

## Seasonal activity patterns of bats in high-elevation conifer sky islands

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In the southern Appalachian Mountains of the southeastern USA, bat communities in high-elevation habitats tend to be relatively under-surveyed. High-elevation habitats may provide important habitat to certain species (i.e., migratory tree bats), and may serve as climate refugia during droughts or high temperatures. We conducted an opportunistic acoustic survey of bat communities in ten survey areas in high elevation (1,585–1,920 m a.s.l.) montane *Picea rubens* (red spruce)-*Abies fraseri* (Fraser fir) forest in the southern Appalachian Mountains of western North Carolina. In each survey area, we randomly placed three full spectrum acoustic detectors ( $N = 30$ ) during three seasons (spring, summer and fall) in 2015. We deployed each detector for two five-day periods during each season ( $n = 900$  survey nights). Although we detected seven bat species/groups during the surveys, 73% of echolocation files were attributed to *Lasiurus cinereus* (hoary bat) and *Lasionycteris noctivagans* (silver-haired bat). Generally rare in the Appalachians and typically present only at low densities in the summer at mid- and low-elevations, both species were detected at all sites during all seasons. Overall, mean nightly activity of bats was higher in the summer than the spring or fall. We observed 3.7–5 times greater activity of *L. cinereus* in spruce-fir forests during the summer compared to spring and fall, whereas *L. noctivagans* had 1.3–5 times more activity in the summer compared to other seasons. After accounting for precipitation events, our finite mixture models showed that season, temperature, elevation, and canopy height influenced *L. cinereus* activity, whereas season and temperature affected *L. noctivagans* activity. Our observations suggest that high-elevation spruce-fir forests are providing summer foraging and possibly day-roosting habitat of tree bats not previously documented this far south in North America.

**Key words:** acoustic surveys, *Lasiurus cinereus*, *Lasionycteris noctivagans*, *Picea rubens*-*Abies fraseri* forests, southern Appalachian Mountains

### INTRODUCTION

Understanding the distribution of bat species is important to determining conservation goals and implementing effective management for these species. With increasing threats to bat populations, especially from white-nose syndrome (WNS) and wind-energy development (Arnett *et al.*, 2008; Turner *et al.*, 2011; O'Shea *et al.*, 2016), filling data gaps in under-surveyed areas is necessary to inform long-term species conservation efforts (Graeter *et al.*, 2015). Often, bat research is conducted at lower or mid-elevation sites and montane or alpine zones are under surveyed (Alberdi *et al.*, 2013, 2015; Chaverri *et al.*, 2016; Caprio *et al.*, 2020). Due to variables related to latitudinal and elevational range of many mountain systems, higher bat abundance, diversity, and activity normally occurs at mid- and lower elevations (Szewczak *et al.*, 1998; Grindal *et al.*, 1999). Conversely, some species occur at higher densities

at higher elevations or are present at higher elevations, but absent from lower elevations (Manga Mongombe *et al.*, 2019).

High-elevation sites may contribute to regional species richness due to interacting factors influencing bat community composition, such as temperature, precipitation, cloud immersion, vegetation types, and topography (McCain, 2007; Odom and Ford, 2020). Several of these factors, notably temperature, may correlate with decreased insect abundance or increased variability of insect populations at higher elevations (Grindal *et al.*, 1999; Cryan *et al.*, 2000; Brooks *et al.*, 2017) and increased physiological restrictions on activities of bats (McGuire and Boyle, 2013). Therefore, these factors can limit the altitudinal distribution of certain bat species. Although there has been bat research in the southern Appalachian Mountains (e.g., O'Keefe *et al.*, 2013, 2019; Hammond *et al.*, 2016), the majority of this work has been restricted to lower and mid-elevation

sites (< 1,200 m) where the threatened *Myotis septentrionalis* (northern long-eared bat) and the endangered *Myotis sodalis* (Indiana bat) occur. Regionally, there has been little effort examining elevational gradient relationships (Hammond *et al.*, 2016; Brooks *et al.*, 2017; Mutherspaugh *et al.*, 2019). Montane boreal forests in the southern Appalachian Mountains have received minimal attention from bat researchers (Graeter *et al.*, 2015), which limits an understanding of the bat community within the region.

