NORTH CAROLINA COASTAL PLAIN

by

John F. Grider

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CHAPTER I

INTRODUCTION

Species distribution maps are often continuous across a region. In reality, however, species distributions are often not continuous. Breaks in the distribution of populations can create metapopulations. A metapopulation is a network of localized breeding populations within a large area that experiences movement between populations (Hanski and Simberloff 1997). Movements happens when there is a net population growth that forces individuals to disperse as habitat patches become crowded (Amarasekare and Nisbet 2001; Stacey et al. 1997). When death rate exceeds recruitment rates dispersal events between metapopulations can help mitigate loss in or reestablish populations (Ronce and Kirkpatrick 2001; Valone and Brown 1995; Stacey et al. 1997).

During the decline of a mammalian species, peripheral populations persist longer than populations in the core (Lomolino and Channell 1995). Peripheral populations are defined as populations that persist in the outer margins of a species' known distribution where populations usually have lower densities and may have different characteristics when compared to populations in the core (Hengeveld and Haeck 1982; Eckert et al. 2008). For example, peripheral populations may be genetically different from core populations and/or may use different behaviors than core populations (Eckert et al. 2008; Kurta et al. 1995). Most conservation efforts are directed toward core populations,

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because this is where most of the individuals reside. A more complete and well-rounded conservation strategy will consider the entire range, including peripheral populations. Currently, core populations of temperate bat species in the eastern United States and Canada are seeing high mortality during hibernation and along migratory routes to and from wintering grounds. Because mortality is associated with core populations during the winter, it is important to understand the winter ecology of peripheral bat populations

In temperate regions during the winter, bats migrate to hibernacula or warmer wintering grounds, or they do not migrate and use short-term torpor on cold days and remain active on warm days. Bats that hibernate in winter, when food becomes scarce, often undertake regional migrations of several hundred kilometers or less (Fleming and Eby 2003). Prior to hibernation, bats increase body mass (Baker et al. 1968; Krulin and Sealande 1972). During hibernation, increased body mass combined with lower metabolic rates allows bats to survive (Malan and Canguilhem 1989). Metabolic rates of bats are reduced in winter months by extended torpor events (Speakman and Thomas 2003) where body temperature approaches ambient temperature (Davis and Reite 1967). Extended torpor events are broken up by periodic arousals (Geiser 2004) that can compromise approximately 80% of a bat's winter energy budget (Thomas et al. 1990). Arousals occur because bats need to restore water lost through evaporation (Thomas and Geiser 1997). Upon arousal, bats may or may not leave the hibernaculum (Whitaker and Rissler 1993; Lausen and Barclay 2006).

Alternatively, some temperate bat species, for example, *Lasiurus borealis*, *Lasiurus cinereus*, and *Lasionycteris noctivagans*, migrate long distances to find suitable

warmer wintering grounds (Cryan 2003; Fleming and Eby 2003). Some bat species move

a thousand kilometers to find suitable wintering sites (Popa-Lisseanu and Voigt 2009;

Cryan 2003). Migration corridors for bats are not known. However, they tend to use

distinct geographic features for navigation, and forested areas for brief stopovers to

forage and roost (Baerwald and Barclay 2009; Furmankiewicz and Kucharska 2009;

McGuire et al. 2012).

Although rare, some individuals in bat populations do not leave their summering

area during winter months, but instead remain resident and active, or remain resident and

use a combination of activity and short torpor bouts (Whitaker and Hamilton 1998; Avery

1985; Rice 1957). Winter residency is possible where nightly temperatures are warm

enough for bats to feed on insects. The temperature threshold for insect flight can vary

by species, but flight can be sustained as low as 8°C (Taylor 1963). On intermittent cold

nights, when foraging is not profitable, bats can use daily torpor events to decease energy

consumption (Wilz and Heldmaier 2000).

Semi-tropical and temperate coastal areas, like those of the coastal plain of the

southeastern United States, may be warm enough for bats to remain active year-round.

These areas have mild winters due to poleward movement of ocean waters that release

heat to surrounding land masses as they move from tropical regions (Berner and Berner

1995; Chahine 1992). The process of land warming through ocean waters has more

substantial influence on temperature during winter months (Berner and Berner 1995).

White Nose Syndrome (WNS) is a disease associated with hibernating bats (Frick

et al. 2010). White Nose Syndrome is characterized by, *Pseudogymnoascus destructans*

(Pd), a white fungus that grows on the skin of bats during hibernation (Blehert et al. 2009). *Pseudogymnoascus destructans*, is thought to have originated in Europe and is an emerging infectious pathogen in the United States (Wibbelt et al. 2010; Frick et al. 2010). White Nose Syndrome spreads from bat to bat and is density dependent, with higher rates of infection among denser concentrations of bats (Langwig et al. 2012). Bats are thought to die from increased evaporative water loss associated with the *Pd* infection (Willis et al. 2011) whereby water loss leads to more frequent arousals during hibernation, which depletes energy reserves to the point of death by starvation (Boyles and Willis 2010; Thomas et al. 1990). White Nose Syndrome has killed >5.5 million bats in the United States (U.S. Fish & Wildlife Service 2014) with mortality impacting, on average, 73% of bats in infected hibernacula (Frick et al. 2010). Bats that do not succumb to WNS in the winter months often show signs of deteriorated wings and poor body condition, which can lower future foraging and reproductive success (Reichard and Kunz 2009).

It has been estimated that hundreds of thousands to over a million bats have died from wind turbines between 2000 and 2011 (Arnett and Baerwald 2013). Theories about why bats are killed at wind turbines, center on pre-existing sensory biases that make turbines attractive to bats (Cryan et al. 2014). Bats may not have the cognitive ability to distinguish turbines from trees and may approach turbines expecting to land at potential roost sites, find insects aggregations on the leeward side, or find other bats as potential mates (Cryan et al. 2014; Kunz et al. 2007). Regardless of why bats are attracted to wind turbines, fatalities are likely increased because of the placement of wind turbines in areas that bats use to migrate such as forested stopover points (Baerwald and Barclay 2009). In

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general, bat fatalities from wind turbines occur in "tree bats" (ie, bats that primarily roost in the foliage of trees) in late summer and early fall, which coincides with their seasonal migration (Cryan 2003; Cryan et al. 2014; Kunz et al. 2007). Thus bats that make seasonal movements associated with the onset and retreat of winter are more susceptible to fatalities from wind facilities than those that can remain in the same area year round.

Understanding winter activity and movement patterns of bats is critical for bat species that are impacted by both WNS and wind energy facilities. There are peripheral populations of bats in the North Carolina coastal plain (Harvey et al. 2011; Morris et al. 2009). Six of the species that occur in peripheral populations in the North Carolina coastal plain have seen significant mortality in core populations due to WNS and wind turbines.

If peripheral populations of these species are active in the coastal plain year round, they could avoid contact with WNS or have reduced mortality from WNS. If the tree bat species do not migrate, then they may also have lower fatalities from wind turbines. The objective of this study was to determine if peripheral populations of bats in the North Carolina coastal plain are more active in winter than non-peripheral populations. High levels of winter activity could potentially allow bats to avoid mortality associated with hibernation at, and/or migration to, wintering sites.

Hypothesis

Bat activity levels and species composition will be related to ambient temperature and season at peripheral (coastal plain) and non-peripheral (piedmont) sites in North Carolina, USA.

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Aims and Predictions

Aim 1 - To determine if there are nightly temperature differences in the winter between peripheral (coastal plain) and non-peripheral (piedmont) regions.

Prediction 1 - Nightly temperatures during the winter will be higher in the peripheral (coastal plain) region compared to the non-peripheral (piedmont) region.

Aim 2 - To determine if the changes in nightly bat activity associated with season and temperature are similar across peripheral (coastal plain) and non-peripheral (piedmont) regions.

Prediction 2-1 - Nightly bat activity will vary with season, however changes in activity between summer and winter in the peripheral (coastal plain) region will be less pronounced when compared to the non-peripheral (piedmont) region.

Prediction -2-2 - Nightly bat activity will be positively correlated with nightly temperature during winter months.

Aim 3 - To determine if bat species composition shifts among seasons at peripheral (coastal plain) and non-peripheral (piedmont) sites.

Prediction 3-1 - Due to seasonal migration of bats in the colder, non-peripheral (piedmont) sites, there will be more changes in species composition among seasons in the non-peripheral sites than the peripheral (coastal plain) sites.

CHAPTER II

METHODS

Study Sites

Field-work was conducted at six sites on public and private lands in the coastal plain and piedmont of North Carolina (Figure 1). These sites were selected because they represent forest types that are commonly found within the piedmont and coastal plain regions of North Carolina. The coastal plain included four sites in a north to south transect: North River Game Land (NR), Parker Tract (PT), Lenoir 1 (L1), and South River (SR) (Figure 1, Table 1). The piedmont included two sites at approximately the same longitude in the central part of North Carolina: Uwharrie National Forest (UNF) and Greensboro (GSO) (Figure 1, Table 1).

Recordings

Bat activity was measured using Song Meter SM2 and SM2+ bat ultrasound detectors (henceforth "detectors"; Wildlife Acoustics, Concord, Massachusetts), which recorded each night (sunset to sunrise) from September 2012 through August 2014. Detectors were powered by 12-volt batteries recharged by solar panels. Microphones were placed 10 to 30 feet off the ground in forest clearings by running microphone cables through 2 cm PVC or mounting the detector on a tall structure. Where needed, electric fencing provided protection from black bear (*Ursus americanus*) and white-tailed deer

(*Odocoileus virginianus*). Detectors recorded at 48 decibels and a high-pass filter was set to 1000 Hertz to attenuate low-frequency noise. Sampling rate was set to 192,000 Hz. Recordings were in .wav format and stored on class 4 or higher SanDisk SDHC cards. All detectors were checked monthly to download calls and ensure functionality.

Relative bat activity was determined by visual examination and counting of all recorded .wav files in Sonobat 3.2 NE (DND Designs, Arcata, California). The majority of files contained a sequence of echolocation pulses; however, some files contained only one echolocation pulse. For this study, files containing at least one bat echolocation pulse were counted as an echolocation sequence for the night it was recorded. Occasionally, files contained echolocation pulses from multiple bats or social calls from bats. Files with multiple bats were still counted as a single echolocation sequence. Files with social calls were only counted as an echolocation pulse if a search phase echolocation pulse could be seen within the file. Total numbers of bat echolocation sequences were tallied for all days where units were operational for the entire night. On select winter nights with high levels of activity echolocation pulse sequences were further examined to determine if they contained feeding buzzes. Feeding buzzes were identified using descriptions in Griffin et al. 1960 and Acharya and Fenton 1992.

Echolocation pulse sequences were analyzed to species using Sonobat 3.2 NE (henceforth Sonobat) and BCID East 2.6a (henceforth BCID; Bat Call Identification Inc., Kansas City, Missouri). Sonobat is an auto classifier that contains all of the bats of the southeastern United, except for the Southeastern Myotis (*Myotis austroriparious*), Seminole bat (*Lasiurus seminolus*) and the Northern yellow bat (*Lasiurus intermedius*).

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Before being analyzed by Sonobat, files were processed through the SM2 Batch

Attributer and Sonobat Batch Scrubber 5.2 (DND Designs, Arcata, California) to

compensate for using xms-ultrasound microphones and to remove low quality recordings.

Settings used for the species analysis were those suggested by Sonobat for SM2 and

SM2+ recordings as follows: maximum number of calls to consider per file =8,

acceptable call quality =0.7, and decision threshold =0.9. Identified echolocation pulse

sequences were not accepted unless a minimum of 3 pulses was identified and there was

"consensus" species decision. All echolocation pulse sequences identified using Sonobat

were then converted to zero cross files using Kaleidoscope software 2.0.7(Wildlife

Acoustics, Concord, Massachusetts). Converted zero cross files were then identified a

second time using a second auto classifier, BCID, to validate the initial classification

made in Sonobat. In BCID the default settings were used and at least five identifiable

pulses were needed to identify a species. The list of species available for the BCID

identification included all of those species potentially present in our study area with the

exception of the Seminole bat and the Northern yellow bat. These two species are hard to

classify due to small call libraries for the species, and or similar spectral characteristic to

other species.

<div align="center">Season and Temperature</div>

I compared relative bat activity to nightly temperature and season to assess

differences in winter activity between non-peripheral (piedmont) and peripheral (coastal

plain) populations. Winter was defined as December, January and February. Summer

was defined as the three warmest moths of the year. Spring was defined as March, April,

and May. Fall (autumn) was defined as September, October, and November. I calculated

a nightly temperature for all recording days by calculating a mean of all hourly

temperature measurements that occurred between sunset and sunrise. Hourly temperature

measurements were obtained from weather stations run by the North Carolina state

climate office (http://www.nc-climate.ncsu.edu). The weather station for each site was

chosen by its proximity to the corresponding recording station (22 km maximum distance

from detector sites). On occasion, hourly temperature data were missing from the North

Carolina state climate office. Nights with missing temperature data were only used if not

more than two hourly temperature measurements were missing and the missing

measurements were non-consecutive.

Mist-Netting

Mist-netting was used to complement acoustic activity data and to confirm the

presence of species detected through acoustic recordings. Mist netting occurred at all

coastal sites between 15 May – 5 August in 2012 and sporadically in the spring and

winter of 2013. Mist-nets were set up on road corridors, forest corridors, or around

bodies of water. Between three and five nets were used on each night. Nets were set

"double high", meaning that one net was set on top of another net, and were between 4

and 12 m wide. On some occasions "single high" nets were used and were 4 or 12 m

wide. Nets were opened at dusk and checked every eight to ten minutes. Barring

inclement weather or very low activity nets remained open for a minimum of five hours.