Within the southern Appalachian Mountains of the eastern USA, montane sky islands of *Picea rubens* (red spruce)-*Abies fraseri* (Fraser fir) forests (hereafter spruce-fir) are distributed on the highest peaks and ridgelines, typically > 1,500 m. These sky islands are disjunct relicts from the glaciated Pleistocene Epoch and are restricted to seven massifs within western North Carolina, eastern Tennessee, and southwestern Virginia (Weigl *et al.*, 1999; Steele and Powell, 1999). Largely surrounded by warm-temperate deciduous forest, high-elevation spruce-fir forests contain the southernmost extent of northern latitude boreal floral and faunal communities in eastern North America (White *et al.*, 1984; Steele and Powell, 1999). Exploitative industrial logging and a subsequent period of widespread wildfire reduced the extent of this already disjunct habitat during the early 20th century (Korstian, 1937; Pyle and Schafale, 1988; Hayes *et al.*, 2006). Many spruce-fir stands, especially those that experienced fire post-logging, were revegetated by faster growing northern hardwood species (Nowacki *et al.*, 2010). These events accounted for an estimated 35–50% loss of spruce-fir forest extent in the southern Appalachian Mountains (Boyce and Martin, 1993).

With the establishment of the Cherokee, Jefferson, Nantahala and Pisgah National Forests, and the Great Smoky Mountains National Park (GSMNP) in the southern Appalachian Mountains in the 1920–1940s (NFRC, 1920; Yarnell, 1998), most remaining spruce-fir forests were protected from further exploitation (Morin and Widmann, 2010). Nonetheless, some declines in the quality and extent of this forest type continued due to decades of air pollution/acid deposition and introduced forest pests such as the *Adelges piceae* (balsam woolly adelgid; Hay *et al.*, 1978; Dull *et al.*, 1988; Eager and Adams, 1992). Additionally, most spruce-fir forests are predicted to be further reduced or possibly eliminated under many climate change scenarios (Iverson *et al.*, 2008; Koo *et al.*, 2015), including stands within GSMNP that contains the largest remaining area of

old-growth spruce-fir in the region (Dull *et al.*, 1988; Burns *et al.*, 2003; Ford *et al.*, 2015). Accordingly, the combination of historic land use and recent/future anthropogenic stressors on southern Appalachian spruce-fir forests make them one of the most endangered ecosystem types in the USA (Noss *et al.*, 1995).

Since bat communities in montane spruce-fir forests are not well known, we conducted opportunistic acoustic surveys encompassing a range in variation in elevation across all major sky islands in the southern Appalachian Mountains using ultrasonic acoustics. From these data, our objectives were to determine 1) seasonal species composition, 2) seasonal variation in activity patterns per species, and 3) environmental factors influencing activity patterns per species of high-elevation sites. As an opportunistic study with few *a priori* expectations, we hypothesized that spring and fall survey periods would show increased activity of migratory species and that resident cave-hibernating species associated with lower elevation temperate deciduous forests, such as *Myotis septentrionalis* or *Myotis sodalis*, would be uncommon.

## MATERIALS AND METHODS

### Study Area

Our study took place in 10 high-elevation spruce-fir forest survey areas within the Blue Ridge Physiographic Region of the southern Appalachian Mountains in western North Carolina, USA. In addition to *Picea rubens* and *Abies fraseri*, other tree species present in the spruce-fir forest type included *Betula alleghaniensis* (yellow birch), *Sorbus americana* (mountain ash) and *Acer spicatum* (mountain maple). Throughout, dense understories of rhododendron *Rhododendron* spp. (rhododendron), *Kalmia latifolia* (mountain laurel) and *Vaccinium* spp. (blueberry) were common. Our survey sites ranged from 1,585–1,920 m in elevation (Fig. 1; Diggins *et al.*, 2020). All study areas showed past infestation of *Adelges piceae* (balsam woolly adelgid; Dull *et al.*, 1988) and 9 of the 10 study areas were logged early in the 20th Century. Our study areas were characterized by mild summers and cold winters (mean temperatures range from 15–30°C and -4–16°C, respectively), high amounts of precipitation (150–200 cm annually), and low cloud immersion (50–75% of the year — McNab and Avers, 1994; Berry and Smith, 2012, 2013).

### Data Collection

We conducted acoustic surveys during April–May, July–August, and September–October 2015 (hereafter spring, summer, and fall, respectively). Within each survey area, we selected three sites per survey area using randomly generated points in ArcGIS 10.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA). We placed Pettersson

D500x full spectrum ultrasonic acoustic detectors (Pettersson Elektronik AB, Uppsala, Sweden<sup>1</sup>)  $\geq 50$  m apart (mean  $137.8 \text{ m} \pm 30.6$ ;  $N = 30$ ). Pettersson D500x is a full-spectrum detector that records in real-time, allowing for multiple nights of passive sampling with detailed temporal data. We surveyed at each site for 10 nights (two 5-night periods) per season (900 survey nights). We programmed detectors to operate between sunset and sunrise. We placed detectors in steel ammunition boxes ( $30.5 \times 15.6 \times 19 \text{ cm}$ ; model MA21, BLACKHAWK!, Overland Park, Kansas, USA) outfitted with a 5.1 cm wide 35° elbow polyvinyl chloride tube to protect microphones from rain. The ammunition box also protected the detectors from damage by *Ursus americanus* (black bear; Britzke *et al.*, 2010; Diggins *et al.*, 2016). We placed detectors 1.5 m high on the bole of a tree with bungee cords, directing the detectors towards the area of the forest with reduced clutter (Weller and Zabel, 2002; Diggins *et al.*, 2016).