Upon capture individual bats were removed from the nets and placed in individual

paper bags. The bag containing the bat was weighed using a 60 g hanging scale (Pesola

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Präzisionswaagen AG, Baar, Switzerland). The bat was then removed from the bag and identified to species. Bat forearm length was measured from the bottom of the elbow to the top of the wrist using calipers (Swiss Precision Instruments, Garden Grove, CA). Wing damage index was assessed to determine if there were signs of WNS, described in Reichard and Kunz (2009). Bats were determined to be juvenile or adult by backlighting the wing and looking for the ossification of finger joints (Burnett and Kunz 1982; Kunz and Anthony 1982). Reproductive classes were assigned as follows. Males were scrotal (testes visible) or non-reproductive (testes not visible). Females were non reproductive (no signs of being pregnant or lactating), pregnant (distended belly), lactating (hairless area around nipples), or post lactating (visible hair growing back in bare area around nipples). After processing, all bats were immediately released at the site of capture. All mist-netting equipment was treated according to the WNS decontamination protocol version 3.15.2012 (North Carolina Wildlife Resources Commission 2012). All animal handling was approved through the University of North Carolina at Greensboro IACUC with permission from the North Carolina Wildlife Resources Commission.

Statistical Analysis

Normality and equality of variance of data were tested using Shapiro-Wilk and Levene's tests, respectively. Data that did not fit the parametric assumptions were normalized using natural log transformations. When transformations failed to normalize data, non-parametric tests were used. Because of missing or limited activity data during parts of some seasons in some years, year could not be used as a unit of replication in my

analysis. Thus, seasons were pooled across years (i.e., a summer night in 2012 and 2013 was simply coded as "summer").

Winter nightly temperature data did not violate parametric assumptions. Therefore, an independent two sample t-test was used to compare winter temperatures between the non-peripheral (piedmont) and peripheral (coastal plain) regions.

Activity data could not be normalized; therefore, non-parametric Kruskal-Wallis tests were used to determine whether there were seasonal differences in activity within each site. A multiple comparison test was used as a post-hoc to the Kruskal-Wallis to identify pairwise differences between seasons (pgirmess; Giraudoux 2014). Since summer and winter were significantly different across all sites a ratio between the sum of summer call sequences and the sum of winter call sequences was calculated to determine how much more likely a summer echolocation pulse sequence was than a winter echolocation pulse sequence. Seasons did not have the same number of recording nights. Therefore, all ratio numerators and denominators were constrained to the same number of sampling nights by averaging the sum of 1000 random subsets of nights from the season with the larger number of recording nights to the number of nights in the season with the smaller number of recording nights. Random subsets were selected using code written by Olav Rueppell in Microsoft Excel (Microsoft Corporation, Redmond, Washington, USA).

Linear regressions were used to analyze the effect of temperature and region (non-peripheral vs peripheral) on activity for each season. Diagnostic plots were used to ensure that data did not validate the assumptions of a linear model. Nights with no activity or average nightly temperatures below seven degrees Celsius were not used in the

regression model because I was only interested in nights that had recorded bat activity or nights that were warm enough for insects to be active.

Program R 3.1.1 (R Core Team 2014) was used for all statistical analyses (packages: lattice (Sarkar 2008), car (Fox and Weisberg 2011), ggplot2 (Wickham 2009), and pgirmess (Giraudoux 2014)).

CHAPTER III

RESULTS

In total, from all sites, I collected acoustic data on 2,878 nights from September

1st 2012 to August 31st 2014. During the winter of 2012, recording stations were missing

the first hour of recording for three days at three sites due to a mistake I made in setting

the recording units. Despite this mistake, I included these nine days even though they

were underestimating activity because one of the three nights at each site was warm and

there was important winter activity to include.

In total, I recorded 171,480 files. I inspected all 171,480 files, and found that

149,264 files contained a bat echolocation pulse sequence. The original 171,480 files

were scrubbed in Sonobat and 165,765 files remained for species identification. There

were more files left after scrubbing (165,765) then actual files containing a bat

echolocation pulse sequence (149,264) because the scrubber was set to ensure that no

potentially useful files were discarded. Of the 165,765 scrubbed files, 36,632 could be

identified to species using Sonobat. Of the 36,632 Sonobat identified files, 7,238 could

be identified to the same species using BCID.

Stations were operational for an average of 479.67 ± 55.38 days during the study.

On average 24,877.33 ± 9,413.93 calls sequences were recorded at each site. Across all

sites an average of 3,471.26 ± 897.72 calls sequences were recorded during each season

(Table 2). I was not able to record on every single night due to batteries losing charge, equipment malfunctions, theft, power outages, or wildlife encounters (Table 2).

As predicted, peripheral (coastal plain) sites had warmer winter nightly temperatures than non-peripheral (piedmont) sites, with peripheral sites being approximately 2°C warmer on winter nights (t = 4.93, df = 746.65, p < 0.001). The average nightly winter temperature in the piedmont sites was 4.14°C whereas the average nightly winter temperature in the coastal plain sites was 6.00°C. Given that cold-tolerant insects are known to be activity at 8°C (Taylor 1963), I calculated the percent of winter nights where average temperature was 8°C or higher for both coastal plain and piedmont sites. In the coastal plain, 34.1% of winter nights had temperatures at or above 8°C whereas in the piedmont 22.4% of winter nights have temperatures at or above 8°C. Echolocation pulse sequences recorded during the winter from both piedmont and coastal plain sites contained feeding buzzes, suggesting that bats were able to feed during winter months.

Overall, the number of echolocation pulse sequences decreased during winter at almost all recording stations regardless of whether they were piedmont or coastal plain sites (Table 3). The exception was PT where the number of echolocation pulse sequences in winter was comparable to other seasons (Table 3). Variation, as expressed by standard error in the number of echolocation pulse sequences tended to be more consistent across seasons in the coastal plain (Table 3).

Season had a significant effect on activity (Table 4). At all sites in both regions, summer had higher activity levels than winter (Figure 2, Table 5).

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At all sites, the chance of recording a bat echolocation pulse sequence was greater in summer than in winter (Table 6). However, ratios were highest in the two non-peripheral (piedmont) sites and L1, a peripheral (coastal plain) site (Table 6). In GSO, for example, for every winter bat echolocation pulse sequence recorded, there were approximately 38 summer bat echolocation pulse sequences recorded, whereas in PT for every winter bat echolocation pulse sequence recorded, there were approximately 1.17 summer bat echolocation pulse sequences recorded.

Linear models assessing effects of temperature and region on bat activity (number echolocation pulse sequences per night) showed an interaction between region and temperature during both summer and fall (Table 7, Figure 3). For both fall and summer, nights with relatively low temperatures had relatively high activity in the coastal plain whereas nights with relatively low temperatures in the piedmont had relatively low levels of activity (Table 7, Figure 3). In spring, temperature was found to be a significant positive predictor of activity in both regions (Table 7, Figure 3). During winter, both temperature and region influenced activity whereby there was a positive relationship between temperature and activity in both the piedmont and the coastal plain however, the coastal plain had higher activity in the winter when compared to the piedmont (Table 7, Figure 3). Winter was the only season where region was a significant predictor on its own of activity suggesting that the coastal plain is an important wintering area for bats.

Although 7,238 recorded files could be identified to species using two automated programs (Table 8), making inferences about species composition and seasonal changes in species composition was impossible at some sites due to small sample sizes (Table 8,

Table 9). There were some seasons with no identifiable calls. Some species of bats were

able to remain active year-round in both the piedmont and coastal plain. Migratory tree

bat (*Lasiurus cinereus* and *Lasionycteris noctivagans*), were only seen intermittently and

occurred during different times of the year in piedmont and coastal plain. In the

piedmont, species composition in the UNF was identical in fall, winter, and summer with

Perimyotis subflavus (PESU) and *Lasiurus borealis* (LABO) being the only species

present (Table 9). However, in spring at UNF, six species were present including

Lasiurus cinereus (LACI), *Lasionycteris noctivagans* (LANO), *Nycticeius humeralis*

(NYHU), *Eptesicus fuscus* (EPFU), LABO, and PESU (Table 9). At NR, species

composition varied by season, but LABO, NYHU and *Myotis septentrionalis* (MYSE)

were recorded year round. Spring was the season with the most diversity at NR, and

species recorded included PESU, MYSE, EPFU, LABO, NYHU, and LANO. At PT no

species was recorded year round. However, summer, fall, and spring had similar species

composition with MYSE and PESU being present in all three season. In winter, LACI

and LANO were the only species recorded at PT (Table 9). At SR, LABO and PESU

were recorded year round and winter was the season with the highest diversity with

LANO, LACI, EPFU, PESU, NYHU, and LABO being recorded (Table 9).

I mist-netted for bats in the coastal plain during 61 nights between the summer of

2012 and winter of 2013 (Table 10). I captured 483 bats. The majority of mist-netting

occurred in 2012 resulting in the capture of 452 bats over 57 nights of mist-netting.

Further mist-netting was conducted to see what species were active during seasons other

than summer. Spring mist-netting resulted in the capture of several species that were

captured during summer (PESU, LABO, MYAU, MYSE, and *Corynorhinus rafinesquii* (CORA)), as well as LANO which was never caught during summer months. Winter mist-netting also resulted in the capture of three species that were captured during summer (NYHU, LABO, and MYAU).

A summary of species-presence data from both mist-netting and automated species identification of acoustic recordings can be found in Table 11. Both identification methods found similar patterns in the presence of species across season (Table 11). Both methods demonstrated year round activity in NYHU and LABO, and the seasonal presence of LANO. Differences between mist-netting and automated species identification of acoustic recordings were seen in the reporting of CORA, MYAU, and *Lasiurus seminolus* (LASE). Although CORA was captured during two different seasons and at multiple sites in the coastal plain, it was rarely identified through automated species identification programs. One of the most frequently captured bats was MYAU and it was captured during every season of mist-netting (Table 10). Furthermore, LASE was captured at L1 and SR in the coastal plain during the summer. However, automated species identification of MYAU and LASE was impossible due to incomplete reference information in the call libraries of BCID and Sonobat.

CHAPTER IV

DISCUSSION

Our findings demonstrate that peripheral bat populations in the coastal plain were able to sustain higher activity levels in winter when compared to non-peripheral bat populations located just a short distance away in the piedmont. Species found active on the coast during winter included those that are known to hibernate throughout most of their species distribution and those that are known to be long distance migrants. Long distance migrants used coastal plain and piedmont regions differently. Long distance migrants used the piedmont as part of the migratory route and the coastal plain as a wintering ground.

For a bat to remain resident in an area over winter, temperatures must be warm enough for bats, and their insects food sources, to stay active (Fleming and Eby 2003). For bats, warmer temperatures are associated with lower physiological stress and higher food availability than cooler temperatures (Fleming and Eby 2003; Hayes 1997). Cold-tolerant insects are able to sustain flight at temperatures as low as 8°C (Taylor 1963). In my study, sites in the coastal plain had average nightly temperatures of 8°C or higher on 34.1% of winter nights, whereas only 22.4% of winter nights in the piedmont had average nightlight temperatures above 8°C, suggesting that the coastal plain offers more opportunities for winter foraging activity by bats.

There were differences in activity between sites with some sites showing higher activity compared to others. In the coastal plain, managed pine forest sites had lower activity than bottomland hardwood sites, with L1 having particularly low activity year-round. Managed pine forests likely had reduced activity because bats favor vertical structure, species diversity, and especially large roost trees in open areas which are not commonly found in managed timber lands (Humes et. al. 1999; Kalcounis et al. 1999; Weller and Zabel 2001; Lacki et. al. 2007). Lower activity at L1 may have also been due to the placement of the microphone in the interior of an unmanaged pine stand where activity is generally lower than on the edge of stands (Morris et al. 2010). On the other hand, UNF, in the piedmont, had the highest level of activity out of all six sites. Increased activity at UNF was likely due to the recording station being located approximately 50 meters from a bright light that illuminated the site at night. Light sources are known to attract insects and the increased concentration of insects attracts bats (Rydell 1992; Fenton and Morris 1976). Site level differences were not known *a priori,* and because of the inherent differences in sites, I did not include site in any of my models. Rather, I focused on differences between seasons within sites or pooled all sites within regions. Previous studies have reported similar differences in activity between study sites (Hayes 1997; Johnson et al. 2011).

Despite differences in activity levels at particular sites, I found consistent patterns between seasons and regions, with winter having lower activity levels than summer. Moreover, as predicted, I found less differentiation in activity between summer and winter at coastal plain sites. For example, activity was almost 38 times higher in summer

than winter at GSO (piedmont), while activity between summer and winter at PT (coastal plain) was nearly equal. Previous studies that investigate year-round activity of bats have observed high activity levels in summer months and low levels of activity in winter (Johnson et al. 2011; Hayes 1997).

Although I found that winter activity was uniformly lower than summer activity across sites, there was still activity at all sites, including piedmont sites, through the winter. While winter activity in temperate regions is relatively low compared to other seasons, activity during this time of year has been reported (Avery 1985; Padgett and Rose 1991; Rice 1957). A previous study of bats in the coastal plain of North Carolina and Virginia showed red bats were able to foraging during winter (Whitaker et al. 1997). My study confirmed winter activity results, and the feeding buzzes I recorded show that bats were feeding during the winter at my study sites.