### Data Analysis

We identified bat echolocation calls using Kaleidoscope Pro 5.1 (Wildlife Acoustics, Maynard, Massachusetts, USA) at the neutral (0) setting that balances sensitivity and specificity in species identification accuracy. We set our species list to include bat species that occur within the southern Appalachian Mountains (Graeter *et al.*, 2015; Etchinson and Weber, 2020). Kaleidoscope Pro was approved by the U.S. Fish and Wildlife Service

for use in the eastern USA, where there are several federally listed bat species: *Myotis sodalis*, *Myotis grisescens* (gray bat), *Corynorhinus townsendii virginianus* (Virginia big-eared bat), and *Myotis septentrionalis*. All of these federally listed species are known to occur in western North Carolina. We considered a bat pass as a call file containing  $\geq 3$  pulses in a sequence. We were interested in total nightly activity rather than presence/absence occupancy measures. Therefore, we used the software nightly maximum likelihood estimator (MLE) values on nightly species identification of  $\leq 0.05$  to accept results whereby identifications with higher MLE values were regarded as unknown bat or noise (Niver *et al.*, 2014). We also visually vetted a random subset of 10% of classified bat call files to confirm species identification, especially those species with high interspecific misclassification rates, i.e., *Myotis* spp. (Britzke *et al.*, 2002). Raw acoustic data is available upon request from the U.S. Geological Survey and Virginia Tech.

To assess elevation as a factor influencing bat activity, we derived elevation from 10 m digital elevation maps (USGS Geospatial Database) in ArcMap 10.2 (Environmental Systems Research Institute, Inc., Redlands, CA). Bats are known to select foraging sites with varying amounts of canopy openness and canopy height depending on their body size (Ford *et al.*, 2005; Menzel *et al.*, 2005) and the main overstory disturbances in our study areas were single-tree canopy gap dynamics (White *et al.*, 1985; Rentch *et al.*, 2010) or canopy loss from balsam woolly adelgid infestation (Dull *et al.*, 1988; Busing *et al.*,