Not surprisingly, our study confirmed that temperature positively influences bat activity (Hayes 1997; Kunz 1973; Lacki 1984; Avery 1985). I recorded bat activity at average nightly temperatures as low -3.4°C. However, it was not until average nightly temperatures reached approximately 7.0°C that activity began to consistently increase with temperature. Both coastal plain and piedmont sites had increased bat activity at higher temperatures. However, in winter the response to temperature was different between regions, with coastal sites seeing greater increases in activity as ambient temperature increased. In other words, for every increase of 1.0°C in the winter, there was a greater increase in activity at the coastal plain than at the piedmont.

My study demonstrates that peripheral populations of bats in the coastal plain of North Carolina have the ability to remain active all year and have higher activity levels than non-peripheral populations of bats in the piedmont, only a short distance away. Elevated levels of winter activity contradict typical behavior of temperate bat species which are normally seen hibernating or migrating during colder parts of the year (Speakman and Thomas 2003; Cryan 2003). Not hibernating could mean lower reproductive success for some species since hibernacula are known as important sites for mating of many temperate bat species (Fenton 1969; Thomas et al. 1979). Alternatively, bats on the coastal plain may not rely on fall mating swarms for mating but instead may mate during other times of the year. There is evidence that bats in warmer temperate areas do not copulate until the spring (Rice 1957). Previous evidence suggested that bats that remain resident in an area year-round are male (Padgett and Rose 1991; Avery 1985). However, my limited winter mist-netting in the coastal plain shows both sexes are present during winter in some species. More intensive mist netting could provide insights into winter sex ratios in the coastal plain during winter and if mating is occurring at times other than fall. If my winter mist-netting results are representative, remaining a resident would not preclude mating. Regardless, bats that forgo migration to stay resident and active on the coastal plain could see reduced mortality from the physiological stresses associated with migration and hibernation in other parts of their range (Fleming and Eby 2003).

In addition to determining whether there were activity differences between the coastal plain and piedmont, I also evaluated species composition of year-round residents

in the coastal plain and piedmont. Species data were critical to determine if the

difference seen in activity, during the winter, between the coastal plain and piedmont

were due to seasonal migrants overwintering on the coast. Of the nearly 150,000 calls

recorded, only 4.88% could be classified to species using both auto classifiers (Sonobat

and BCID). I was especially conservative with species identification to ensure calls were

identified correctly. Reasons for low rate of species identification include: plasticity in

the structure of bat echolocation (Obrist 1995), difficulty in classifying some species

echolocation pulses (Parsons and Jones 2000), and incomplete reference information for

particular species in the auto classification programs. Despite the low rate of

classification, 7,238 calls were identified to species and because of the conservative

nature of species identification, I am confident about species presence based on acoustic

sampling.

In the coastal plain, year round residents included *Myotis septentrionalis*,

Lasiurus borealis, *Nycticeius humeralis*, *Perimyotis subflavus*, and *Myotis*

austroriparious. Although, auto-classifiers were unable to identify *Myotis*

austroriparious, I captured this species at NR, a coastal plain site, in spring, summer, and

winter. Along with *Myotis austroriparious*, *Lasiurus borealis* was caught in every season

when mist-netting occurred and *Nycticeius humeralis* was captured in both winter and

summer. Acoustic identification from the piedmont also demonstrates that *Lasiurus*

borealis and *Perimyotis subflavus* remain active year round.

Lasiurus cinereus, Lasionycteris noctivagans, and *Lasiurus borealis* are the three

species of bats associated with long distance migration in the study area (Fleming and

Eby 2003; Cryan 2003). *Lasiurus borealis* was recorded year round in both coastal plain and piedmont sites and was often one of the most common species captured or recorded during each season. *Lasiurus cinereus* and *Lasionycteris noctivagans* were only seen intermittently and occurred during different times of the year in the piedmont and coastal plain. *Lasiurus cinereus* and *Lasionycteris noctivagans* were present almost exclusively during the winter on the coastal plain whereas they were present in the piedmont during spring. These results suggest that piedmont sites were used as stopover points along spring migratory routes while the coastal plain was used as wintering grounds for migrants. Previous studies have shown that stopover points are commonly used during bat migration and can be important sites for bats to rest along their migratory pathway (McGuire et al. 2012; Taylor et al. 2011). While migratory species were seen in large number in the spring at piedmont sites, they were never seen in the fall in the piedmont, suggesting that bats are using different migratory routes for fall migration than those used in spring. In the coastal plain, *Lasionycteris noctivagans* was recorded at every site where year round species data were available, but *Lasiurus cinereus* was primarily recorded in sites that were composed of managed pine forests. This suggests that bottomland hardwood forests may be important overwintering winter habitat for *Lasionycteris noctivagans* whereas bottomland hardwood forest maybe important overwintering habitat for *Lasiurus cinereus.*

Long distance migratory bat species face a growing threat from encounters with wind turbines along their migratory corridors (Arnett et al. 2008; Kunz et al. 2007). My results show year round activity of *Lasiurus borealis,* suggesting that some individuals

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are not migrating and may not experience mortality from wind facilities. On the other hand, my results show that *Lasionycteris noctivagans* and *Lasiurus cinereus* were present only during parts of the year suggesting that these species are making seasonal migrations which put them at risk for mortality associated with wind facilities (Arnett et al. 2008).

Myotis septentrionalis and *Perimyotis subflavus*, the former of which is proposed for listing as an endangered species, were found to be active on the coast year-round. Both of these species have seen mortality from WNS in other parts of their range ("White-Nose Syndrome Map | White-Nose Syndrome" 2014). Throughout most of their range, *Myotis septentrionalis* and *Perimyotis subflavus* are known to make seasonal movements to caves for hibernation (Caceres and Barclay 2000; Fraser et al. 2012), where there is high mortality from WNS (Blehert et al. 2009). However, my study shows that these species can remain active year round and may not need to migrate to hibernacula where WNS is found.

WNS has been found in hibernacula in the North Carolina mountain region and all bordering states ("White-Nose Syndrome Map | White-Nose Syndrome" 2014). White Nose Syndrome has not been found in the piedmont or coastal plain of North Carolina. Thus individuals remaining resident and active on the coastal plain are potentially suffering less mortality from WNS. Furthermore, warm coastal temperatures likely give bats a better chance of surviving WNS if they are exposed to the spores of *Pseudogymnoascus destructans*. Mortality from WNS is associated with arousal from hibernation with frequent arousal events leading to death (Reeder et al. 2012). However,

in the coastal plain, year-round residents are normally active through winter which should increase survival in the face of WNS.

Previous research showed that bats displayed different behavior throughout their range (Kurta et al. 1995; Rice 1957). My study provides further evidence that peripheral populations of bats in the coastal plain of North Carolina sustain more consistent activity levels year round than inland populations. These populations' ability to sustain higher activity throughout winter could result in less mortality associated with WNS (Frick et al. 2010) and anthropogenic factors, such as wind facilities, found in other parts of the species range (Kunz et al. 2007). These factors could ultimately lead to peripheral populations of bats in the coastal plain becoming source or rescue populations for re-colonization of locally extinct of depleted core populations. My results suggest that peripheral populations are valuable for conservation efforts of some bat species.

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Table 1. Details of field sites in North Carolina, USA. The six field sites used for acoustic bat recording are outlined with respect to forest type, maximum size of forest that defines the site (hectares), county, and GPS coordinates. The two non-peripheral (piedmont) sites are GSO and UNF. The four peripheral (coastal plain) sites are NR, PT, L1, and SR.

Site	Forest Type	Size (hectares)	County	Coordinates
GSO	Urban Temperate Mixed Forest	85	Guilford	36.0689, -79.8067
UNF	Southeastern Mixed forest	20,495	Montgomery	35.3159, -79.9763
NR	Bottomland Hardwood Forest	8,069	Camden	36.2789, -75.9901
PT	Managed Loblolly Pine Forest	4,000	Washington	35.8347, -76.6823
L1	Managed Loblolly Pine Forest	1,267	Lenoir	35.2616, -77.4646
SR	Bottomland Hardwood Forest	55	Bladen	34.6784, -78.3422

Table 2. Summary table of total number of echolocation pulse sequences recorded and number of nights that recording units were operational at all sites in all seasons. For each season, the number on the left is the number of echolocation pulse sequences (EPS) recorded that season and the number on the right is the number of nights (#N) that the recording station was operational during that season. Seasons where units were not deployed are denoted as N/D and seasons where units were deployed but not operational are denoted as N/A.

	Fall 2012		Winter 2012-13		Spring 2013		Summer 2013		Fall 2013		Winter 2013-14		Spring 2014		Summer 2014		Total	
Site	EPS	#N	EPS	#N	EPS	#N	EPS	#N	EPS	#N	EPS	#N	EPS	#N	EPS	#N	EPS	#N
GSO	1069	90	69	89	1297	89	2688	85	878	62	46	82	649	79	1753	88	8449	664
UNF	N/D	N/D	N/D	N/D	N/D	N/D	29647	56	6361	59	1933	90	18298	73	N/D	N/D	56239	278
NR	842	24	1680	87	14608	90	11212	79	2507	73	280	83	4669	70	2578	82	38376	588
PT	70	35	627	87	280	60	803	72	682	42	468	36	1	8	648	67	3579	407
L1	70	23	93	79	183	58	96	36	26	80	12	60	521	70	1023	74	2024	480
SR	4651	42	2922	52	7143	89	13310	81	4995	48	N/A	N/A	1755	57	5821	92	40597	461
Total	6702	214	5391	394	23880	385	57756	409	15449	364	2739	356	25893	357	11823	405	149264	2878

Table 3. Mean and standard error of the mean number of echolocation pulse sequences recorded at each site during each season. Seasons where units were not deployed are denoted as N/D and seasons where units were deployed but not operational are denoted as N/A.

	Fall 2012		Winter 2012-13		Spring 2013		Summer 2013		Fall 2013		Winter 2013-14		Spring 2014		Summer 2014	
Site	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
GSO	11.88	1.46	.78	.14	15.57	1.75	31.62	3.26	14.16	5.03	.56	.14	8.22	1.02	19.60	2.00
UNF	N/D	N/D	N/D	N/D	N/D	N/D	529.41	38.56	107.81	30.92	21.48	8.99	250.66	34.72	N/D	N/D
NR	35.08	9.42	19.31	4.39	162.31	19.99	141.92	9.50	34.34	3.76	3.37	1.16	66.7	9.8	31.44	3.56
PT	2	2.32	7.21	1.73	4.67	.77	11.15	.67	16.24	8.77	13	7.90	.13	.125	9.67	.91
L1	3.04	1.33	1.18	.61	3.16	.65	2.67	3.30	.33	.08	.2	.1	7.44	1.66	13.82	3.05
SR	108.37	18.70	56.19	15.08	84.40	10.86	164.32	26.19	104.06	11.81	N/A	N/A	30.79	3.67	63.27	6.61

Table 4. Results from Kruskal-Wallis tests comparing number of echolocation pulse sequences per night among seasons at each site.

Site	X^2	df	p	Number of nights
GSO	276.1047	3	<0.001	664
UNF	155.6537	3	<0.001	278
NR	209.0154	3	<0.001	588
PT	95.0742	3	<0.001	407
L1	128.5685	3	<0.001	480
SR	54.3973	3	<0.001	461

Table 5. Results of post-hoc comparisons of Kruskal-Wallis tests comparing number of echolocation pulse sequences per night among seasons at each site. Boxes filled in with grey indicate that there was not a significant difference between the two seasons at a p value of < 0.05.

Site	Summer Winter	Summer Spring	Summer Fall	Spring Fall	Spring Winter	Winter Fall
GSO				■		
UNF				■		
NR		■		■		
PT				■	■	
L1		■				■
SR			■			

Table 6. Adjusted ratios of the sum of summer echolocation pulse sequences divided by the sum of winter echolocation pulse sequences. Ratios were adjusted to account for differences in the number of days sampled between summer and winter.

Site	Ratio
GSO	37.79
UNF	24.70
NR	7.63
PT	1.17
L1	13.46
SR	2.50

Table 7. Results from linear models predicting bat activity (number of echolocation pulse sequences per night) by season based on temperature and region. Interactions between temperature and region were seen only during fall and summer. Temperature was a significant predictor of activity during both spring and fall and region was a significant predictor of activity in winter.

	Numerator Degrees of Freedom	Denominator Degrees of Freedom	Adjusted R-squared	F-statistic	Parameter	t-statistic	p-value
Fall	3	403	0.06	9.544			
					Temperature	0.618	0.537
					Region	-3.759	<0.001
					Interaction	3.94	<0.001
Winter	2	175	0.14	15.37			
					Temperature	4.98	<0.001
					Region	-2.219	0.023
Spring	2	510	0.05	13.89			
					Temperature	5.240	<0.001
					Region	1.282	0.2
Summer	3	757	0.03	8.97			
					Temperature	0.509	0.611
					Region	-1.526	0.127
					Interaction	2.015	0.044

Table 8. Number of echolocation pulse sequences classified to species at each site. Four letter species abbreviations are as follows; *Myotis septentrionalis* (MYSE; Northern long-eared bat), *Myotis austroriparius* (MYAU; southeastern Myotis), *Lasiurus borealis* (LABO; eastern red bat), *Lasiurus cinereus* (LACI; hoary bat), *Lasionycteris noctivagans* (LANO; silver-haired bat), *Nycticeius humeralis* (NYHU; evening bat), *Perimyotis subflavus* (PESU; tricolored bat), *Eptesicus fuscus* (EPFU; big brown bat), and *Corynorhinus rafinesquii* (CORA; Rafinesque's big-eared bat).