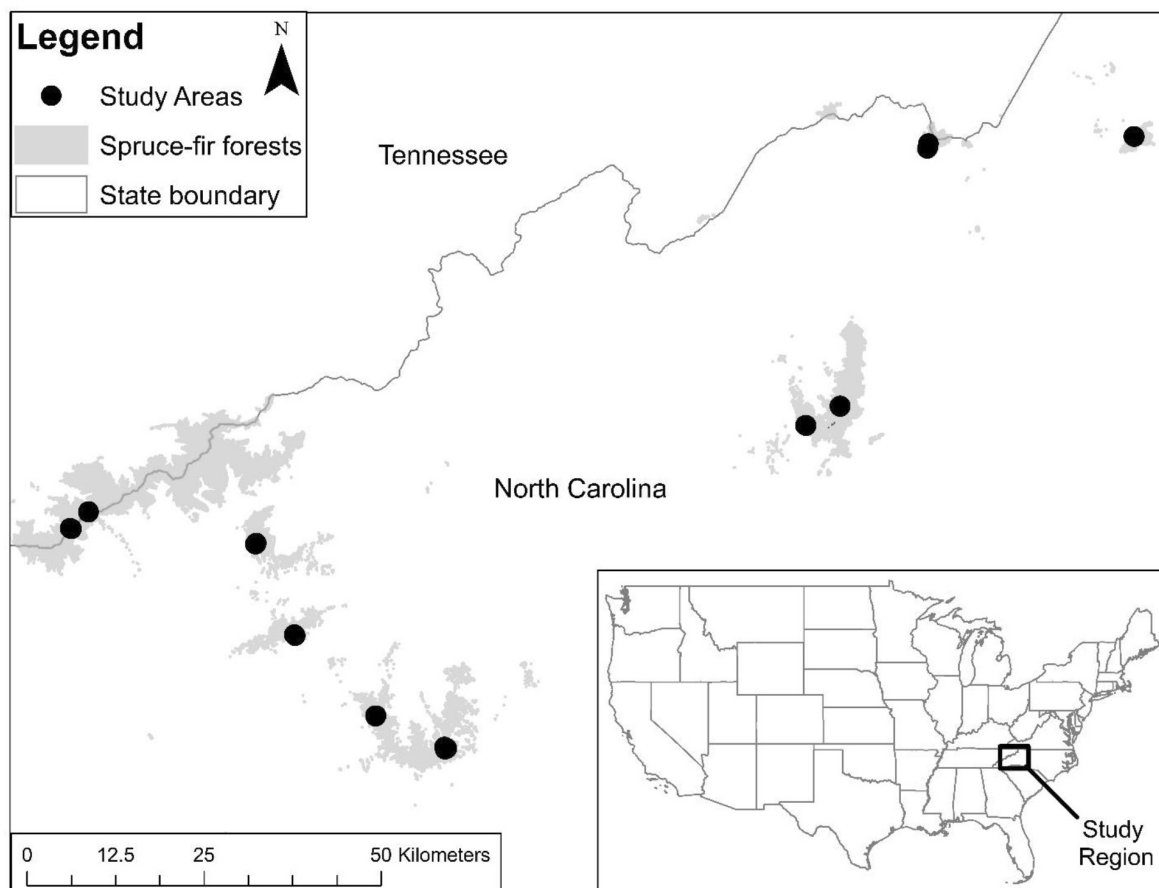


FIG. 1. Study areas for bat acoustic monitoring in montane *P. rubens*-*A. fraseri* forests in the southern Appalachian Mountains of western North Carolina, U.S.A. during spring, summer, and fall of 2015

2004). Therefore, we used a 22.8 cm vertical resolution LiDAR (light intensity and data ranging; Newcomb, 2012) data to estimate canopy height for 100 m surrounding each deployed detector to determine relationship of forest canopy height to bat activity response. Bat activity often is reduced on nights with precipitation or reduced temperatures (Voight *et al.*, 2011), so we matched each study area with the nearest high-elevation (> 1,350 m) weather station and included precipitation and temperature as covariates in our model. We coded survey nights with rain events (precipitation > 0.1 mm) or non-events (precipitation < 0.1 mm). We obtained weather data from the North Carolina Climate Retrieval and Observations Network of the Southeast Database (<https://climate.ncsu.edu/cronos>).

To analyze the relationships of season (spring, summer and fall), elevation, forest canopy height, mean daily temperature, and precipitation on bat activity, we ran finite mixture models (PROC FMM) in SAS version 9.4 (SAS Institute, Cary, North Carolina, USA). These models fit a truncated Poisson distribution of nightly bat species activity with season, elevation, forest canopy height and an elevation\*forest canopy height interactive term following a mixing adjustment for the binary influence of precipitation on simple nightly presence or absence for each bat species.

## RESULTS

We recorded 859 detection nights over the course of our study, corrected for detector failure. We detected 4,125 bat call passes: 1,173 in spring, 2,363 in summer, and 589 in fall. The few *Myotis* spp. echolocations we recorded were attributable to

*Myotis sodalis*, *Myotis septentrionalis* and *Myotis leibii* (eastern small-footed bat), however, owing to high nightly MLE scores and low number of detections per species, we chose to combine all *Myotis* spp. as a group. Accordingly, bat call passes for six species and one group were identified: 2,189 *Lasiurus cinereus*, 824 *Lasionycteris noctivagans*, 92 *Eptesicus fuscus* (big brown bat), 85 *Myotis* spp., 20 *Perimyotis subflavus* (tri-colored bat), 19 *Lasiurus borealis* (eastern red bat), and 10 *Nycticeius humeralis* (evening bat). A total of 876 calls were not identified to species. Mean activity levels for each species varied between seasons, although summer activity was higher for all species (Table 1). *Lasiurus cinereus* and *L. noctivagans* were the only species with enough detections to model with environmental variables. Both species were detected at all sites in all seasons and had nightly activity patterns positively related to temperature. Relationships between elevation and canopy height and activity were significant for *L. cinereus* and equivocal for *L. noctivagans* (Table 2). Still, both species tended to be most active at sites with lower canopy heights at the highest elevations surveyed, particularly in the fall, though *L. cinereus* activity during the summer did increase with increasing canopy height (Fig. 2). *Lasiurus cinereus* concentrated

TABLE 1. Average bat echolocation activity (i.e., nightly bat passes) across all acoustic sites in high-elevation *P. rubens*-*A. fraseri* forests in the southern Appalachian Mountains, North Carolina, USA during spring, summer, and fall 2015. The number of survey nights per season was 205 nights in spring, 146 nights in summer, and 158 nights in fall

| Species                                              | Season | Mean | SE   |
|------------------------------------------------------|--------|------|------|
| <i>Eptesicus fuscus</i> (big brown bat)              | Spring | 0.04 | 0.02 |
|                                                      | Summer | 0.52 | 0.12 |
|                                                      | Fall   | 0.04 | 0.02 |
| <i>Lasiurus borealis</i> (eastern red bat)           | Spring | 0.04 | 0.01 |
|                                                      | Summer | 0.06 | 0.03 |
|                                                      | Fall   | 0.01 | 0.01 |
| <i>Lasiurus cinereus</i> (hoary bat)                 | Spring | 1.92 | 0.23 |
|                                                      | Summer | 9.53 | 2.16 |
|                                                      | Fall   | 2.55 | 0.65 |
| <i>Lasionycteris noctivagans</i> (silver-haired bat) | Spring | 1.89 | 0.33 |
|                                                      | Summer | 2.45 | 0.92 |
|                                                      | Fall   | 0.49 | 0.12 |
| <i>Myotis</i> spp.                                   | Spring | 0.19 | 0.06 |
|                                                      | Summer | 0.29 | 0.08 |
|                                                      | Fall   | 0.02 | 0.01 |
| <i>Nycticeius humeralis</i> (evening bat)            | Spring | 0.01 | 0.01 |
|                                                      | Summer | 0.03 | 0.02 |
|                                                      | Fall   | 0.02 | 0.02 |
| <i>Perimyotis subflavus</i> (tri-colored bat)        | Spring | 0.01 | 0.01 |
|                                                      | Summer | 0.06 | 0.02 |
|                                                      | Fall   | 0.06 | 0.03 |
| Unidentified bat                                     | Spring | 1.60 | 0.42 |
|                                                      | Summer | 3.23 | 0.68 |
|                                                      | Fall   | 0.54 | 0.12 |

TABLE 2. Parameter estimates for truncated Poisson models for *L. cinereus* and *L. noctivagans* echolocation activity (i.e., nightly bat passes) in high-elevation *P. rubens*-*A. fraseri* forests in the southern Appalachian Mountains, North Carolina, USA during spring, summer and fall, 2015. Nightly precipitation (< 0.1 mm or > 0.1 mm) served as the finite mixing factor. Summer is the reference season for the model

| Model                            | Estimate | Standard error | z value | Pr >  z |
|----------------------------------|----------|----------------|---------|---------|
| <i>Lasiurus cinereus</i>         |          |                |         |         |
| Intercept                        | -29.48   | 2.21           | -13.34  | < 0.001 |
| Fall                             | -0.17    | 0.09           | 1.79    | 0.074   |
| Spring                           | -0.21    | 0.09           | -2.30   | 0.021   |
| Summer                           | 0.00     | —              | —       | —       |
| Average temperature (°C)         | 0.22     | 0.02           | 13.35   | < 0.001 |
| Elevation (m)                    | 0.02     | 0.001          | 13.29   | < 0.001 |
| Forest height (m)                | 1.21     | 0.14           | 8.45    | < 0.001 |
| Elevation × Height               | -0.001   | 0.0001         | -8.45   | < 0.001 |
| Intercept <sup>1</sup>           | 0.37     | 0.11           | 3.23    | 0.001   |
| Precipitation (mm) <sup>1</sup>  | -0.55    | 0.18           | -2.96   | 0.003   |
| <i>Lasionycteris noctivagans</i> |          |                |         |         |
| Intercept                        | -3.78    | 4.35           | -0.87   | 0.385   |
| Fall                             | -1.24    | 0.20           | -6.14   | < 0.001 |
| Spring                           | -0.05    | 0.15           | 0.33    | 0.739   |
| Summer                           | 0.00     | —              | —       | —       |
| Average temperature (°C)         | 0.07     | 0.03           | 2.39    | 0.017   |
| Elevation (m)                    | 0.003    | 0.003          | 1.19    | 0.233   |
| Forest height (m)                | -0.43    | 0.33           | -1.32   | 0.186   |
| Elevation × Height               | 0.0002   | 0.0002         | 1.09    | 0.276   |
| Intercept <sup>1</sup>           | -0.76    | 0.12           | -6.35   | < 0.001 |
| Precipitation (mm) <sup>1</sup>  | -0.17    | 0.20           | -0.83   | 0.408   |

<sup>1</sup> — Parameter estimates for mixing probabilities

foraging activity between above 1,650 m in the spring, between 1,760–1,840 m in the summer, and above 1,700 m in the fall (Fig. 2A1–A3). *Lasionycteris noctivagans* typically foraged above 1,750 m, although elevation did not significantly influence foraging activity for this species (Fig. 2B1–B3). When fall was set as the reference season, activity of *L. cinereus* was greater in the fall than spring period ( $P < 0.01$ ) whereas spring and fall did not differ for *L. noctivagans*.