Site	MYSE	LABO	LACI	LANO	NYHU	PESU	EPFU	CORA	Total
GSO	0	94	1	107	21	30	68	0	321
UNF	0	855	598	134	4	215	11	0	1817
NR	93	2787	0	3	454	178	32	1	3548
PT	44	16	3	3	2	5	0	1	74
L1	0	0	0	0	0	0	3	0	3
SR	9	1255	2	13	21	118	57	0	1475
Total	146	5007	604	260	502	546	171	2	7238

Table 9. Species identified from recorded echolocation pulse sequences at each site in each season. Numbers indicate how many recorded echolocation pulse sequences files were identified for a given species during a particular season. Seasons are abbreviated S (spring), M (summer), F (fall), and W (winter). Four letter species abbreviations are as follows; *Myotis septentrionalis* (MYSE; Northern long-eared bat), *Myotis austroriparius* (MYAU; southeastern Myotis), *Lasiurus borealis* (LABO; eastern red bat), *Lasiurus cinereus* (LACI; hoary bat), *Lasionycteris noctivagans* (LANO; silver-haired bat), *Nycticeius humeralis* (NYHU; evening bat), *Perimyotis subflavus* (PESU; tricolored bat), *Eptesicus fuscus* (EPFU; big brown bat), and *Corynorhinus rafinesquii* (CORA; Rafinesque's big-eared bat).

Site	MYSE		LABO		LACI		LANO		NYHU		PESU		EPFU		CORA		Total	
Season	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M
	F	W	F	W	F	W	F	W	F	W	F	W	F	W	F	W	F	W
GSO	0	0	4	90	0	1	0	107	1	20	3	27	1	67	0	0	9	312
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UNF	0	0	481	275	598	0	134	0	4	0	37	167	11	0	0	0	1265	442
	0	0	94	5	0	0	0	0	0	0	4	6	0	0	0	0	98	12
NR	82	5	1863	895	0	0	1	0	276	170	142	35	28	4	0	1	2392	1110
	2	4	15	14	0	0	0	2	7	1	1	0	0	0	0	0	25	21
PT	11	29	9	7	0	0	0	0	0	2	1	3	0	0	0	1	19	44
	4	0	0	0	0	3	0	3	0	0	1	0	0	0	0	0	5	6
L1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3
SR	0	2	623	77	0	0	0	0	12	3	23	59	2	1	0	0	669	142
	7	0	15	531	0	2	0	13	0	6	3	33	0	54	0	0	25	639

Table 10. Number of bats captured, by species, at each site during mist-netting in summer 2012 and spring and winter 2013. Four letter species abbreviations are as follows; *Myotis septentrionalis* (MYSE; Northern long-eared bat), *Myotis austroriparius* (MYAU; southeastern Myotis), *Lasiurus borealis* (LABO; eastern red bat), *Lasiurus cinereus* (LACI; hoary bat), *Lasionycteris noctivagans* (LANO; silver-haired bat), *Nycticeius humeralis* (NYHU; evening bat), *Perimyotis subflavus* (PESU; tricolored bat), *Eptesicus fuscus* (EPFU; big brown bat), and *Corynorhinus rafinesquii* (CORA; Rafinesque's big-eared bat).

Summer 2012 (14 May to 5 August)										
Site	MYSE	MYAU	LABO	LANO	LASE	NYHU	PESU	EPFU	CORA	Total
NR	6	36	55	0	0	88	8	18	13	224
PT	2	0	23	0	0	22	5	8	0	60
L1	0	0	27	0	3	0	3	5	0	38
SR	0	6	68	0	4	7	34	4	7	130
Total	8	42	173	0	7	117	50	35	20	452

Spring 2013 (11 March and 12 April)										
Site	MYSE	MYAU	LABO	LANO	LASE	NYHU	PESU	EPFU	CORA	Total
NR	1	2	2	1	0	0	2	0	2	10
PT	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
L1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
SR	0	0	5	0	0	0	0	0	0	5
Total	1	2	7	1	0	0	2	0	2	15

Winter 2013 (20-21 December)										
Site	MYSE	MYAU	LABO	LANO	LASE	NYHU	PESU	EPFU	CORA	Total
NR	0	15	2	0	0	5	0	0	0	22
PT	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
L1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
SR	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Total	0	15	2	0	0	5	0	0	0	22

Table 11. Summary table of bat species presence for each site and season from both mist-netting captures and acoustic recordings. Shaded boxes indicate that the species was identified. Seasons are abbreviated S (spring), M (summer), F (fall), and W (winter Four letter species abbreviations are as follows; *Myotis septentrionalis* (MYSE; Northern long-eared bat), *Myotis austroriparius* (MYAU; southeastern Myotis), *Lasiurus borealis* (LABO; eastern red bat), *Lasiurus cinereus* (LACI; hoary bat), *Lasionycteris noctivagans* (LANO; silver-haired bat), *Nycticeius humeralis* (NYHU; evening bat), *Perimyotis subflavus* (PESU; tricolored bat), *Eptesicus fuscus* (EPFU; big brown bat), and *Corynorhinus rafinesquii* (CORA; Rafinesque's big-eared bat).

Site	Season	MYSE S	MYSE M	LABO S	LABO M	LASE S	LASE M	LACI S	LACI M	LANO S	LANO M	NYHU S	NYHU M	PESU S	PESU M	EPFU S	EPFU M	CORA S	CORA M
GSO	S/M			■	■				■	■	■	■	■	■	■	■	■		
GSO	F/W																		
UNF	S/M			■	■			■		■		■		■	■	■			
UNF	F/W			■	■									■					
NR	S/M	■	■	■	■				■			■	■	■	■			■	■
NR	F/W	■	■	■	■						■	■	■	■					
PT	S/M	■	■	■									■		■	■			■
PT	F/W	■						■		■				■					
L1	S/M				■	■									■	■			
L1	F/W															■			
SR	S/M		■	■	■		■					■	■	■	■				■
SR	F/W	■		■	■			■				■	■			■			

FIGURES

Figure 1. Map showing location of field sites in the piedmont and coastal plain regions of North Carolina, USA. The two non-peripheral (piedmont) sites are GSO and UNF. The four peripheral (coastal plain) sites are NR, PT, L1, and SR.
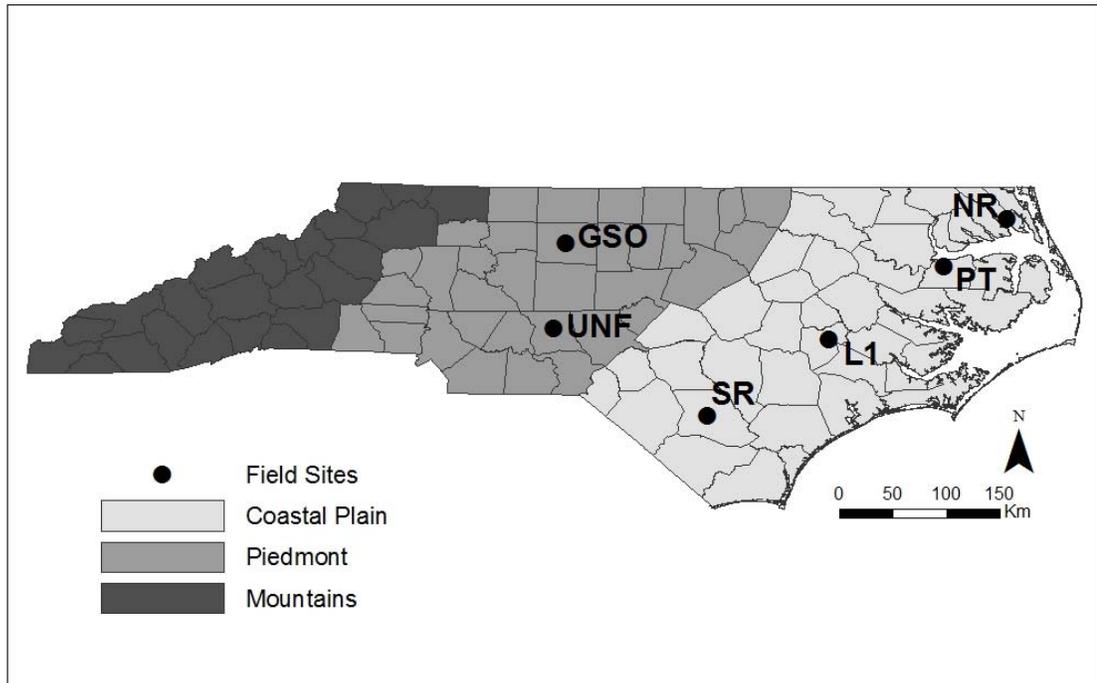
Figure 2. Boxplots of the natural log number of echolocation pulses recorded per night by site and season. Whiskers represent minimum and maximum, the box represents the 25% to 75% quartiles, dark points represent the median natural log number of calls per night, and outliers are hollow points.
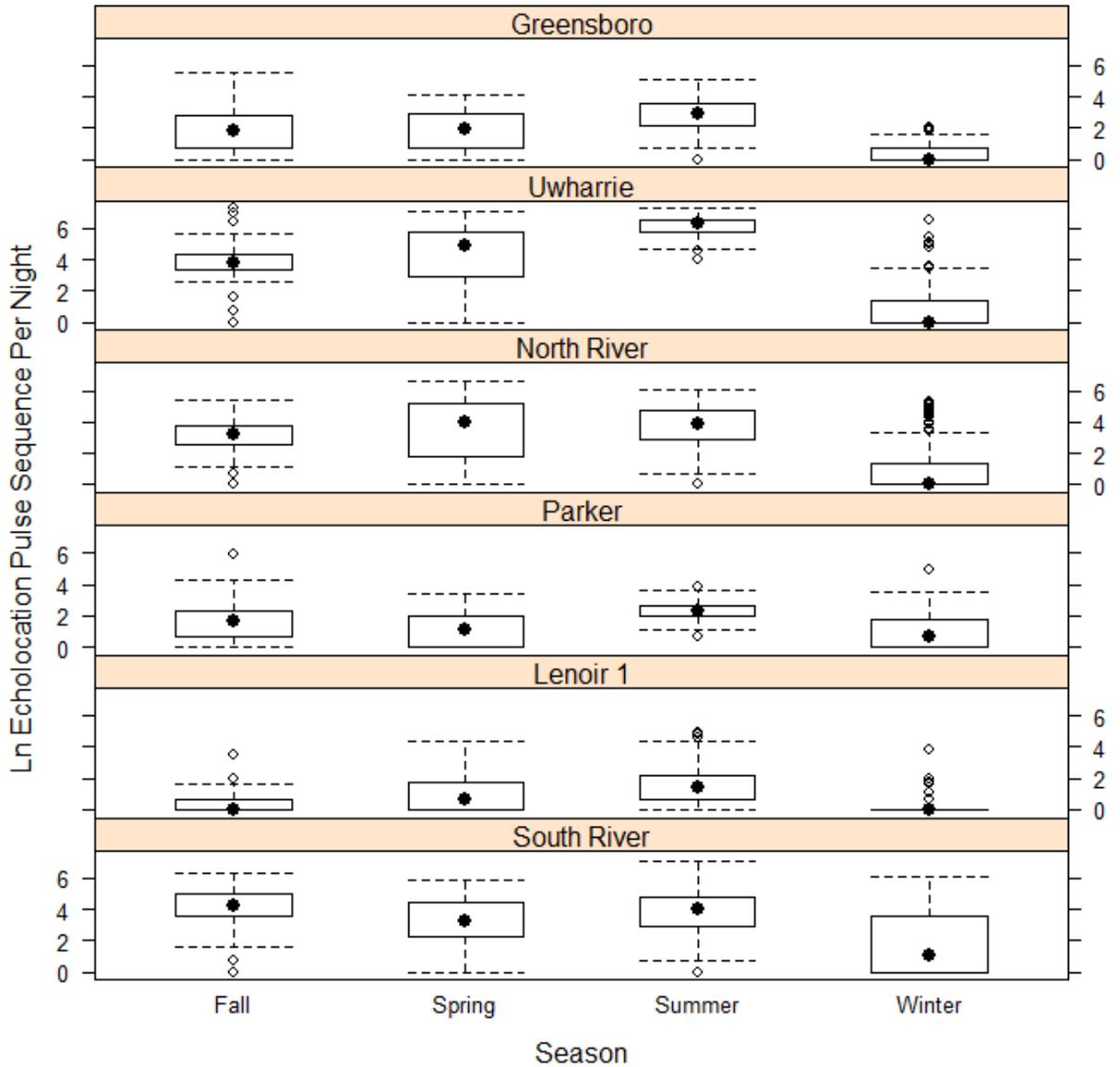
Figure 3. Scatterplots of the natural log number of echolocation pulses recorded per night showing by average nightly temperature, by region, within each season. The data are taken from all six sites (four in the coastal plain and two in the piedmont) in North Carolina from fall 2012 to summer 2014. Solid circles and lines represent the coastal plain. Open circles and dashed lines represent the piedmont. Lines represent the best fit for the data and show the relationship between temperature and activity.