## DISCUSSION

Generally, bats show decreasing species richness with increasing elevation, as climatic factors at local and regional scales drive bat community richness (McCain, 2007). Although we detected several species at our high-elevation sites, only two species were detected during all seasons and at all survey areas. *Lasiurus cinereus* and *L. noctivagans* were the most detected species with 53% and 20% of call files attributed to these species, respectively. The tree bats, such as *L. cinereus* and *L. noctivagans*, are migratory and are believed to use landscape features such as the Atlantic coastline or the Appalachian Mountains as flyways from southern wintering

grounds to northern maternity sites and back (Cryan, 2003; Muthersbaugh *et al.*, 2019). We expected to see variation in the seasonal activity patterns for these bat species and potential shifts in the bat community due to migration events or alterations in activity when temperatures changed. However, we saw greater levels of *L. cinereus* and *L. noctivagans* bat activity in the summer that approached activity levels more often observed along the temperate-boreal tension zone in the northern USA or Canada where maternal females are present (Cryan, 2003; Nocera *et al.*, 2019). Decreases in activity in relation to taller spruce-fir forest canopies largely were consistent with observations of *L. cinereus* activity in forests of the central Appalachians Mountains (Ford *et al.*, 2005), where foraging activity could occur both underneath a mature forest canopy and above (Menzel *et al.*, 2005). Activity in spruce-fir stands < 15 m in height was probably occurring only above the canopy as conditions below would be too cluttered for these large-bodied, low echolocation frequency bats (Menzel *et al.* 2005, Rentch *et al.* 2010). Alternatively, shorter forest canopy height also was more associated with the survey sites that approached 2,000 m in elevation where *Abies fraseri* becomes more dominant and factors such as

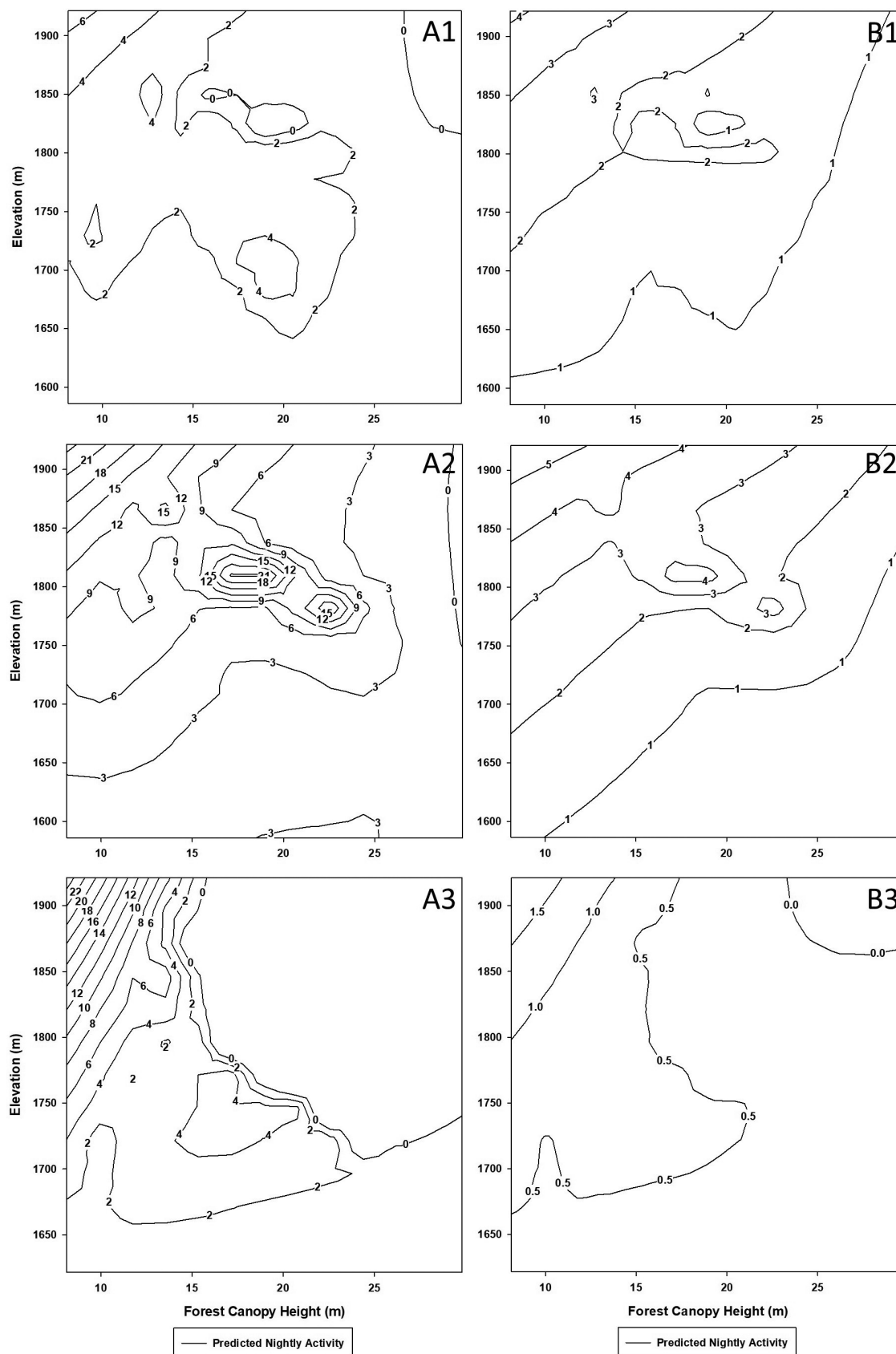


FIG. 2. Predicted seasonal activity (e.g., nightly bat passes) patterns by elevation and canopy height for A — *L. cinereus* and B — *L. noctivagans* in the 1) spring, 2) summer, and 3) fall in high elevation *P. rubens*-*A. fraseri* forests in the southern Appalachian Mountains of western North Carolina, USA in 2015. Isoclines represent mean nightly activity

temperature, shorter growing seasons, and higher winds decrease forest growth rates (Nicholas and Zedaker, 1992), representing growth conditions that are found in Canada or the extreme northeastern USA (Oosting and Billings, 1951).

*Lasiurus cinereus* and *L. noctivagans* were thought to be largely absent from the southeastern USA in the summer (Findley and Jones, 1964; Cryan, 2003; but see Perry and Thill, 2007) and occur at relatively low levels only farther north in the central Appalachian Mountains (Ford *et al.*, 2005; Austin *et al.*, 2018a, 2018b). On the mid-Atlantic Coast, these species typically are encountered during spring or fall migration (Johnson *et al.*, 2011). Therefore, we expected higher activity levels of tree bats during the spring and fall, when they are known to use high-elevation ridgelines in the central Appalachian Mountains to the north as migration corridors (Muthersbaugh *et al.*, 2019). However, we observed average higher activity levels in the summer: 3.7–5 times higher for *L. cinereus* and 1.3–5 times higher for *L. noctivagans*. Vaughan and Krutzsch (1954) found *L. cinereus* were present within the highest elevations in the montane areas of southern California during parts of the summer. A few summer records of *L. noctivagans* in the southern Appalachian Mountains are known, but this species is rarely encountered (Cryan, 2003; Bernard and McCracken, 2017). For the southern Appalachian Mountains, our data suggests that under-sampling of high-elevation areas may have led to the assumption that these species are absent or rare from this is region during the summer. Conversely, our study suggests that *L. cinereus* and *L. noctivagans* remain or perhaps end their spring migration in these sky islands from their wintering grounds (Hayes *et al.*, 2015; Ford and Cherry, 2019).

Within our study area, models showed *L. cinereus* exhibited seasonal elevational shifts within spruce-fir forests themselves, whereas *L. noctivagans* activity was not driven as much by elevation. In the summer, *L. cinereus* concentrated activity within a 100 m band, but had higher activity over a range of elevations in the spring and fall. This may be due to temperature fluctuations in spring and fall, which could influence insect activity and abundance (Muthersbaugh *et al.*, 2019), requiring bats to vary which elevations they forage in depending on nightly temperatures. Some bat species are known to show local elevational migration, although the mechanisms of this type of migration are not well understood (McGuire and Boyle, 2013). Even though *L. cinereus* and *L. noctivagans* are known to

seasonally migrate to northern latitudes along parts of the Appalachian Mountain chain (Muthersbaugh *et al.* 2019), there may be local elevational migration occurring. The elevational range of our sites was relatively narrow (ca. 335 m) and surveys over a greater elevational range may better highlight seasonal elevational shifts. Without additional documentation (i.e., from band recoveries or stable-isotope analyses from the hair of captured bats; Britzke *et al.*, 2009) determining whether these individuals are local migrants from the surrounding lower elevations or more long distant migrants (e.g., the coastal region of the southeastern U.S.A.) remains unknown. *Lasiurus cinereus* and *L. noctivagans* are locally common in the spring and fall in the northern and central Appalachian Mountains (Cryan, 2003; Ford *et al.*, 2005) and are summer residents in much of the northeastern USA (Johnson *et al.*, 2011). Although there are winter records of *L. noctivagans* in the GSMNP (Bernard and McCracken, 2017) and *L. cinereus* may occupy habitats at lower elevations in the southern Appalachians Mountains during colder months of the year (Hayes *et al.*, 2015), it could be that some individuals are year-round residents that exhibit elevational migration during the spring and fall. We did not survey along an elevation gradient from valleys up to high-elevation sites, therefore, our inference on elevational shifts for these species is limited and is restricted only to comparisons from other research in the area from low- to mid-elevations that report little activity of these two species (e.g., Loeb and O’Keefe, 2006).

Acoustic surveys are limited because demographic information, such as sex and reproductive condition cannot be obtained (Hayes 2000). Tree bat species are known to segregate their distribution seasonally due to geographic factors, including those related to elevation (Cryan *et al.*, 2000; Cryan, 2003; Kurta, 2010). Whether or not summer residents of these two species show sex-ratio bias as seen latitudinally with *L. borealis* (Ford *et al.*, 2002) is also unknown. For some bat species in temperate zones, females often occupy warmer lowlands whereas males occupy cooler uplands during the summer (Grindal *et al.*, 1999; Ford *et al.*, 2002; McGuire and Boyle, 2013). Colder temperatures at higher elevations may present high energetic demands on pregnant and lactating females or deleterious thermogenic constraints on their pups, potentially influencing their occupancy of lower versus higher elevation sites (Cryan *et al.*, 2000; McGuire and Boyle, 2013). Still, because both *L. cinereus* and *L. noctivagans* are associated with habitats with

boreal affinities, it is possible that spruce-fir sky islands in the southern Appalachians may actually provide summer maternity habitat despite being at a southernly latitude.

Our study took place four years after the initial detection of WNS in western North Carolina in 2011 (Graeter *et al.*, 2015). White-nose syndrome has caused precipitous declines of *Myotis* spp. and *P. subflavus* throughout the region (O’Keefe *et al.*, 2019). We detected low activity levels of WNS-affected cave bat species (i.e., *Myotis* spp. and *P. subflavus*) in montane spruce-fir forests. The majority of our detections for these species occurred only in the summer, albeit at low levels of activity. Due to a lack of previous surveys at high-elevation sites, however, it is unclear whether the activity levels we observed can be attributed to disease-related declines or to *Myotis* spp. lack of association with spruce-fir forests. Using a combination of acoustic observations, mist-netting captures and day-roost locations, Ford *et al.* (2015) observed that while present, use of the northern hardwood transition to the spruce-fir forest type was limited by *M. septentrionalis* in West Virginia. Hammond *et al.* (2016) predicted low *M. sodalis* presence in the GSMNP at elevations > 600 m, far below where spruce-fir forests occur. Post-WNS, there has been some evidence of competitive release of non-impacted bat species following declines of *Myotis* spp. (Brooks, 2011; Ford *et al.*, 2011; Jachowski *et al.*, 2014; Nocera *et al.*, 2019). Population declines due to WNS may have influenced our low observations of cave bats compared to tree bats, however, it is unlikely these species were abundant in spruce-fir forests prior to WNS due to reduced insect prey base, fewer suitable day-roost opportunities (i.e., cavities in deciduous trees), and dense understory and mid-story forest conditions (Silvis *et al.*, 2016).

Whereas WNS has reduced cave bat populations in the region, wind-energy development threatens tree bat populations (Kunz *et al.*, 2007). The highest bat mortality levels are observed at wind-energy sites in the central Appalachian Mountains ca. 400–500 km north of our study area (Arnett *et al.*, 2008; Arnett and Baerwald, 2013; Muthersbaugh *et al.*, 2019). Declines of *L. cinereus* have been observed there and elsewhere in the USA (Ford *et al.*, 2011; Jachowski *et al.*, 2014; Rodhouse *et al.*, 2019). Presently, there are no wind-energy sites in this part of the southern Appalachian Mountains. However, current and proposed development of wind-energy in the region as well as to the north along the central Appalachian flyways may have negative impacts on

high-elevation bat communities in the southern Appalachian Mountains.

Our study, although opportunistic and limited to one year, was the first sky island study in the Appalachians and should be viewed as an initial assessment of bat activity rates in these high-elevation forests. Clearly, there may be inter-annual variation in bat use of high-elevation spruce-fir forests depending on a variety of environmental/climatic factors and hence this should be viewed as a valuable baseline effort that provides data to initially explore patterns and hypotheses about a little studied component of bat ecology. As such, further research on bat activity generally, and demographics specifically, in high-elevation spruce-fir forests are needed and surveys could be incorporated into regional monitoring programs. This is especially urgent, as climate change may cause elevational or latitudinal ranges shifts in bat species (Sherwin *et al.*, 2013).

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